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Ecological and phylogenetic comparative studies of avian lice

PhD thesis

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List of abbreviations and denotations

AIC	Akaike Information Criterion
BIC	Bayesian Information Criterion
C.I.	Confidence Interval
CAIC format	“Comparative Analysis by Independent Contrasts” application’s format
CHD1	Chromodomain Helicase DNA Binding Protein 1
CRR	Converse Rensch's rule
FBSSD	Female-biased sexual size dimorphism
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
H₀	Null hypothesis
HR	Harrison's Rule
IOC	International Ornithologists' Union (formerly International Ornithologists' Committee)
MA	Major axis regression
MBSSD	Male-biased sexual size dimorphism
N	Sample size
p	p-value
PCR	Polymerase chain reaction
pRMA	Phylogenetic reduced major axis regression
R²	Coefficient of determination
RMA	Reduced Major Axis regression
RR	Rensch's rule
S.D.	Standard deviation
SSD	Sexual Size Dimorphism
WII	Wildlife Institute of India
α	Type I. error
λ	Pagel's λ - phylogenetic signal

*“And these several sorts of men, each followed such a profession as was most proper
for the nature of their species, which the Empress encouraged them in ...
The bear-men were to be her experimental philosophers, the bird-men her astronomers,
... and lice-men her mathematicians ...”*

Margaret Cavendish: *The Blazing World*, 1666

1 Summary

Avian Lice (Phthiraptera: Amblycera, Ischnocera) are common, low pathogenic ectoparasites of birds. Their long coevolutionary history with their hosts make them worthy subjects for studying the ecology and evolution of parasitism.

Ecology of Avian lice

The abundance and population dynamics of lice are mainly affected by their host's defensive efforts, life cycle, individual and species-specific traits. The host's body size and development stage has been known to influence their louse load. Seasonal changes have also been long observed and suspected to be related to the host's breeding season or moulting. Small falcon species are good subjects to study these questions as they are frequently infected with lice. They are also in the focus of many scientific and conservation programmes that provide valuable data on the birds.

Our studies aimed to investigate how individual traits of falcons affect their louse load at different stages of their life. The first one investigated how the sex, maturity, and clutch size of Common Kestrel (*Falco tinnunculus*) nestlings affect the abundance of their lice. Our second study investigated how static and dynamic traits of colonial Red-footed Falcons (*Falco vespertinus*) interplay with 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' (*Falco amurensis*) sex, age and body size on the abundance of their lice at a vast autumn migratory stop-over site.

We collected ectoparasite samples from Common Kestrels in Hungary. We analysed the effect of the host's sex, wing length and clutch size on the abundance of their lice.

We sampled Red-footed Falcon (*Falco vespertinus*) nestlings in two and adults in one breeding season. On the nestlings, we modelled the mean abundance of their louse species using the 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, as explanatory variables.

We sampled Amur Falcons in Nagaland, India, at major roosting sites. We modelled the abundance of their lice using the host age category (juvenile or adult) and wing length, both in interaction with sex, as explanatory variables.

We collected all ectoparasite samples with dust ruffling. We analysed the data using generalised linear (mixed) models with negative binomial distribution and log-link.

The ischnoceran *Degeeriella rufa* (Burmeister, 1838) and the amblyceran *Colpocephalum subzerafae* (Tendeiro, 1988b) occurred on all three studied bird species

frequently. We analysed the abundance of these species in detail. *Laemobothrion (Laemobothrion) tinnunculi* Linnaeus, 1758 was only rarely found on Red-footed and Amur Falcons.

On Common Kestrel nestlings, none of the investigated variables had a significant effect on *C. subzerfae* abundance. Contrarily, clutch size had a significant effect on *D. rufa* abundance. In small clutches (3–4 nestlings), the mean abundance of *D. rufa* was 3.7 times higher than in large (5–6 nestlings) clutches.

On Red-footed Falcons, *D. rufa* abundances increased with the nestlings' wing length. In one year, this trend was steeper on females. Initially, both louse species exhibited higher abundances on adult, breeding females, but it decreased subsequently through the breeding season. Contrarily, abundances were constantly low on adult males.

On Amur Falcons, host age significantly affected the abundance of *C. subzerfae*, being nearly four times higher on juveniles than adults. Juveniles were also more infested with *D. rufa* than adults. Additionally, the abundance of the latter species was lower on adult male Falcons than on adult females.

We can think of two non-exclusive explanations why Common Kestrel nestlings in larger broods are more parasitised with lice. 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. According to the dilution hypothesis, lice can be considered long life-cycle ectoparasites. These are incapable to significantly raise their subpopulation size till the fledging of the chicks. This results 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.

It seems *D. rufa* postpones transmission until Red-footed Falcon nestlings develop juvenile plumage and choose the more feathered individual among siblings. On adult birds, the sexual difference in abundance could either be caused by the different plumage or the females' preference for less parasitised 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.

Both louse species showed juvenile bias on Amur Falcons. Juvenile bias in ectoparasite infestation is common in nature, probably due to juveniles being immunologically naïve, more resource-limited, and may be inexperienced in body maintenance behaviours. Again, we found evidence of female-biased infestations. Being

sister species, the reasons for this could be similar for both Amur and Red-footed Falcons.

In conclusion, we have seen that the louse load of small falcons is a subject of various traits starting from the early days of their life. Longitudinal studies could reveal more on this phenomenon if they could overcome the associated methodological hurdles.

Evolution of sexual body size dimorphism in Avian lice

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 escape preening, while the sexes' relative size should still 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 converse RR occur in many free-living animal taxa.

2 General Introduction

It would be hard to find an ecological interaction that is both so ubiquitous and so neglected at the same time as parasitism. Parasitism is the most common nutrient obtaining strategy among animals (Goater et al., 2013), and parasites show exemplary biodiversity (De Meeûs and Renaud, 2002). Parasites mostly evoke interest for their (possible) pathogenicity. However, their role in nature goes much deeper than that, whether we talk about subtle behaviour modifying effects (Poulin, 2010) or being one of the major shaping forces in evolution (Clayton et al., 2015; Rózsa, 2005). In this dissertation, I investigate the life of parasites through case studies on falcon lice and an evolutionary analysis demonstrating that not just coevolutionary processes act on avian lice.

“The classical definition of parasitism holds that it is an intimate relationship between two organisms in which one lives on, off and at the expense of the other”

(Esch and Fernández, 1993).

Some issues arise regarding such traditional definitions, one being that “harm” is a relative term, making it impossible to quantify. Some authors tried to develop more precise definitions for parasitism (Crofton, 1971), while others intentionally leave it vague (Goater et al., 2013). Even though it is less evident to label some species as parasites and many species are parasitic at certain life stages only, parasitism is still extremely widespread. The list of described parasite species ranges from protozoans, through helminths to arthropods and even vertebrates in the animal kingdom (Rózsa, 2005; Schmidt, 1992).

Parasites are often studied in relation to their hosts, but they can have a broader effect on their environment. Although they can be considered predators (Raffel et al., 2008), they can also serve as preys. Apart from more apparent examples as concomitant predation — the parasite’s host is consumed by a predator — or grooming, free-living stages of parasites are regularly consumed not just in aquatic ecosystems (Johnson et al., 2010) but in terrestrials as well. Ticks, such as *Rhipicephalus* species, may serve as prey for mice, lizards, birds and ants (Mwangi et al., 1991; Sutherst et al., 2000). Since the biomass of parasites can be huge in certain ecosystems (Kuris et al., 2008), generalist parasites may affect food web attributes (Thompson et al., 2005). Studying the trophic relations of parasites may be vital to understand their evolutionary history, such as the emergence of complex life cycles (Parker et al., 2003).

Going beyond their direct trophic effects, parasites can also shape communities by parasite-mediated competition. A classic example is the case of *Anolis* lizard species on

St. Maarten island. *A. gingivinus* seems to have a competitive advantage over *A. watti*; however, the latter shows more resistance to their malarial parasite (*Plasmodium azurophilum*). The two species only coexist locally, where malaria is also present. Its negative effect on *A. gingivinus* indirectly helps the local *A. watti* population (Schall, 1992). The opposite can also be true when carrying pathogens can work in favour of their host. The invasive grey squirrel (*Sciurus carolinensis*) gradually replaced the native red squirrel (*Sciurus vulgaris*) on the British Isles over the last century. Grey squirrels may attribute their success to a parapoxivirus they are carrying (Tompkins et al., 2003).

By seeing these intricate relationships, it is not surprising that parasitism is deeply rooted in the tree of life. There are well-known monophyletic parasitic taxa; for example, monogeneans, cestodes and trematodes all had a common parasitic ancestor (Littlewood et al., 2008). The same holds for nematomorphs (Hanelt et al., 2005), acanthocephalans (Herlyn et al., 2003) and parasitoid hymenopterans as well (Whitfield, 1998). While specific parasitic clades are diverse and ancient, parasitism has evolved more than 200 times in the Animal kingdom (Weinstein and Kuris, 2016). Although their origins may differ, the parasitic lifestyle exerts similar selective pressures even on distantly related species making them follow similar evolutionary trajectories. These convergent evolutionary processes can be responsible for the emergence of only a handful of parasitic strategies that most described parasites follow (convergent evolution; Poulin, 2011a).

Micropredators feed off multiple host individuals during their life cycle, usually without being strictly species-specific. They come to relatively brief contact with their host when they feed on it. Feeding can be followed by significant life-history events like moulting (ticks, Ixododa; Goater et al., 2013) or reproduction (mosquitoes, Culicidae; Taylor et al., 2015). Leeches (Hirudinea), ticks (Ixodida) and fleas (Siphonaptera) can all be considered micropredators.

However, most parasites tend to form lasting associations with their hosts, often with multiple species. Commonly, they reach sexual maturity and reproduce in their definitive host. Before that, they may have one or more intermediate hosts where they undergo morphological development or even asexual reproduction. Definitive hosts are often on higher trophic levels in food webs, and usually, they are vertebrates (Goater et al., 2013).

Trophically transmitted parasites find their way to their definitive host by predation. They are usually more virulent in the intermediate host (Poulin, 2011a) and less virulent in the definitive host. It is easy to see this strategy's adaptive advantage, as it facilitates the successful predation of the intermediate host by the definitive host. Trematodes

(except for schistosomes), cestodes and certain protozoans like sarcocystiid species are all trophically transmitted (Schmidt, 1992; Taylor et al., 2015).

Vector transmitted parasites use blood-feeding micropredators to spread between their vertebrate hosts. Malaria is one of the biggest epidemiological concern of our date (Snow et al., 2005), caused by *Plasmodium* species (primarily, but not exclusively by *P. falciparum*) distributed by female *Anopheles* mosquitoes (Zekar and Sharman, 2020). Reduviid hemipterans spread Chagas' disease (*Trypanosoma cruzi* infection; Bern, 2015). Babesiosis is spread by ticks (Vannier and Krause, 2020) and can cause serious infections commonly accompanied by weakness and depression (Taylor et al., 2015).

Not all parasites rely on multiple host species in their life cycle. *Directly transmitted parasites* (Poulin, 2011a) could be interesting subjects for ecological and evolutionary parasitology as these organisms' environment and evolutionary constraints are more specified. Despite their similarities, they can vary considerably in their virulence, life cycle and origin. Parasitic turbellarians (Cannon and Lester, 1988) are scarce endoparasites of marine fish. Usually, they are not virulent; they may complete their life cycle without hosts. Monoxenous¹ parasitic nematodes also have free-living stages; they only invade the host in their third larval stage (Schmidt, 1992). They may also have both free-living and parasitic reproductive cycles, like *Strongyloides* species (Taylor et al., 2015).

Lice (Phthiraptera) are special in this sense. Not only they spend their entire life-cycle in immediate contact with their host (Clayton et al., 2015), but as large-bodied ectoparasites, they are also relatively easy to study. These properties alone would make them instructive models of parasite ecological and evolutionary studies; they alone deserve attention for being a diverse, entirely parasitic clade. Although their phylogeny and origins are not fully resolved, they are undoubtedly ancient. Lice are closely related to bark and book lice (Psocoptera). Although the two latter are not parasitic, they often live in nests or burrows of birds and mammals feeding on organic matter (Light et al., 2010). Liposcelidid booklice are considered the closest free-living relatives of lice. The earliest known fossil from the Liposcelididae family dates back 100 million years (Grimaldi and Engel, 2006).

Lice are dorsoventrally compressed, wingless ectoparasites of nearly all birds and some mammals. The adults are around 0.8–11 mm long. Females are usually larger than males. They either have no or small eyes. They have sensory organs on their antennae and in their mouths (Johnson and Clayton, 2003). All lice have similar, hemimetabolous life cycles. The females lay operculate eggs (often called nits) that they glue with

¹ One host in their life cycle

glandular cement to the host's feathers or hair (Taylor et al., 2015). These are usually visible to the naked eye; they are often easier to detect than the lice themselves (Johnson et al., 2003). The nymphs (larvae) hatch from the eggs after 4–10 days of incubation. They tend to be less sclerotized and more achromatic, especially in their earlier nymphal stages. Nymphs have no reproductive organs, so they cannot be sexed morphologically in contrast to adults. They reach maturity after three moults. The instars² need 3–12 days to proceed to their next stage. The females lay 1–10 nits a day during their 1–2 month-long adult life.

Phthiraptera has four suborders: Anoplura, Rhynchophthirina, Ischnocera and Amblycera. Anoplura are blood sucking lice of mammals. Their mouthparts adapted to pierce the host's skin. Most sucking lice are known from rodents, but they occur on 20% of all mammal species. Humans also have lice: the head louse (*Pediculus humanus capitis*), the body louse (*Pediculus humanus humanus*) and the pubic louse (*Phthirus pubis*). Human lice spread between persons in most cases. Body lice may be vectors of diseases (Bonilla et al., 2013; Raoult and Roux, 1999), namely the louse-borne relapsing fever (caused by *Borrelia recurrentis*), trench fever (caused by *Bartonella quintana*) and epidemic typhus (caused by *Rickettsia prowazekii*). Nowadays, louse infestations are not considered a serious public health issue since they are usually easy to treat with pediculicides. However, the increasing pediculicide resistance observed in head lice may be concerning (Durand et al., 2012; Marcoux et al., 2010). This trend may emphasize the use of traditional (Mumcuoglu et al., 2021) and new non-chemical (Bush et al., 2011) remedies against pediculosis. For veterinary medicine, primarily the species of the Haematopinidae and Linognathidae families may be significant (Taylor et al., 2015).

Rhynchophthirina is the sister clade of Anoplura, also the smallest suborder. We only know three species from elephants (*Loxodonta africana* and *Elephas maximus*), warthogs (*Phacochoerus aethiopicus*) and river hogs (*Potamochoerus porcus*). The other two remaining suborders are the Ischnocera and Amblycera. These three are often called chewing lice after their chewing mouthparts. "Chewing lice" is now an informal name for these groups as the Mallophaga suborder turned out to be paraphyletic. Chewing lice feed on dead skin, skin products, secretions, blood, or feather material, but not on hair (Johnson et al., 2003). About 12% of chewing lice species live on mammals the others parasitise birds (Aves). More than 3900 louse species were described from avian hosts (Price et al., 2003). Although an exceptionally host-generalist species, *Menacanthus eurysternus*, is known from 175 host species, most avian lice are more or

² Development stage between two moults

less host-specific (Clayton et al., 2015). Typically, there are 2–4 louse species on a bird species, with considerable variations across host taxa. Hummingbird individuals usually accommodate no or a single louse species, compared to eight on some procellariiform birds (such as petrels; Galloway and Lamb, 2021).

The relationship of birds and lice dates back at least 40 million years (Wappler et al., 2004). During this period, adaptations and counter-adaptations formed an “arms race” in which bird and lice species shaped each other’s characteristics (Clayton et al., 2015). This makes them ideal models to study not just macroevolutionary but also microevolutionary processes. Birds do not just evoke the interest of the general public (Baldassarre, 2020), they are probably the most researched vertebrate taxa as well (Titley et al., 2017). The long coevolutionary history and the rich background knowledge on the hosts make birds and their lice a valuable study system.

Birds try to cope with their lice in many different ways, most notably by grooming (preening or scratching; Clayton et al., 2010). Preening is one of the primary ways for birds to combat their lice (Bush and Clayton, 2018). The morphology of the beak partly adapted for the removal of ectoparasites. Beak-trimmed hens could be eight times more infested with lice than hens with intact beaks (Chen et al., 2011). In Rock pigeons (*Columbia livia*), the shortening of the upper beak drastically increases the number of lice while not hindering them in feeding (Clayton et al., 2005). 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 (Solt, 1998). Scratching may be less efficient, but it is vital in body parts that a bird cannot preen (Bush et al., 2018). Of course, other birds can help where self-grooming comes short. Apart from having important social functions, allopreening may even be more efficient than self-preening (Villa et al., 2016b). The uropygial oil of birds is known to have antibiotic and antifungal effects. It can also act against lice and other ectoparasites not just chemically but also by impeding their movement or suffocating them (Clayton et al., 2010). Sun-, dust-, and water-bathing can also help to combat lice, as these radically alter the otherwise more or less constant microclimate of the plumage (Clayton et al., 2010). Felső and Rózsa (2007) even showed that the diving behaviour of birds reduces the genera richness of their lice.

Avian lice mainly feed on feather material (that is why they were previously considered among “chewing lice”). Endosymbiotic bacteria help them break down their keratin-rich food and provide them vitamins (Clayton et al., 2015; Perotti et al., 2008). Some groups may feed on skin debris or blood by chewing on developing feathers (Johnson et al., 2003). Lice are typically low pathogenic parasites, causing more severe symptoms if present in higher numbers on a host (Taylor et al., 2015). The amount of feather material

consumed by the lice can affect the host's thermoregulation (Booth et al., 1993). They may also be vectors of microbial infections (Rózsa, 2003).

On the one hand, louse subpopulations can often overgrow in the absence of adequate defence, as the examples have shown above. On the other hand, an extreme infestation worsens the host's condition (Brown et al., 1995). The direction of causality between the infestation and the birds' health status is not always clear. However, the levels of their infestations still covaries with host health status for two reasons. First, birds with poor body condition may invest fewer resources into antiparasitic defenses, thus allowing more parasites to infest, survive and multiply on their bodies. Second, the rise of ectoparasite infestations exerts an increasing metabolic cost on the hosts. Lice typically exhibit aggregated distributions in the natural populations of birds, similar to other parasites. Many birds are not or only slightly infected, while a smaller portion is heavily infected (Rózsa, 2005). It follows that their impact also reflects this distribution on the host population.

Lice are flightless insects; they can spread by direct physical contact between their hosts. Some lice show phoretic behaviour when they attach themselves to louse flies (Hippoboscidae) to travel between hosts (Harbison et al., 2009). 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, fighting or roosting. Vertical transmission occurs among related hosts, especially parents and offspring, or between siblings until the nestlings are still in the nest together. Parental care offers ample opportunities for lice to disperse from their parents to the nestlings when they feed, brood or shade their young. While the nestlings are still together, lice have the opportunity to choose a nestling with better surviving prospects (or a live one, in a more extreme case). While vertical transmission arguably offers a more robust opportunity for dispersal, the short-term survival chances of nestlings may be lower than adult birds. In most cases, lice probably make decisions about their dispersal (Brooke, 2010), but we know little about this behaviour. We do not entirely understand what lice perceive about their environment. Still, they can show complex behaviours like avoiding moulting and seeking newly developing feathers (Moyer et al., 2002) or leaving dead hosts (Johnson et al., 2003; Rózsa, 2003). Their dispersal behaviour is most likely affected by the donor and recipient host's expected survival and reproduction chances (Brooke, 2010; Darolova et al., 2001).

As we have seen, the dispersal opportunities for avian lice are pretty rare compared to their expected lifetime. This means that most louse subpopulations live mostly in isolation that results in inbreeding. This phenomenon is further amplified by the fact that

lice seldom have the opportunity to spread between different host species, as interspecies physical interactions of hosts are rare. These, along with the constant coevolutionary pressures, amplify the divergence and eventually the diversification of avian lice.

Lice try to evade host defences in various ways. Since birds primarily counter lice by preening, most of the lice's counter adaptations have evolved against that. Some amblycerans may try to evade preening by quickly moving in the plumage or seeking hard to reach refugia. Ischnoceran lice may try to burrow deep into the birds' plumage or hide in the interbarb ditches of wing or tail feathers. Some lice specifically occur on hard to reach body regions as the head or the neck (Johnson et al., 2003). Body size also has a vital role in escaping host defences. Fecundity selection is expected to drive louse body size larger. However, lice cannot grow too large as they would fall victim to their host more easily (Clayton et al., 2015). This is supported by the fact that lice respond to selection on their body size rapidly (Villa et al., 2019). Even on macroevolutionary scales, larger hosts tend to host larger lice (as known as Harrison's rule; Harnos et al., 2017). This phenomenon illustrates that different kinds of selection pressures — some related to parasitism, some not — can act on lice.

As outlined in this section, lice and birds offer a rich model system to learn about the ecology and evolution of parasitism. In the first half of this thesis, I try to gain some insight into the ecology of avian lice by studying how their abundance is related to their hosts' individual traits. In the second half, I investigate whether a generally observed pattern in sexual size dimorphism holds true for these ectoparasites.

3 Ecology of Avian lice

3.1 Introduction

The abundance of ectoparasites can vary markedly between individuals and a considerable part of this variation can be explained by certain individual host traits. Both static and dynamic host traits can influence infestation levels; like sex, age, body size, and behaviour. Considering both trait types simultaneously in parasite ecological studies could help us better understand the biology of host-ectoparasite interactions and explain their dynamics.

Body size is one of the most relevant characteristics of host organisms; larger birds tend to harbour more lice in comparisons both within³ (Chu et al., 2019; Galloway and Lamb, 2017) and across species (Harnos et al., 2017; Rózsa, 1997). Larger hosts probably provide more durable 'habitat patches', with larger surface areas, and more diverse sets of topographic refugia (Poulin, 2011b; Rózsa, 1997) for lice. Since it is easy to measure, wing length is often used as a proxy of body size when examining nestlings under field conditions.

Sex has also frequently been associated with louse abundance with contradictory overall results. In some cases, the males (Durkin et al., 2015; Rivera-Parra et al., 2014), in others the females (Brooke, 2010; Potti and Merino, 1995) were more heavily infested, while other studies found no evidence for bias (Kettle, 1983; Touleshkov, 1965).

It has been recognised early that louse abundance can change dynamically throughout the year but based on the existing studies it is difficult to find clear associations with the life cycle stages of the host. Foster (1969) found that the amblyceran lice of the Orange-crowned Warbler (*Leiothlypis celata*) timed their breeding to match the host's breeding period. Lamb and Galloway (2015) revealed that Woodpecker lice breed throughout the year, but their prevalence and intensity was the lowest at the end of the hosts' breeding period. Contrarily, both Galloway and Lamb (2015) and also Kettle (1983) showed that different species of lice on the same host can exhibit distinct seasonal patterns, and none of these matches the reproductive cycle of the hosts. Moulting was also hypothesised to affect louse abundances (Foster, 1969; Kettle, 1983), but this is challenged by both field studies (Galloway et al., 2015) and experiments (Moyer et al., 2002). Although the relationship of louse population dynamics and the breeding period of the birds remained unclear, this life cycle stage has a profound

³ For a counter example see Darolova et al. (2001)

impact on the birds' physiology and behaviour which could change their ability to combat lice.

Avian lice heavily rely on vertical transmission routes from parents to offspring (Clayton and Tompkins, 1995) and, therefore, their dispersion opportunities mainly open up during the host breeding season. Lice infesting nestlings in a brood have the chance to prefer particular siblings against others, due to the direct bodily contacts among them. This period offers opportunities even for lice with poor transmission capabilities to choose the most appropriate host, taking multiple host characters like body size, plumage development, and sex into account. The louse load of a particular nestling, therefore, depends substantially on its individual characters as compared to its nestmates' number and their characters. Richner and Heeb (1995) introduced the so-called Dilution Hypothesis, claiming that ectoparasites like lice can disperse to more nestlings in larger broods, lowering the average abundance on individuals. This effect may be accentuated by the individual differences between parents: birds in poor condition likely to have fewer offspring, but being more infested themselves, they also transmit more lice to the clutch (Whiteman and Parker, 2004).

High parasite burdens could constitute both a cause and a consequence of poor health status in birds (Clayton et al., 2015). This is particularly true for large-bodied bird species like raptors, because they tend to host relatively high ectoparasite burdens (Rózsa, 1997). Furthermore, since several populations have declined dramatically, many raptors are considered vulnerable to extinction. Thus, the importance of monitoring the health status of their populations, as judged from levels of parasite infestations, is increasingly important for conservation purposes (Liébana et al., 2011; Órdenes et al., 2005; Saxena, 2017; Tinajero et al., 2019; Yosef et al., 2019). Moreover, avian ectoparasites may also be threatened by extinction and constitute conservation values themselves (Bulgarella and Palma, 2017; Dougherty et al., 2016; Kwak, 2018; Kwak et al., 2019; Rózsa and Vas, 2015b; West et al., 2019). Establishing baseline values for parasite infections in natural populations must necessarily be controlled for the most important factors affecting individual ectoparasite loads. Most notably, host age, sex, and body size likely affect individual infestation levels, and the seasonality of infestation dynamics must also be taken into account (Lamb and Galloway, 2016; Yunik et al., 2016).

To study the ecology of avian 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. Taking the falcons as an example, the Falconidae family consists of 63 species (Gill et al., 2021). The Falconinae subfamily is cosmopolitan, but most species breed in the

Palaearctic region (Fuchs et al., 2015). Many of them are long-distant migrants, like Lesser Kestrels (*Falco naumanni*; Cox, 2010), Red-footed Falcons (*Falco vespertinus*; Fehérvári, 2016; Palatitz et al., 2018) and Amur Falcons (*Falco amurensis*; Bildstein, 2006). Others may be partially migratory, like Common Kestrels (*Falco tinnunculus*) in Europe (Holte et al., 2016). Falcons generally show sexual size dimorphism. The females, on average, are larger than the males (Krüger, 2005). They may also show sexual plumage colour dimorphism to a varying degree. While male and female adult Hobbies (*Falco subbuteo*) can be tricky to sex based on their plumage, Red-footed Falcons show quite marked dimorphism in colour (Forsman, 1998). Falcons' beak has a characteristic trait, the tomial tooth. The tomial tooth is a triangularly shaped protrusion preceded by a notch. It is hypothesised that it helps to sever the neck of their prey (Miller and Fowler, 2014). Its relation to preening — best to my knowledge — has not been studied. Falcons often forage in mid-air or open areas like grasslands. They frequently prey on vertebrates, often on other birds. The smaller species also consume insects, sometimes even more than vertebrates (Forsman, 1998; Palatitz et al., 2018). Falcons are (mostly) socially monogamous, but extra-pair fertilisations may also occur (Magonyi et al., 2021). None of the falcon species build nests. They either occupy nests of other bird species (the so-called nest-host species) or breed in cliff ledges, tree cavities, or even buildings. Most species breed solitarily, but some can be colonial based on their nest-host species like Red-footed Falcons or Common Kestrels. Migratory species often gather on roosting sites preceding migration or during wintering (Fehérvári, 2016; Fehérvári et al., 2014).

In this chapter, I aimed to study how the individual traits of the hosts relate to the abundance of their lice. For this, I chose three small-bodied falcon species, the Common Kestrel, the Red-footed Falcon and the Amur Falcon. These birds are frequently infected with lice (Piross et al., 2015; Vas et al., 2012). This allows us to study louse ecology with a reasonable research effort that also relieves the birds from unnecessary disturbance. The Common Kestrel is widespread and has been intensively studied for decades (Village, 2010). Both Red-footed Falcons and Amur Falcons are subjects of great conservational concerns internationally (Aiyadurai and Banerjee, 2019; Palatitz et al., 2018). The background data from ongoing conservation programmes like these offer invaluable opportunities and data to conduct such studies. We researched the louse abundance of these falcons at different stages of their life. We studied Common Kestrel and Red-footed Falcon nestlings, breeding Red-footed Falcons and roosting Amur Falcons during their autumn migration. These species mostly share their louse fauna,

which can hopefully help in the generalisation of our findings. Our question was how the individual traits of the birds relate to the abundance of their most common louse species.

3.2 Statistical analysis of parasite infestations

3.2.1 The nature of parasite abundance data

Describing the infestation level of the host population is a central topic of parasite ecology. Although we can measure this from different viewpoints, the data can be structured simplistically, allowing a wide variety of statistics to be calculated. When gathering parasite samples, the individual hosts can be taken as sampling or observational units. For each sampled host, we can record the number of parasites collected. This is usually logged on a per-species basis, and it is referred to as infrapopulation size (Reiczigel et al., 2019). According to the analyses' aims, parasites can also be categorised by different developmental stages, sexes, or different taxonomic ranks. It is worth noting that it is hard or even impossible to collect all parasites from a given host in most cases. Different sampling methods estimate ectoparasite abundance with different accuracy (Clayton and Drown, 2001), which most likely depends on both the host and the parasite species. Without knowing the exact bias, it is not possible to account for it in the statistical analyses. Still, it is worth keeping in mind when interpreting the results that the actual ectoparasite abundances are most likely higher than the estimates.

Based on the possible infrapopulation sizes, we can draw the observed distribution of hosts among the infestation classes (i.e. the number of hosts with 0, 1, etc. parasites). These distributions are discrete and usually aggregated (Poulin, 2007). Most hosts are not infected or carry only a handful of parasites, while a few hosts are more heavily infected. The discrete and aggregated nature of these data limits what kind of procedures we can use for the statistical analyses.

3.2.2 Infection indices and descriptive statistics

Following the recommendations of Reiczigel et al. (2019), the parasite infection can be characterised from different perspectives using the following indices:

Abundance is defined as the number of parasites found on a host (infected or noninfected). The mean and the median of the observed abundances can describe the parasite load of the host population.

Intensity is the number of parasites on an infected host. Again, the mean and median are commonly used to characterise the host population's infected part.

Prevalence is “the proportion of infected individuals within the host sample or population” (Reiczigel et al., 2019). Prevalence can be expressed as a percentage of infected individuals or as a probability that a randomly chosen individual is infected.

Aggregation indices measure how unevenly are the hosts distributed among the infestation classes. The two most commonly used are the variance to mean ratio and exponent r of the fitted negative binomial distribution.

Crowding expresses the infrapopulation size from the parasite’s perspective. Crowding equals intensity, but the statistical measures are calculated over the number of parasites rather than the number of hosts. While the mean intensity estimates the expected number of parasites on a randomly chosen host, mean crowding expresses the expected size of the infrapopulation to which a randomly chosen parasite belongs (Reiczigel et al., 2008, 2005).

It is possible to compute confidence intervals for the indices mentioned above (Rózsa et al., 2000) and compare them between host populations using statistical tests (Reiczigel et al., 2019, 2013).

3.2.3 Statistical modelling of parasite abundance

Statistical tests allow us to compare the parasite loads of two — in some cases, more — host populations (e.g. sexes, age groups, biological populations, etc.), but they cannot describe more complex infestation patterns. The generalised linear models (GLM) can model various infection indices (Zuur et al., 2009). They can also be used for hypothesis testing to determine which explanatory variables significantly affect the birds’ louse load. These models consist of three parts.

The (i) systematic component (also known as the linear predictor) is a linear combination of the explanatory variables that estimates a function (ii link function) of the response variable. The (iii) random component describes the distribution of the response variable. Moreover, the distribution must be parametric and be part of the exponential family (Keener, 2010). Commonly, but not exclusively, the Normal (Gaussian), Binomial, Poisson and Negative binomial distributions are used as random components.

The whole model formula can be given as:

$$g(E(Y)) = \beta_0 + \beta_1 X_1 + \dots + \beta_i X_i$$

Y : response variable

$g(\cdot)$: link function

The systematic component describes the expected value of Y , where the link function transforms Y .

$$g(E(Y)) = \beta_0 + \beta_1 X_1 + \dots + \beta_i X_i$$

$E(Y)$: the expected value of Y

It is worth keeping in mind that we do not automatically get the estimated expected values from the model results. Each distribution family has a canonical link function to transform the models' expected values (Agresti, 2003; Gelman and Hill, 2007). We can apply their inverse on the model estimates to transform them back to their original scale. The most commonly used distribution families, their canonical link function and their inverse are listed in Table 1.

Table 1 Types of GLMs used to model different infestation indices. These models differ in which distribution families are used in the random component of the model. The canonical link function and their inverse is also reported.

Infection index	GLM model	Canonical link function	Inverse function
Abundance	Poisson	$\ln(E(Y))$	$e^{E(Y)}$
	Negative binomial		
	Quasi-Poisson		
	Zero-inflated Poisson		
	Zero-inflated negative binomial		
Hurdle ⁴			
Intensity	Zero-truncated Poisson	$\ln(E(Y))$	$e^{E(Y)}$
	Zero-truncated negative binomial		
	Hurdle ^{Error! Bookmark not defined.}		
Prevalence	Binomial	$\ln\left(\frac{E(Y)}{1 - E(Y)}\right)$	$\frac{e^{E(Y)}}{1 + e^{E(Y)}}$
	Hurdle ^{Error! Bookmark not defined.}		

The distribution family used in these models depends on both the modelled infection index and the nature of the data itself. Abundance is usually modelled with discrete distributions such as the Poisson or the negative binomial distribution. The Poisson distribution has a single parameter, the expected value (traditionally denoted by λ). The Poisson distribution has an interesting property that its variance equals its expected value. However, this not always true for real-life data.

⁴ Hurdle models consist of two models. A binomial model for all zeros and either a Zero-truncated Poisson or a Zero-truncated Negative binomial for non-zero values)

Overdispersion occurs when variance exceeds the mean. This is more common than underdispersion (the variance is less than the mean). According to Hilbe (2007), overdispersion can either be apparent or real. Apparent overdispersion arises when the model is insufficiently specified. There could be several reasons for that. For example, important explanatory variables or interactions are missing from the model. There are outlying data points in it, or the response variable and its link function have a non-linear relationship with the predictors. Overdispersion causes standard errors to be underestimated and could cause certain predictors to appear significant when they are not. There are ways to handle apparent overdispersion if the root of the problem is identified.

Real overdispersion can be dealt with in many different approaches (Hilbe, 2007; Zuur et al., 2009). There are two common cases when the Poisson distribution does not seem to fit our data. In the first one, the variance is just simply higher; the distribution is more right-skewed than the Poisson distribution with the same mean. In this case, Quasi-Poisson models are applicable: These scale the standard errors post-hoc to correct for their inflation. Alternatively, count data can also be modelled with the negative binomial distribution. The negative binomial distribution has two parameters, the mean and a dispersion parameter, which controls the distribution's skewness.

Overdispersion can also be caused by zero-inflation. Zero-inflation means there are more zero observations than expected from a Poisson or negative binomial distribution. In this case, our model should account for this excessive number of zeros. There are at least two modelling approaches for this. Zero-inflated and Hurdle models both assume a complex data generating process. In the first binary part, a random process decides whether the outcome is necessarily zero or not with a certain probability (Bernoulli process). A possible interpretation in this context is whether a bird even had a chance to contract lice. In the second process, if the bird had a chance to get infected, another random process decides how many lice it had. The two approaches differ in this second part: zero-inflated models assume that the parasite counts come from regular Poisson or negative binomial distributions. This means, even if the bird had a chance to contract parasites, it did not necessarily have. Hurdle models use zero-truncated Poisson or negative binomial distributions to model parasite counts. These distributions do not have a possible zero outcome. Otherwise, they are the same as their regular counterparts. This can be interpreted as if a bird had a chance to get infected it had. A detailed description of these models is available in Achim et al. (2008).

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

Based on: 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

3.3.1 Introduction

Common Kestrels (*Falco tinnunculus*) are small falcons (Falconidae) common in Hungary, where they breed in agricultural areas and towns. Like other falcons, they occupy nests of other bird species instead of building their own. Depending on which species' nests they occupy, they either breed solitarily — for example, in nests of Hooded Crows (*Corvus cornix*) or Eurasian Magpies (*Pica pica*) — or colonially in Rook (*Corvus frugilegus*) and Western Jackdaw (*Corvus monedula*) colonies. Their diet usually consists of small rodents, lizards, occasionally birds and insects. Two major — non-independent — governing factors of their brood size are food availability and breeding commencement. According to Finnish studies (Korpimäki and Wiehn, 1998), the abundance of Common Voles (*Microtus arvalis*) and Bank Voles (*Myodes glareolus*) — local main preys — varies cyclically over the years. When the abundance of the voles was low, the kestrels commenced their breeding later and laid fewer eggs. However, parental quality seems to be the most influential factor. The breeding pairs take their condition and survival chances into account when investing their resources (nutrients, energy) into breeding. It follows that brood size indicates parental quality (Tolonen and Korpimäki, 1994). Parents provide more food for larger broods (Masman et al., 1989), but they do not increase the amount when the brood size is artificially increased (Tolonen and Korpimäki, 1996). The sex of Kestrel nestlings (see Photo 1) can be morphologically determined (Forsman, 1998), which allows investigating the effect of sex on the abundance of lice efficiently.

In this study, we investigated how Common Kestrel nestlings' sex, maturity, and brood size (number of siblings) affect their common louse species' abundance.



Photo 1 Kestrel (Falco tinnunculus) nestling in a nest-box. Photo by Péter Palatitz.

3.3.2 Materials and methods

We collected the samples between 09-11. 06. 2017. at Cserebökény, Vásárhelyi-puszta and Csanádi-puszták, areas belonging to Körös-Maros National Park, Hungary. Birdlife Hungary's (MME) Red-footed Falcon Workgroup and staff of the National Park Directorate monitor raptors' breeding in the area (Kotymán et al., 2015).

We took ectoparasite samples from Common Kestrel nestlings older than 15 days. We sampled entire broods, all at the same time. We kept the nestlings separate from each other to prevent cross-contamination. Before sampling, we measured their wing length and determined their sex based on morphological traits (Clark and Yosef, 1998; Forsman, 1998).

We used the dust-ruffling technique using a pyrethrin powder to sample for ectoparasites. We applied the powder on the nestling's plumage and held it over a white tray for five minutes. After this period, we gently riffled the plumage of the bird to dislodge the remaining ectoparasites. We collected the ectoparasites into small centrifuge tubes containing 70% ethyl-alcohol. For the identification, we used a stereo microscope with 20x and 40x magnification. We based the identification on Price et al. (2003).

For modelling the abundance of the different louse species, we used generalised mixed models with negative binomial distribution and log-link (Zuur et al., 2009). The nestling's sex, wing length, the brood size were fixed variables; the nest ID was a random variable in the initial models. Brood size was treated as a categorical variable: We considered broods with 3–4 nestlings small (N=5), broods with 5–6 nestlings large (N=7). This categorisation was necessary to account for the effect of this variable with the current — low — sample sizes. We used deviance ratio tests for model selection. We left out fixed variables from the initial model one-by-one, and we compared these models to the other, still containing that variable. When leaving out a variable would have significantly worsened the model fit, we kept it in the model. We considered results significant at a 5% level. For calculating the descriptive statistics, fitting the models and preparing the figures, we used R 3.4.4. (R Core Team, 2018) statistical environment and the following libraries: glmmTMB 0.1.1 (Brooks et al., 2017), lsmeans 2.25-5 (Lenth, 2016), RcmdrMisc 1.0-5 (Fox, 2016), ggplot2 2.2.1 (Wickham, 2009).

3.3.3 Results

Altogether we sampled 54 nestlings from 12 different broods. We found two louse species on the nestlings: the amblyceran (Amblycera: Menoponidae) *Colpocephalum subzerfae* and the ischnoceran (Ischnocera: Philopteridae) *Degeeriella rufa*. We found

neither *Laemobothrion tinnunculi* — associated with Common Kestrels in the most recent Hungarian checklist (Vas et al., 2012) — nor *Nosopon lucidum* — in the global checklist (Price et al., 2003) — on the nestlings. Table 2 contains the descriptive statistics on nestlings' infestation with *C. subzerafae* and *D. rufa*. See Figure 1 for the distributions of conspecific lice.

None of the investigated explanatory variables had a significant effect on the abundance *C. subzerafae*. Brood size had a significant effect (p-value=0.0099) on the abundance of *D. rufa* (Figure 2). In small broods, with 3–4 nestlings, the estimated *D. rufa* abundance was 15.5 (95% C.I.: 8–30), while in large broods, with 5–6 nestlings, it was 4.2 (95% C.I.: 2.3–7.4).

Table 2 Descriptive statistics of the Colpocephalum subzerafae and Degeeriella rufa infestation of Common Kestrel (Falco tinnunculus) nestlings in small (3-4 chicks) and large (5-6 chicks) clutches.

	<i>C. subzerafae</i>			<i>D. rufa</i>		
	3–4 nestlings	5–6 nestlings	All	3–4 nestlings	5–6 nestlings	All
Number of infected nestlings	9	6	15	17	30	47
Number of investigated nestlings	17	37	54	17	37	54
Prevalence	53%	16%	28%	100%	81%	87%
Mean abundance	1.5	0.3	0.7	16.7	5.5	9
Median abundance	1	0	0	15	4	7
Mean intensity	2.8	2	2.5	16.7	6.8	10.4
Median intensity	2	2	2	15	5	7
Variance/Mean	3.5	2.8	3.6	6.9	5.7	9.3

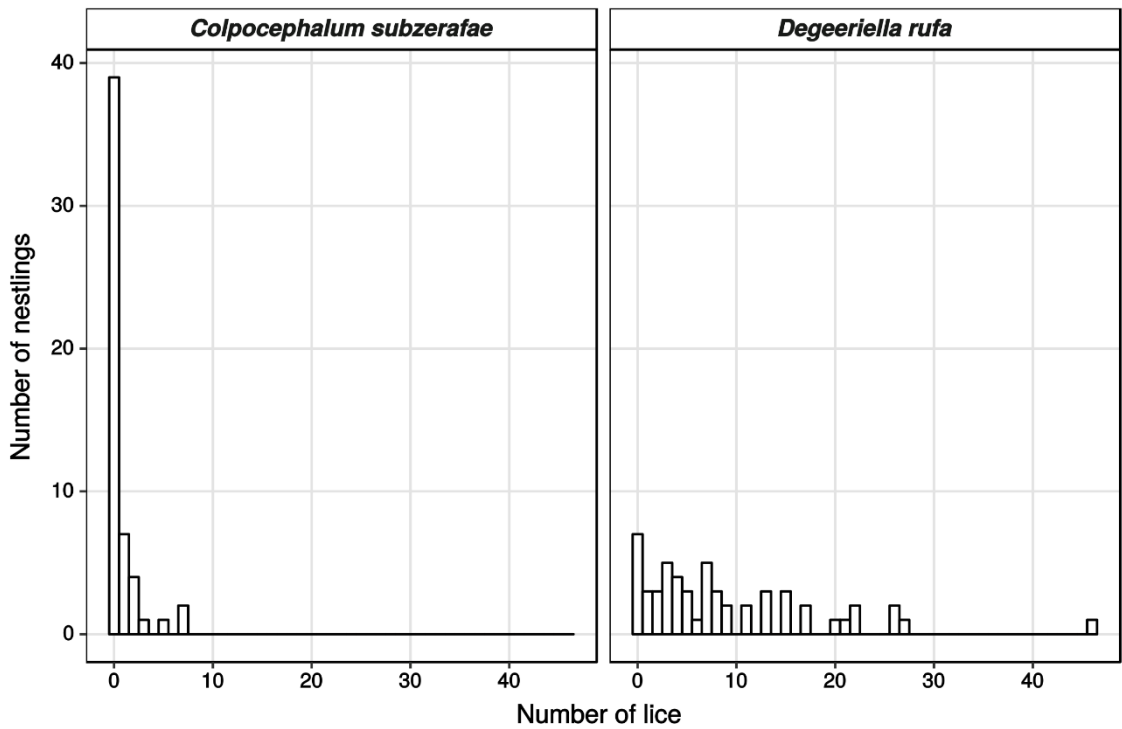


Figure 1 Distribution of the number of *Colpocephalum subzerafae* and *Degeeriella rufa* lice on Common Kestrel (*Falco tinnunculus*) nestlings. The number of examined birds was 54.

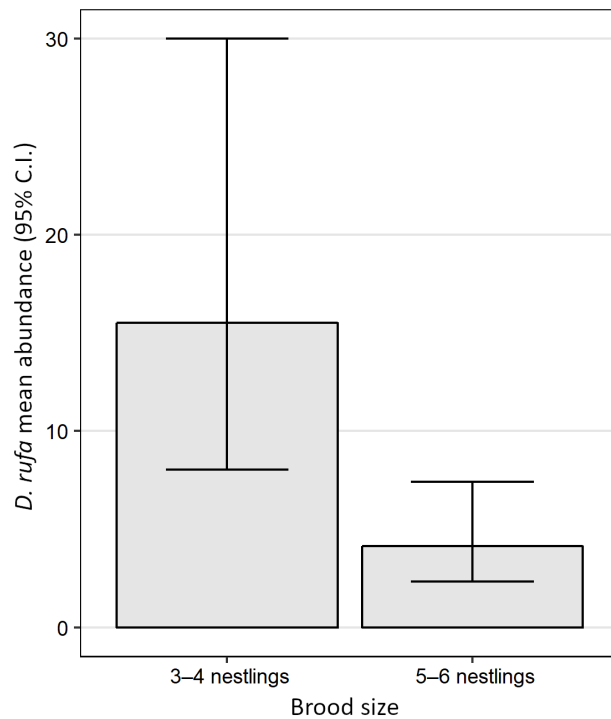


Figure 2 Mean abundance (95% confidence interval, C.I.) of *Degeeriella rufa* on Common Kestrel (*Falco tinnunculus*) nestlings in small (3-4 chicks) and large (5-6 chicks) broods.

3.3.4 Discussion

According to our results, Common Kestrel nestlings are more heavily infected with *D. rufa* lice in smaller broods. We can explain this in two ways: by the parental quality and that in larger broods, lice can disperse to more nestlings (Richner et al., 1995).

We conducted our study within a few days in similar habitats and with similarly old nestlings. Based on this, we believe that the variance observed in brood size is mainly due to parental quality. The pattern observed could be explained by parental quality if parents in poorer condition, laying smaller broods are also more infested with *D. rufa*. Similar results were found in Galapagos Hawks, where birds in poorer condition were more heavily infested with lice, and their condition predicted their territory ownership as well (Whiteman et al., 2004).

The reproduction rate of lice can provide an alternative explanation for the observed higher abundances in smaller broods. Richner and Heeb (1995) explained the relationship between brood size and ectoparasite infestations by the parasites' life cycle. The authors reason that a shorter life-cycle — compared to the time spent in the nest by the nestlings — also means that the ectoparasites multiply faster. These species establish subpopulations with roughly the same size on each nestling, meaning that the total number of ectoparasites in a brood depends on its size. Møller (2000) observed this phenomenon on Barn Swallows (*Hirundo rustica*) and their haematophagous mites *Oritonissuss bursa*. Contrarily, ectoparasites with a long life-cycle (e.g. lice), cannot significantly increase their subpopulations sizes by the time the nestlings fledge. This leads to the so-called dilution hypothesis: the migrating ectoparasites disperse in the brood, meaning that their total number in the brood does not depend on its size, and the subpopulation sizes will be smaller in larger broods (Richner et al., 1995).

This may also be true for our tested system, as Kestrel nestlings are most likely to be infected with lice vertically (from their parents or by their siblings). In this case, we should also assume that the likelihood of lice moving from parents to offspring does not depend on the brood size. We know little about how lice decide whether they should spread to another host given they have an opportunity. Brooke (2010) did not even find clear evidence that the number of lice on the parents would affect the number of lice dispersing to the nestlings. We observed a similar pattern with *C. subzerafae*; however, we do not have strong enough evidence of this phenomenon. Based on our findings, it seems that the Common Kestrels' parental investment not only affects the number and condition of their nestlings but their ectoparasite load as well.

3.4 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

3.4.1 Introduction

Red-footed Falcons (*Falco vespertinus* Linnaeus, 1766) are colonially breeding raptors showing marked sexual dimorphism in adult plumage (but not in juvenile plumage; see Photo 2Photo 5) and different sex roles during breeding. Their habitat use and behaviour in the breeding period are broadly studied (Palatitz et al., 2018). These falcons typically raise 3–4 nestlings of similar age (Solt, 2018a), and host relatively high lice loads (Piross et al., 2015). Siblings of the same clutch tend to be genetically similar, receive similar parental care, and have an equal chance to contract lice from their parents and each other. Studying the ectoparasite-host relationship in this system, therefore, allows us to rule out known influential factors such as large-scale environmental differences, and also allows us to focus on the effects of individual host traits.

The aim of this work was to investigate how certain host characteristics affect the abundance of lice on both nestling and adult Red-footed Falcons during the breeding period. We examined the role of body size, sex, time elapsed since the commencement of breeding (in case of adults only), and clutch size (in case of nestlings only).



Photo 2 Adult male Red-footed falcon Falcon (Falco vespertinus). Photo by Péter Palatitz.



Photo 3 Adult female Red-footed falcon Falcon (Falco vespertinus). Photo by Péter Palatitz.



Photo 4 Young Red-footed Falcon (Falco vespertinus) nestling. Photo by Péter Palatitz.



Photo 5 Red-footed Falcon (Falco vespertinus) fledgling with fully developed juvenile plumage. Photo by Péter Palatitz.

3.4.2 Materials and methods

3.4.2.1 Sampling

Red-footed Falcon louse sampling took place in Vásárhelyi-pusztá, an area within the municipality borders of Hódmezővásárhely, Békéssámson, Székkutas, Orosháza and Kardoskút (N 46°28'25", E 20°37'30"), belonging to the Körös-Maros National Park, Hungary. This landscape is dominated by alkaline grasslands interspersed with arable fields, temporary saline lakes or marshes, farms and dirt roads. In this area, most Red-footed Falcons breed in artificial nest-boxes fixed on trees, but a minority of them occupies natural nest-sites built by corvids. They readily breed colonially, but solitary breeding is also frequent (Kotymán et al., 2015). The breeding performance of the local population is closely monitored, and the vast majority of nestlings is ringed with individual colour rings and weighed and measured according to a standard protocol. This entails body mass and wing length measurements.

In 2012, two (in one case three) nestlings (N=95) — a presumed male and a presumed female (Ristow, 2003) — from each clutch were sampled for lice (N=67). In 2014, entire clutches (87 nestlings from 32 clutches), together with adult birds (N=60) were sampled. The sampled clutches and adults were selected to be independent of each other to avoid cross contamination caused by the ectoparasite collection method (see below for details). Adults were trapped in the vicinity of their nests using mist nets and were colour ringed. All focal nests were subsequently revisited and observed at least twice on separate days to observe and identify colour ringed individuals associated with the clutch. An adult bird was considered as the social parent of the clutch if some sort of parental care (incubation, feeding etc.) was observed on both occasions. Nest-boxes were monitored 6-12 times throughout the breeding season allowing to pin-point egg laying dates to a 24-hour precision (see Kotymán et al., 2015 for further details).

Dust-ruffling (Clayton et al., 2001) was used to remove the lice from the hosts. The plumage was treated with pyrethrin powder and the birds held over a white tray for 5 minutes. Lice falling off were collected into a centrifuge tube containing 70% ethanol. After five minutes, the plumage was gently ruffled to dislodge the remaining parasites. The identification of lice was based on Price et al. (2003), using a stereoscopic microscope (Zeiss Stemi DRC).

3.4.2.2 Molecular sexing of the nestlings

The sex of the nestlings was determined by molecular methods. For this purpose, three developing feathers were plucked from the back during the ringing procedure. The samples were stored in absolute ethanol at -20 °C until further use. The feather samples

were analysed in the molecular laboratory of the Institute of Biology, University of Veterinary Medicine Budapest. Total genomic DNA was extracted from the feather shaft using NucleoSpin Tissue Kit (Macherey-Nagel). Sex was determined by amplifying the CHD1-W and CHD1-Z gene introns, using the 2550F and 2718R primer pair (Fridolfsson and Ellegren, 1999). To verify the molecular sexing results, two methods were used: first, another intronic part of the CHD1 gene was parallelly amplified using the primer pair (CHD1-i16F and CHD1-i16R; Suh et al. 2011) in a subset of samples (N=10). Second, 18 adult birds with known sex were additionally analysed. Both primer pairs gave congruent results, and sex determined by molecular analysis agreed with adult phenotypic sex in each case. PCR reactions were performed using the conditions as described by the authors publishing the primers. PCR products were evaluated by agarose gel-electrophoresis.

3.4.2.3 Statistical methods

We used generalized mixed models with negative binomial distribution and log-link (Zuur et al., 2009) to evaluate the effect of the explanatory variables on the abundance of *Colpocephalum subzerafae* (Tendeiro, 1988b) and *Degeeriella rufa* (Burmeister, 1838) respectively. In the case of nestlings, we analysed the samples from 2012 and 2014 separately. This was necessary for two reasons. First, different sampling procedures were implemented in the two years. Second, the distribution of lice differed so much (Piross et al., 2015, p. 20) that incorporating both years into a single model that fits the data was infeasible. We tested the effect of host sex by comparing siblings. To do this correctly, we only used data from nestlings where we sampled both males and females in the same clutch. We hypothesised that the difference in louse abundance between siblings of different sex is caused by the preference of lice for male versus female host, and this is possible only if both sexes are present in the clutch. In case of the adults, we removed observations with missing values in the explanatory variables. We centred (subtracted the mean) of every continuous variable before modelling to improve model fit. We used deviance-ratio tests for model selection. We removed the explanatory variables from our initial models one-by-one, and if the two models (with and without the variable) did not differ significantly ($\alpha=0.05$), we left out the variable from the model. For the nestlings, the fixed variables for the initial models were clutch size and sex (as categorical variables), wing length (mm) and its interaction with sex. We used the clutch identifier as a random factor. This approach allows to measure clutch effects of variables such as sex. For the adults, the fixed variables were sex, wing length (mm), their interaction, the number of days after the first egg was laid, its interaction with sex. We also used the breeding colony as a random factor.

For all analyses and figures we used R 3.6.1 (R Core Team, 2019) and the ggplot2 3.2.0 (Wickham, 2016), glmmTMB 0.2.3 (Brooks et al., 2017, p. 201), gridExtra 2.3 (Auguie, 2017), lsmeans 2.30-0 (Lenth, 2016) and the RcmdrMisc 2.5-1 (Fox, 2018, p. 201) packages.

3.4.3 Results

Three louse species were found on the Red-footed Falcons. *Colpocephalum subzerafae* and *Degeeriella rufa* are associated with this host species in the latest world checklist (Price et al. 2003), and the scarce occurrence of *Laemobothrion* (*Laemobothrion*) *tinnunculi* Linnaeus, 1758 was also reported in Piross et al. (2015). *L. tinnunculi* was found only on two adult birds. We have not found any *Nosopon lucidum* Rudow 1869a in our samples (Price et al., 2003). The descriptive statistics (Reiczigel et al., 2019) of the *C. subzerafae* and *D. rufa* infestation are presented in Table 3.

Table 3 Descriptive statistics of the louse infestation of the Red-footed Falcons (*Falco vespertinus*) by age, louse species, year and sex.

Age	Louse species	Year	Sex	Infected	Hosts	Prevalence	Mean abundance	Median abundance	Mean intensity	Median intensity	Variance/Mean
nestlings	<i>C. subzerafae</i>	2012	male	34	42	81%	5.5	3	6.7	5	8.6
			female	41	51	80%	5.9	5	7.4	7	6.9
			all	75	95	79%	5.6	4	7.1	6	7.7
		2014	male	14	38	37%	1.1	0	3.0	2	5.3
			female	15	46	33%	0.9	0	2.7	2	5.1
			all	29	87	33%	1.0	0	2.9	2	5.2
	<i>D. rufa</i>	2012	male	34	42	81%	3.2	2	4.0	2	3.5
			female	40	51	78%	2.7	2	3.4	2	3.2
			all	74	95	78%	2.8	2	3.7	2	3.4
		2014	male	22	38	58%	2.2	1	3.9	2	6.3
			female	31	46	67%	1.9	2	2.9	2	2.9
			all	53	87	61%	2.0	1	3.3	2	4.6
adults	<i>C. subzerafae</i>	2014	male	8	33	24%	4.2	0	17.4	7	55.2
			female	4	27	15%	0.2	0	1.5	2	1.5
			all	12	60	20%	2.4	0	12.1	4	53.9
	<i>D. rufa</i>	2014	male	22	33	67%	6.1	1	9.1	4	19.8
			female	12	27	44%	1.0	0	2.2	2	1.5
			all	34	60	57%	3.8	1	6.7	2	19.1

Our models indicate that louse abundance on nestlings was affected by their sex and wing length. In 2012, a marginally significant (slightly above the prescribed level of significance, $p=0.0565$), but relevant difference was found in the abundance of *C. subzerafae* between male and female siblings. Estimated abundance was 3.5 (95% C.I. 1.7–7.2) on females compared to 2.1 (95% C.I. 1.0–4.4) on their male siblings. In 2014, none of the investigated variables had any significant effect on *C. subzerafae* abundance (see Appendix 1).

In 2012, only wing length ($p=0.0482$), in 2014 sex, wing length, and their interaction had a significant effect ($p=0.0387$) on the nestlings' *D. rufa* abundance. The predicted *D. rufa* abundance was 0.7 (95% C.I.: 0.2–2.1) on the smallest nestlings (wing length=109 mm) and 3.4 (95% C.I.: 1.6–7.2) on the largest ones (wing length=167 mm). In 2014, the

predicted abundance for the smallest male nestlings (wing length=109 mm) was 1.6 (95% C.I.: 0.4–5.9) and 0.3 on females (95% C.I.: 0.1–1.4). On the largest male nestlings (wing length=167 mm) it was 1.0 (95% C.I.: 0.3–3.3) and 3.4 (95% C.I.: 1.2–9.6) on the females. This shows that wing length has a different effect on the louse abundance depending on sex. See **Error! Reference source not found.**, Figure 3 and Figure 4 and Appendix 1 for further details.

Table 4 Abundances (and their 95% C.I.) of the different louse species on the Red-footed Falcon (Falco vespertinus) nestlings predicted by the GLMMs. Wing length statistics were calculated using data from both 2012 and 2014 for better comparability of the results.

Data	Wing length (mm)	sex	Abundance estimate	95% C.I.	
<i>C. subzerafae</i> , nestlings 2012		female	3.5	1.7 7.2	
		male	2.1	1.0 4.4	
<i>D. rufa</i> , nestlings 2012	minimum	109	0.7	0.2 2.1	
	1 st quartile	133	1.4	0.8 2.4	
	median	143	1.8	1.1 2.8	
	3 rd quartile	152	2.3	1.4 3.7	
	maximum	167	3.4	1.6 7.2	
<i>D. rufa</i> , nestlings 2014	minimum	109	0.3	0.1 1.4	
	1 st quartile	133	0.8	0.4 1.7	
	median	143	female	1.2	0.7 2.1
	3 rd quartile	152		1.8	1.0 3.3
	maximum	167		3.4	1.2 9.6
	minimum	109		1.6	0.4 5.9
	1 st quartile	133		1.3	0.7 2.4
	median	143	male	1.2	0.7 2.1
	3 rd quartile	152		1.2	0.6 2.3
maximum	167		1.0	0.3 3.3	

Both louse species showed a similar abundance pattern on adult falcons. Sex, the number of days elapsed since laying the first egg, and the interaction of these two variables all had a significant effect on both the *C. subzerafae* ($p=0.0361$) and *D. rufa* ($p<0.0001$) abundance. In general, the males show a low, and nearly constant level of abundance as compared to females in both species. In the earlier days of breeding (day 11) the predicted *C. subzerafae* abundance was 0.4 (95% C.I.: 0.1–3.6) and *D. rufa*

abundance was 2.0 (95% C.I.: 0.8-5.0). In the later days (day 54) it was 0.1 (95% C.I.: 0.0–1.4) for *C. subzerafae* and 0.6 (95% C.I.: 0.2–1.7) for *D. rufa*.

Contrarily, females show higher abundances in the early days that rapidly declines during the breeding period. At day 11 the predicted abundance for *C. subzerafae* was 8.5 (95% C.I.: 0.8–84.8), for *D. rufa* it was 25.0 (95% C.I.: 11.7–53.6), while at day 54 it was 0 (95% C.I.: 0.0–0.5) for *C. subzerafae* and 0.2 (95% C.I.: 0.1–0.6) for *D. rufa*. See Table 5 and Figure 5 for further details. The results of the deviance tests and the AIC and BIC values of the models are available in Appendix 1.

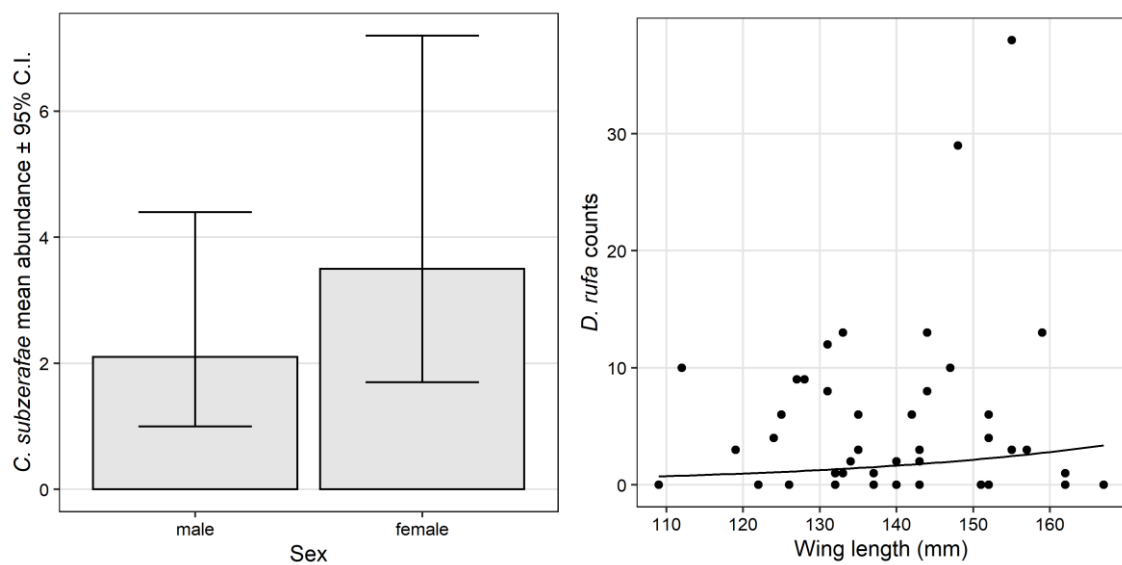


Figure 3 GLMM modelling results of the mean abundance of the louse species on the Red-footed Falcon (*Falco vespertinus*) nestlings in 2012. In the case of the *Colpocephalum subzerafae*, a non-significant difference can be seen between the two sexes. In the case of *Degeeriella rufa*, the mean abundance increases with the wing length of the nestlings.

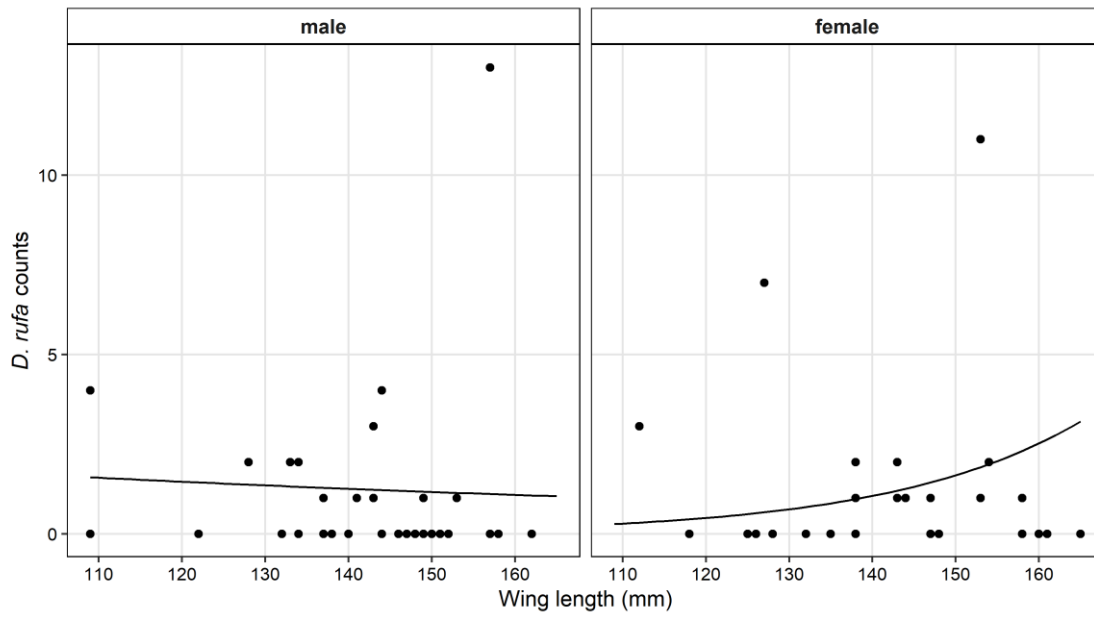


Figure 4 GLMM modelling results of the mean abundance of *Degeeriella rufa* on the Red-footed Falcon (*Falco vespertinus*) nestlings in 2014. There is an interaction between sex and wing length. The mean abundance increases with wing length in the case of the females.

Table 5 Abundances (and their 95% C.I.) of the different louse species on the adult Red-footed Falcons (*Falco vespertinus*) predicted by the GLMMs. Statistics on the days after first egg laid were calculated using combined data from both males and females for better comparability of the results.

data	Days after first egg laid	sex	Abundance estimate	95% C.I.		
<i>C. subzerfae</i> , adults 2014	minimum	11	0.4	0.1	3.6	
	1 st quartile	19	0.3	0.1	1.8	
	median	30	male	0.2	0.1	0.9
	3 rd quartile	48		0.1	0.0	1.1
	maximum	54		0.1	0.0	1.4
	minimum	11		8.5	0.8	84.8
	1 st quartile	19		2.5	0.6	11.4
	median	30	female	0.5	0.1	1.7
	3 rd quartile	48		0.0	0.0	0.6
	maximum	54		0.0	0.0	0.5
<i>D. rufa</i> , adults 2014	minimum	11	2.0	0.8	5.0	
	1 st quartile	19	1.6	0.8	3.2	
	median	30	male	1.1	0.7	2.0
	3 rd quartile	48		0.7	0.3	1.6
	maximum	54		0.6	0.2	1.7
	minimum	11		25.0	11.7	53.6
	1 st quartile	19		10.1	6.0	16.9
	median	30	female	2.9	1.8	4.5
	3 rd quartile	48		0.4	0.1	1.0
	maximum	54		0.2	0.1	0.6

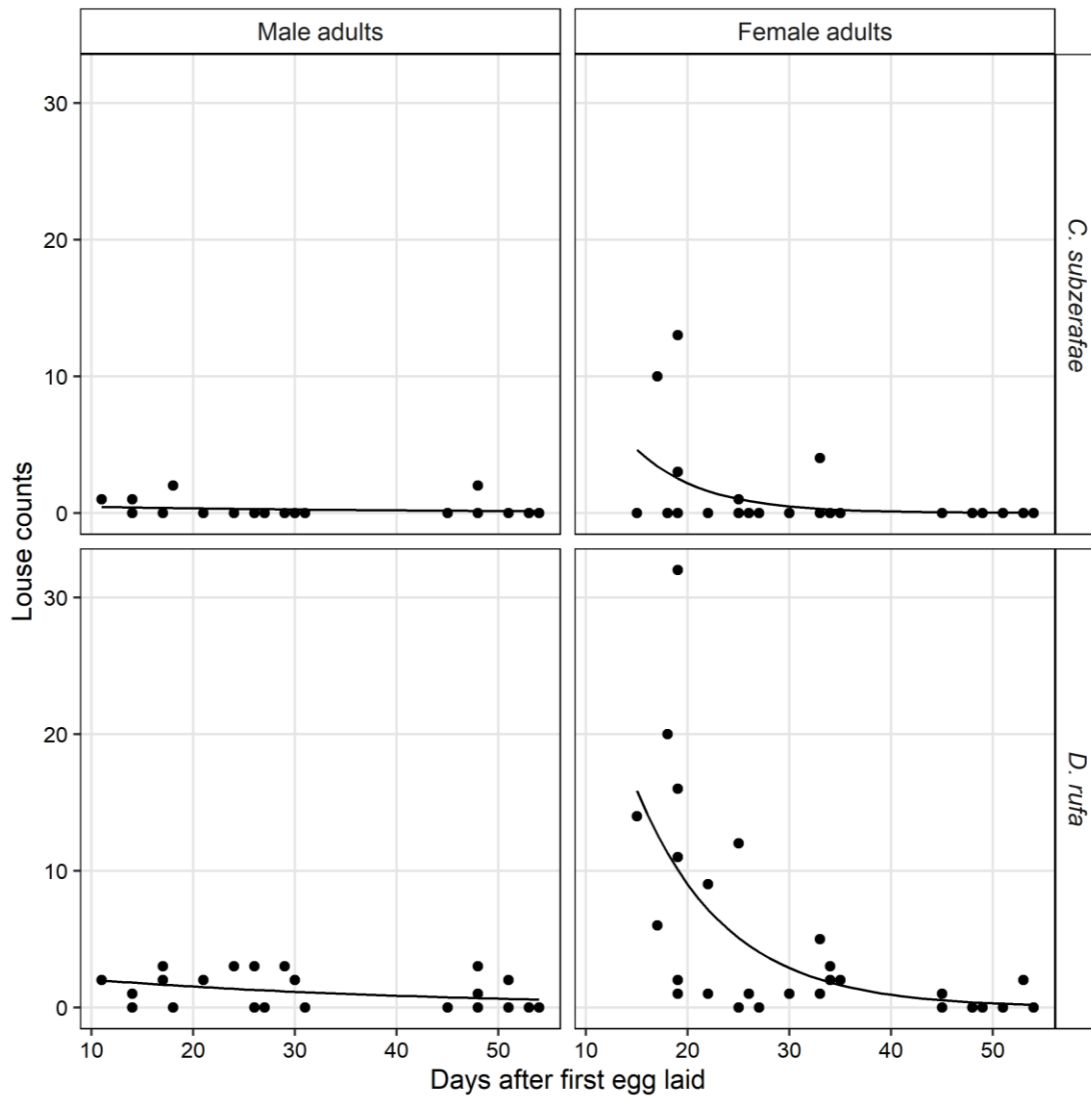


Figure 5 GLMM modelling results of the mean abundance of the louse species on the adult Red-footed Falcons (*Falco vespertinus*) in 2014. There is an interaction between sex and the number of days after the first egg was laid in both louse species. The mean abundance of lice decreases with the number of days passed on female birds, while males maintain a low abundance level.

3.4.4 Discussion

Here we showed that the two examined louse species can exhibit sex-biased infestation patterns that are interconnected with different host traits across different life-history stages. Our generalized mixed-effect modelling approach enabled us to take several factors and their interactions into account, revealing the invading parasites' preference for female nestlings and possibly show examples of both parasite- and host-mediated sex-biased infestation.

Wing length (a proxy of body size) exhibited noticeable effects on the abundance of lice infesting nestlings in case of *D. rufa*, while *C. subzerafae* was seemingly unaffected by the size of the nestlings (Table 4 **Error! Reference source not found.**, Figure 3 and Figure 4). These two lice belong to different suborders that exhibit different evasion mechanisms to reduce mortality due to host defences. Amblycerans, like *C. subzerafae*, often avoid preening by running swiftly in the plumage, and also on the skin surface. Contrarily, ischnocerans — like *D. rufa* — can hide and attach themselves to particular topographic refugia in the host plumage (Johnson et al., 2003). The two suborders tend to rely on different diets as well. Ischnocerans mostly graze feather barbules, while amblycerans also chew skin fragments and consume blood. Consequently, ischnocerans probably rely more heavily on host plumage than amblycerans (Johnson et al., 2003). Our findings corroborate this hypothesis as *D. rufa* possibly postpones infestation of nestlings until the juvenile plumage is well developed.

Nestlings' sex also affects louse abundances to some extent. In one of the two study years, we found weak evidence that female nestlings harbour ~60% more on average of *C. subzerafae* than their male siblings (see Table 4 and Figure 3). In 2014 — but not in 2012 —, an increasing trend of *D. rufa* abundance was also detected on female nestlings, but not on males (see Table 4 **Error! Reference source not found.** and Figure 4). Since the nestling period is not much longer than the typical generation time of avian lice (Johnson and Clayton 2003), we assume that this increase was not caused by the multiplication of lice on falcon nestlings rather they represented the influx of lice transmitted from the parents. This implies that the sexual differences in nestling infestation levels are probably caused by parasite preferences for female hosts. As far as the nestlings stay in the nest their bodily contacts enable lice to move freely across and probe all members of the clutch providing ample time and opportunity for individual lice to decide on their final host.

An alternative to this hypothesis would be to presume that male and female nestlings are equally infested, but their antiparasitic defences are different. The most important

avian defences against lice are preening and grooming (Clayton et al., 2010), with the immune response also involved in case of amblyceran lice (Møller and Rózsa, 2005). In this case, however, we would expect the female sex to exhibit more effective defences and lower infestation rates (Poulin, 1996; Zuk and McKean, 1996), an opposite to the phenomenon documented above.

Further, Red-footed Falcons at this age hardly show any morphological dimorphism aside from that females tend to be slightly larger, but body size (measured as wing length) was taken into account in our statistical procedure. Therefore, there is no apparent explanation why lice should prefer female nestlings over their male siblings on the short term. On the long term, arguably, lice on female Red-footed Falcons may achieve higher fitness due to their ability to establish larger subpopulations on adult females. Moreover, female hosts arguably offer better dispersal chances for their lice, since they come closer and more frequent contact with their nestlings. Similar results were found on the closely related (Fuchs et al., 2015) Amur Falcons (*Falco amurensis*), where *D. rufa* abundances were higher on adult females than adult males (see 3.5.3; Piross et al., 2020a). This assumes a behavioural adaptation of lice: they need to make adaptive decisions on which host individual to choose in the nest.

In 2014, the nestlings were less infested (see Table 1; Piross et al., 2015) with both louse species, which may explain why we found different patterns in the two years. Considering *C. subzerfae*, the evidence for sex-biased infestation was weak in 2012. Since the lice were scarcer in 2014, a similarly slight difference — if present — was impossible to detect.

On the adult birds, louse abundances show complex temporal dynamics in interaction with sex. While male birds tend to maintain a nearly constant, low level of abundance for both investigated species, females' initially higher louse abundances decrease over the breeding period (see Table 5 and Figure 5). Although it would be tempting to assume that the lice transferring from mothers to the offspring are causing this phenomenon, there is temporal mismatch between the increase in *D. rufa* abundance on the nestlings and the decrease in louse abundance in general on the females. Red-footed Falcon nestlings hatch 28 days after the first egg was laid (Solt, 2018b). By this time, the abundance of both louse species has been already dropped (Figure 5). It seems likely that host behavioural changes are behind this decrease. Both sexes incubate the eggs, however males while not incubating hunt for both themselves and their mates, whereas females are more inactive and tend to rest in the vicinity of the nest when not incubating (Solt, 2018a). Therefore, females may allocate more time to body maintenance behaviours like preening and grooming, since they are mostly relieved from foraging

during the incubation period. Possibly, this sex role differentiation in the hosts allows females to decrease their own ectoparasite load and consequently lower the future parasite load of their offspring.

It is less clear what causes the initial difference in louse abundance on adult males and females. It has long been hypothesised that parasites negatively affect the chances of males finding mates (and see experiment in Clayton, 1990; Hamilton and Zuk, 1982). Males may therefore invest more into anti-parasitic behaviour prior to the commencement of breeding to increase their chances during mate choice. Furthermore, males have in general a darker, melanised plumage compared to females. Melanin was hypothesized to be less digestible for lice (Bonser, 1995), thus males may comprise less favourable habitats for lice, but no evidence was found in the case of Rock Doves (Bush et al., 2006b).

Our study has shown sexual biases in the louse infestations of Red-footed Falcon nestlings that show intricate patterns in interaction with other host traits. Such biases can either arise due to adaptive host-preference decisions by the parasites (i.e. parasite-mediated), or different time allocation to anti-parasite defences (i.e. host-mediated), depending on the life stage of the birds. Learning from the nestlings' example, it is also worth exploring further whether sexually monomorphic species or life stages could exhibit sex-biased louse infestation.

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

Based on: 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

3.5.1 Introduction

Amur Falcons (*Falco amurensis*) breed in East Asia (Transbaikalia, Amurland, North-Eastern China) and winter in southern Africa making their migratory route the longest among raptors (Meyburg et al., 2017). They form huge, high-density aggregations at communal roosting sites in northeast India during post-nuptial migration (Kumar, 2014), where hundreds of thousands of birds can gather (see Photo 6). At this stage of their life cycle, Amur Falcons constitute exemplary subjects of parasite ecological studies for the following reasons. First, parasite transmission is enhanced by their nocturnal behaviour leading to close body proximity (Kumar, 2014). Therefore, it is reasonable to assume that the individuals' observed louse load depends mainly on their actual resistance and less on their individual history, whether they had contracted lice formerly or not. Second, unlike during the breeding season, the different sexes and age groups live a similar way of life at these stopover sites.

In the current study, we aimed to utilise this unique opportunity to investigate how the abundance of lice depends on the host's body size, sex and age during the Amur Falcons' autumn migratory stopover period at their large Indian roosting sites.



Photo 6 Amur Falcon (Falco amurensis) roosting site in Nagaland, India. Photo by Péter Palatitz.



Photo 7 Second calendar-year male Amur Falcon (Falco amurensis) showing characteristics of both adult and juvenile plumage. Photo by Péter Palatitz.



Photo 8 Second calendar-year female Amur Falcon (Falco amurensis). Its plumage still shows some resemblance to its juvenile form. Photo by Péter Palatitz.

3.5.2 Materials and methods

3.5.2.1 Study site

Data collection took place in Nagaland, India (N25.67, E94.11), where Amur Falcons were trapped and ringed within the framework of an ongoing research project led by the Wildlife Institute of India (WII). Birds were mist-netted at three different roost sites in November of 2016. The three sites were located approximately 50 km from each other, two of them were located in secondary sub-tropical evergreen rainforests and the third one by a teak tree plantation. Two sites each had over 100 000 individuals at the time of trapping, while one site was utilised by over 15 000 roosting individuals.

3.5.2.2 Data collection

We ringed and recorded the age and sex of all the 50 Amur Falcons trapped. Only juveniles (i.e. 1st calendar-year birds) and adult (at least 3rd calendar-year) birds were selected for the analyses. The plumage of second calendar-year birds can show characteristics of both adult and juvenile plumage (see Photo 7 and Photo 8). We recorded wing length, as a proxy of body size that is easy to measure under field conditions. Blood samples were also collected by puncturing the brachial vein of the wing, and subsequently stored in 70% ethanol. These samples were later used to identify the sex of juvenile birds.

Dust-ruffling (Clayton et al., 2001) was used to remove lice from hosts. The plumage was treated with pyrethrin powder over a white tray. Lice falling off were collected into a centrifuge tube containing 70% ethanol. After five minutes, the plumage was gently ruffled to dislodge the remaining parasites. Ectoparasite sampling was carried out solely by Fehérvári, P. The identification of lice was carried out by Siliwal, M. and Kumar, R. S. at the Wildlife Institute of India (WII) using a stereoscopic microscope based on Price et al. (2003).

3.5.2.3 Molecular sexing of the juveniles

The molecular sexing of the juveniles was carried out at the WII by Siliwal, M. and Kumar, R. S. Total genomic DNA was extracted from the collected blood samples using Qiagen® DNeasy Blood & Tissue Kit (Qiagen Valencia CA.). Sex was determined by amplifying the CHD1-W and CHD1-Z gene introns, using the 2550F and 2718R primer pair (Fridolfsson et al., 1999). To verify the molecular sexing results, two methods were used: first, another intronic part of the CHD1 gene was amplified in parallel using the primer pair (CHD1-i16F and CHD1-i16R; Suh et al., 2011) in a subset of samples (N=10). Second, 18 adult birds with known sex were additionally analysed. Both primer pairs gave congruent results, and sex determined by molecular analysis agreed with adult

phenotypic sex. PCR reactions were performed using the conditions as described by the authors publishing the primers. PCR products were evaluated by agarose gel-electrophoresis.

3.5.2.4 Statistical methods

We applied generalised linear models (GLM) with negative binomial error distribution and log-link (Zuur et al., 2009) to model the mean abundances of the two common louse species, *Colpocephalum subzerafae* Tendeiro, 1988b and *Degeeriella rufa* Burmeister, 1838. Since the sample size only allows us to investigate the effect of a handful of explanatory variables, we chose to incorporate the biologically most relevant potential predictors into our initial model. These were the following: the bird's age class (juvenile or adult), their wing length (mm) as a proxy of body size, and these variables' interaction with sex. We chose not to incorporate the roosting localities into our models since the birds change their nocturnal roosting sites frequently within the season, and we saw no relevant differences between the sites from this study's point of view. We used likelihood-ratio tests for model selection. We removed explanatory variables from our initial models, and if this caused the model to fit significantly worse ($\alpha=0.05$), we kept the variable in the model. Our initial models contained sex, wing length (mm) and their interaction, age (juvenile or adult) and its interaction with sex. We centred the wing length variable (subtracted the mean) to stabilise model fit. For all analyses and for preparing the figures we used R 3.6.1 (R Core Team, 2019) and the ggplot2 3.2.0 (Wickham, 2016), glmmTMB 0.2.3 (Brooks et al., 2017), gridExtra 2.3 (Auguie, 2017), lsmeans 2.30-0 (Lenth, 2016) and the RcmdrMisc 2.5-1 (Fox, 2018) packages.

3.5.3 Results

We found three louse species on the Amur Falcons, all of which have been described from this host previously (Piross et al., 2015; Price et al., 2003). *Laemobothrion (Laemobothrion) tinnunculi* Linnaeus, 1758 was scarcely found on birds with only five hosts infested and each one carried only a single louse individual. Contrarily, both *Colpocephalum subzerafae* and *Degeeriella rufa* were abundant on birds, thus providing large enough samples for statistical analyses. The descriptive statistics (Reiczigel et al., 2019) of their infestation are provided in Table 6.

Our models indicated that only age exerted a significant effect ($p=0.0006$) on the mean abundance of *C. subzerafae* (see Appendix 2). The mean abundance on adults was 1.8 (95% C.I. 1.0–3.3) compared to 7.1 (95% C.I. 4.8–10.4) on juveniles (see Table 7 and Figure 6).

In the case of *D. rufa*, on the other hand, sex, age, and their interaction exhibited a significant effect ($p=0.0006$) on mean abundance (see Appendix 2). The mean abundance was 9.4 (95% C.I. 7.3–12.2) on juvenile males and 10.4 (95% C.I. 7.3–14.6) on juvenile females. In the case of adults, the abundances were lower and differed between the two sexes. Adult females showed a higher mean of *D. rufa* abundance (4.9, 95% C.I. 3.2–7.6) than males (1.8, 95% C.I. 1.0–3.1; see Table 7). The results of the likelihood ratio tests and the AIC and BIC values of the models are provided in Appendix 2.

Table 6 Descriptive statistics of the louse infestation of the Amur Falcons (*Falco amurensis*) by age, louse species and sex (SD: standard deviation).

Louse species	Age	Sex	Infected	Hosts	Prevalence	Mean abundance \pm SD	Median abundance	Mean intensity \pm SD	Median intensity	Variance/ Mean
<i>C. subzerafae</i>	juveniles	male	15	20	75%	6 \pm 6.8	4	8.1 \pm 6.7	4	7.5
		female	10	11	91%	8.9 \pm 7.9	8	9.8 \pm 7.7	8	7.0
		all	25	31	81%	7.1 \pm 7.2	4	8.8 \pm 7	7	7.3
	adults	male	6	10	60%	1.8 \pm 2.1	1	3 \pm 1.9	3	2.4
		female	6	9	67%	1.9 \pm 1.7	2	2.8 \pm 1.2	3	1.5
		all	12	19	63%	1.8 \pm 1.9	1	2.9 \pm 1.5	3	1.9
<i>D. rufa</i>	juveniles	male	20	20	100%	9.4 \pm 5.1	9	9.4 \pm 5.1	9	2.8
		female	11	11	100%	10.4 \pm 4.5	9	10.4 \pm 4.5	9	1.9
		all	31	31	100%	9.7 \pm 4.8	9	9.7 \pm 4.8	9	2.4
	adults	male	6	10	60%	1.8 \pm 2.5	1	3 \pm 2.7	2	3.6
		female	9	9	100%	4.9 \pm 4.8	3	4.9 \pm 4.8	3	4.7
		all	15	19	79%	3.3 \pm 4	2	4.1 \pm 4.1	2	4.9

Table 7 Abundances (and their 95% C.I.) of the different louse species on Amur Falcons (*Falco amurensis*) predicted by the GLMs.

Louse species	Age	Sex	Abundance estimate	95% C.I.
<i>C. subzerafae</i>	juvenile		7.1	4.8 – 10.4
	adult		1.8	1.0 – 3.3
<i>D. rufa</i>	juvenile	male	9.4	7.3 – 12.2
		female	10.4	7.3 – 14.6
	adult	male	1.8	1.0 – 3.1
		female	4.9	3.2 – 7.6

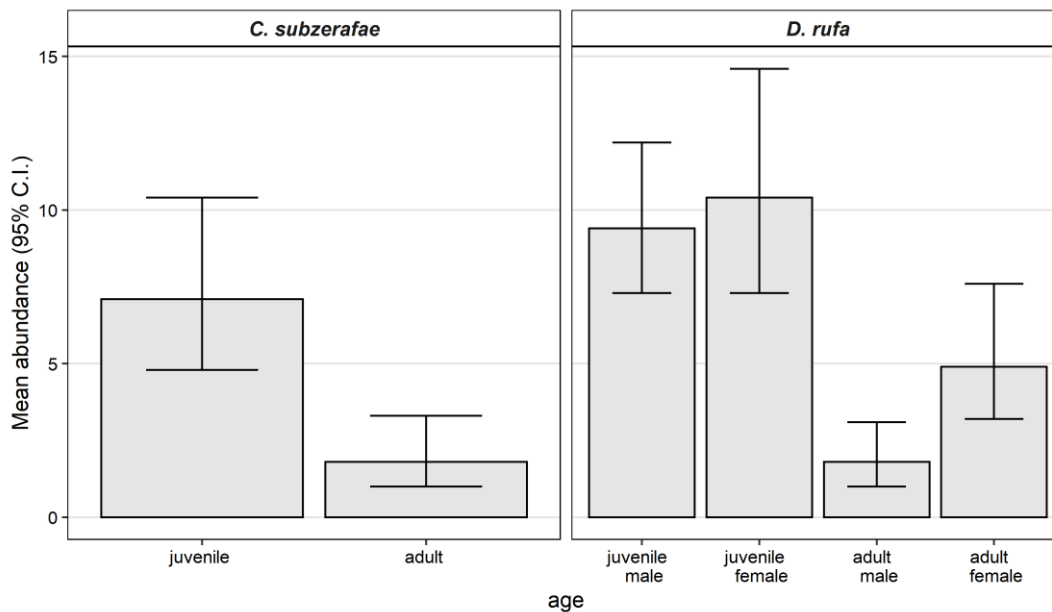


Figure 6 GLMM modelling results of the mean abundance of the louse species on the Amur Falcons (*Falco amurensis*). The mean abundance of *Colpocephalum subzerafae* is higher on juveniles than on adults. In the case of *Degeeriella rufa* we found interaction between the sex and the age of the birds. The mean abundance of *D. rufa* is similarly high among juveniles for both sexes, while it is higher for adult females than adult males.

3.5.4 Discussion

There is a growing body of information concerning the environmental factors influencing the distribution and abundance of lice in comparison across different bird species (Galloway et al., 2017; Lamb and Galloway, 2019; Moyer et al., 2002; Rózsa, 1997). Contrarily, it is much less understood how host individual factors (like age, body size and their interaction with sex) influence the distribution of lice within a particular bird population (Durkin et al., 2015; Leonardi et al., 2018; Leonardi and Quintana, 2017; but see Palma et al., 2002; Szczykutowicz et al., 2006).

We have collected lice from Amur Falcons sampled in Nagaland, India at a migratory stopover site, where these birds gather to form huge autumn roosting flocks before crossing the Indian subcontinent and the Arabian Sea towards their African wintering grounds. Our aim was to investigate the effect of falcon sex, age and body size on the abundance of their two most abundant species of lice. We applied generalised linear models to model parasite abundance using host age, wing length and their interaction with sex as explanatory variables.

We demonstrated that the age class (juvenile vs. adult) of Amur Falcons covaries with the abundance of both *C. subzerafae* and *D. rufa* so that juveniles were more infested than adults. Juvenile-biased levels of ectoparasite infestation have been frequently reported by other authors (Hamstra and Badyaev, 2009; Potti et al., 1995; Rivera-Parra

et al., 2014), probably due to several reasons. First, juveniles are immunologically naïve, and the amblyceran lice (including *C. subzerfae*) partially feed on living tissues and, thus, interact with the host immune system (Møller et al., 2005). Second, young birds may not be able to allocate as much time to body maintenance behaviours like preening (birds' primary defence mechanism against lice) as the adult birds. Finally, the efficacy of preening may well depend on individual practice, even though the effect of experience could not be experimentally verified in domestic Rock Pigeons (*Columba livia*; Villa et al., 2016a).

The results presented here indicate that *D. rufa* also exhibits female-biased infestation during the autumn period at a migratory stopover site, where the falcons' habitat usage and behaviour are presumed to be uniform across sexes. Female-biased infestations are not unprecedented; Ortego et al. (2007) showed that the *D. rufa* infestations in Lesser Kestrels (*Falco naumanni*) tend to be female-biased. However, it is far more often the male sex that hosts higher levels of infection (Morales-Montor et al., 2004; Poulin, 1996; Zuk et al., 1996). For example, male-biased louse infestations were found among White-throated Dippers (*Cinclus cinclus*; Doyle et al., 2005) and various seabirds (Rivera-Parra et al., 2014).

The causes of female bias observed here are not known, but several possible reasons can be put forward to explain this phenomenon:

First, one could hypothesize that females constitute more optimal hosts for these lice due to their somewhat larger body size. This seems unlikely since we have statistically controlled for body size (using wing length as a proxy for it) in the present study, and also in our other study on Red-footed Falcons (*Falco vespertinus*; see 3.4.4; Piross et al., 2020b).

Second, Red-footed Falcons — previously considered conspecific with Amur falcons — also exhibit female-biased infestations by the same two louse species examined here, at least during the early days of the breeding period (see 3.4.3; Piross et al., 2020b). During the breeding season, the female-biased infestations might be driven by a difference in how sexes allocate their time; females may allocate less time to body maintenance. The Amur falcons' female-biased infestations with *D. rufa* during the autumn migration could simply be a remnant of a previous infestation difference that built up during the summer breeding season. However, this does not explain why only *D. rufa* showed female-biased infestation. A notable difference between the two species is that they evade preening differently. *D. rufa*, similarly to some other ischnocerans attaches itself to feathers. Amblycerans, on the other hand, tend to use more active evasion

techniques and different refugia. *Colpocephalum* species, for example, may hide inside of feather shafts (Johnson et al., 2003). Assuming that there is a difference here in the efficacy of the two broad evasion strategies, we hypothesize that the females may be able to reduce the number of *C. subzerafae* more quickly; however, this explanation lacks empirical evidence.

Lastly, female-biased parasitism can be attributed to sexual dichromatism. Adult male Amur Falcons and Red-footed Falcons display a dark bluish-grey colouration based on melanin pigments. Since melanin is known to make feathers more resistant to mechanical abrasion (Bonser, 1995), dark feathers may be harder to chew for lice. Contrary to this expectation, however, Bush et al. (2006b) showed that dark colouration in rock pigeons provided no defence against the pigeon wing lice, *Columbicola columbae*. However, the ischnoceran wing lice like *C. columbae* and *D. rufa* graze the barbules of the down feathers that tend to be unpigmented, but they do not feed on the heavily pigmented, interlocked barbs of the vane of cover feathers (Clayton et al., 2015). Therefore, the difference in the melanin pigmentation between the sexes is unlikely to cause the infestation differences we documented.

Overall, we conclude that birds can show age- and sex-biased levels of louse infestation even during migration, when birds of different age and sex live an apparently similar way of life. Our study highlights the importance of following the seasonal changes of sex-biased parasite infections through the whole life cycle of the host to develop a better understanding of host-parasite systems.

3.6 Conclusions

This chapter investigated the louse abundance on three falcon species at different stages of their life. While these studies were unable to cover the whole life cycle of the hosts, they most certainly provided at least some insight into the population dynamics of their lice.

The abundance of *D. rufa* was higher on Common Kestrel nestlings of larger broods and increased with the body size of Red-footed Falcon nestlings (see 3.3.3). *D. rufa* was also more numerous on adult female Amur Falcons than males (see 3.5.3). Both *D. rufa* and *C. subzerafae* were more abundant on juvenile Amur Falcons than adults during migratory roosting (see 3.5.3). Both showed the same pattern on breeding Red-footed Falcons, where their abundance decreased over the breeding period on females and constantly remained low on males (see 3.4.3).

Some of these findings are more or less in line with what we expected from the literature. The two most unexpected outcomes were the higher louse abundance on females in specific scenarios and its relation with brood size. The latter would be interesting to study in species with much variance in brood sizes like Buzzards (*Buteo buteo*) or Montague's Harriers (*Circus pygargus*), and Hen Harriers (*Circus cyaneus*). Although we should not forget that brood size is subject to many governing factors that may also be related to ectoparasite loads — for example, food availability, weather conditions and other factors that directly affect the birds' physical condition (Krüger, 2004; Millon et al., 2002).

Differences in louse abundance between the sexes were not ubiquitous, but in all cases, they were female-biased. Although male-biased infestations may be more common, female bias is not at all unprecedented (Garbarino et al., 2013). Where we found an effect of sex, it was in interaction with another variable like age, size, or time passed since the start of breeding. Recent findings suggest that the difference in the immune response of the sexes can show seasonality, the difference being more expressed in the breeding season (Valdebenito et al., 2021). These results suggest that we should pay more attention to possible interactions and life-cycle events, especially when investigating sex biases. Sexual dimorphism is commonly more expressed in adult age. The breeding period has substantial effects on both the behaviour and the physiology of both sexes but mainly on the females. These could give rise to or enhance already existing differences in the defensive capabilities of the sexes.

It is worth noting that the repeatability of our studies may not be high for the following reasons. First, these were observational studies where the lack of control over the

studied system severely limits the inferences we can make. Second, we see that the population dynamics of lice are complex, and certain factors like sex and age may interact with each other. Taking only snapshots are not ideal for studying a constantly changing dynamic system. This leads to the third problem: our sampling methodology may interfere with the natural state of the louse populations. Field examination of louse abundances assumes the removal of lice, as the visual examination is not reliable. The usage of fumigation chambers or dust-ruffling does not remove all lice from the host but almost surely kills most, if not all of them (lice on the head or the bird's neck have better chances of survival). This makes the proper longitudinal monitoring of louse subpopulations impossible. Also, surveying lice with these methods on a larger scale may affect the whole louse population. If most subpopulations are eradicated or shrank, they do not have the same chances to regenerate as only a few of them were affected. Of course, these are extreme assumptions, the circumstances may be fairly better in systems that rely heavily on horizontal transmission (Darolova et al., 2001), or the overall louse loads are high. Still, this aspect of these sampling methods should be kept in mind when designing surveys of louse populations of wild birds.

An evident approach would be to conduct more experiments. Specific bird and louse species can be kept well under laboratory conditions like Rock Doves (*Columba livia*) and their lice *Columbicola columbae*, and *Campanulotes bidentatus*. A vast portion of our current knowledge on avian lice comes from experimental studies like these (Clayton et al., 2015). However, many aspects of lice's life history cannot be studied under artificial conditions. First of all, these restrict the number of host and louse species investigated. Moreover, many life-history events like bird migration cannot be replicated in experiments. The hurdles of field studies are not easy to overcome, but they are worth it since many questions are waiting to be answered. The seasonality of louse abundance has been studied for a long time, yet it is not fully understood (Galloway et al., 2021). We still do not know whether lice actively respond to the reproductive state of the host. It is suspected that this would benefit them as their dispersal chances could be better in the breeding period. Studies where whole broods and their parents are sampled simultaneously (Brooke, 2010) would tell us a lot more about this topic.

There is still a lot to uncover about the population dynamics of lice outside the breeding period on the falcon species we studied. Both Amur and Red-footed Falcons overwinter in subequatorial Africa, and we are still discovering their wintering behaviour. It seems that Red-footed Falcons may use vast roosting sites before the spring migration. At the largest roosting site observed in Angola, many of the roosting birds were Amur Falcons (Péter Fehérvári pers. comm.). This would mean that horizontal transmission

may play a significant role in their lice's dispersion. Moreover, this would provide ample opportunities for inter-species transmission, which are usually rare across other bird species. This highlights that studying the migratory behaviour of birds may be important to understand the dynamics of their louse infestations.

Common Kestrels — as partially migrating species — would also be worthy subjects for such studies. Also, along with the Red-footed Falcons, they could be useful in investigating the consequences of sociality. Colonial birds tend to be more heavily infested with lice (Rózsa, 1997), because the more frequent interactions help the dispersal of lice. Contrarily, some argue that colonial birds allopreen more, which should lower their overall louse load. (Galloway et al., 2021). Allopreening is not common in these two falcon species, but we can find both colonies and solitaire pairs in the same habitat where we conducted our studies. This would allow for direct comparisons between the two breeding strategies replicated in two species. Hopefully, our studies and ideas drew attention to falcons as subjects for studying the ecology of lice.

4 Evolution of sexual body size dimorphism in Avian lice

4.1 Introduction

Apart from the rare and brief transmission periods between host individuals, permanent ectoparasites have no direct contact with any other components of the environment other than the host body itself. Thus most studies on the evolution of ectoparasites focus on adaptations and evolutionary processes attributed to parasitic lifestyle (Clayton et al., 2015). However, many animal parasites reproduce sexually — or at least partially sexually — therefore, sexual selection is likely to exert selection pressure on their body size. This effect is often overlooked, as very few studies ever addressed sexually selected morphological traits in animal parasites (Pap et al., 2013; Poulin, 1997; Rózsa et al., 2015a; Tryjanowski et al., 2009).

Body size is a rapidly evolving trait in avian lice (Villa et al., 2019), and it seems that for each host-lice association exists an optimal size for lice. Various selection pressures shape this optimum. We can see these effects in inter-species comparisons of body size. Harrison's rule postulate that larger hosts tend to harbour larger parasites. Harnos et al. (2017) recently confirmed this rule on a large set of avian louse species. Preening is considered a major selection force acting on the body size — and shape — of avian lice. Lice relatively large compared to the host are more vulnerable to preening, especially species that tend to hide in inter-barb spaces of feathers (Bush and Clayton, 2006a). This could explain why smaller birds have smaller lice, but not the other way around. Poulin's increasing variance hypothesis (Poulin, 2011b) claims that the ectoparasites' body size variance also increases with the host body size. Harnos et al. (2017) also confirmed this hypothesis for several groups of lice. Bush and Clayton (2006a) documented that relatively smaller lice may also have smaller fitness on a larger host even when the birds were impaired in preening. Alternatively, it was shown by Villa et al. (2018) that larger female lice could lay more eggs, which could drive selection for a larger female body size when possible. Based on this experiment, it is not apparent why a larger body size would benefit males. Villa et al. (2019) showed that *Columbicola columbae* males that were relatively smaller or larger than the female had difficulties copulating successfully with their partner.

This suggests that the male to female body size ratio should be constant, but avian louse species show considerable variance in sexual body size dimorphism (see 4.3.3;

Piross et al., 2019). This chapter investigates a pattern in the sexual body size dimorphism of a large set of louse species.

4.2 Phylogenetic comparative analysis of body size allometry

Allometry is the study of size and its consequences in biology (Niklas, 2004). It is a common question in this field how two size measures scale against each other. This is commonly done by fitting a regression line to describe a bivariate allometric relationship. All regression models have an error term describing deviances from the fitted line (Reiczigel et al., 2007). Type I and type II regression models differ in our assumption about the explanatory variable's randomness (X) and its relation to the dependent variable (Y). Type I models assume that Y depends directly on X because a) X is not a random variable since the experimenter set it or b) it is, but X 's values are measured accurately, and Y depends on these values. Type II models consider X to be measured with error (Legendre and Legendre, 2012), so they are typically used in allometric studies (Warton et al., 2006). The two most commonly used type II models are the major axis (MA) and the reduced (or standardised) major axis (RMA⁵ or SMA) regressions. MA models minimise the sum of the squared distances between the points and the regression line perpendicular to it. RMA regression is the same as performing a major axis regression on standardised data, then transforming the variables back (Warton et al., 2006). Both methods are used in allometry, and both can perform better under specific scenarios from different viewpoints (Jolicoeur, 1990; Warton et al., 2006). Warton et al. (2006) propose RMA for general use since it estimates the regression line with higher precision.

These regression models assume the independence of observations (Legendre et al., 2012). This assumption cannot necessarily be held when we study allometry across species because we expect closely related species to exhibit similar traits. Phylogenetic comparative methods handle this by analysing the data in the species' historical framework (Garamszegi, 2014). Phylogenetic comparative methods require a phylogenetic tree that represents our hypothesis on the investigated taxa's evolutionary history (Paradis, 2011). By examining these taxa's ancestor-descendant relationship and the intermediate ancestors, we can infer on the shared ancestry to describe the expected similarity in phenotypic traits. The general approach is to assign a covariance parameter

⁵ RMA can also stand for ranged major axis regression (Legendre et al. 2012.), which is not the same as the standardised or reduced major axis regression.

to each pair of species and organise this in a variance-covariance matrix. In this matrix, the off-diagonal elements quantify the two given species' or taxa's shared evolutionary history. The diagonal elements will be equal to the distances from the tree's tips to its root. This variance-covariance matrix can be used in weighted regression models to represent the residuals' expected covariance structure (Garamszegi, 2014).

The similarity of the traits depends on their evolutionary stability. We expect unstable traits to be more dissimilar than expected from the phylogenetic tree. The simplest approach to mitigate this problem is to do the analyses with and without phylogenetic control. However, more subtle solutions exist. The phylogenetic signal is a scalar value that describes the statistical relationship between the phylogeny and the observed traits. We can view it as a measure of the evolutionary stability of the trait. High phylogenetic signals indicate gradual changes over time. Low values indicate either extreme stability or instability of the trait. Both mean that the phylogeny and the trait are not in strong relation with each other (Garamszegi, 2014). There are multiple phylogenetic signal measures (Blomberg et al., 2003; Gittleman and Kot, 1990; Grafen and Hamilton, 1989). One of the most commonly used is Pagel's λ (Pagel, 1999, 1997). Pagel's λ scales between 0 (no phylogenetic signal) and 1 (strong phylogenetic signal).

We used phylogenetic reduced major axis regression (pRMA) models in this chapter based on Clarke (1980) and McArdle's (1988) work that considers both the allometric and the phylogenetic aspects of the problem.

4.3 Rensch's rule in avian lice: contradictory allometric trends for sexual size dimorphism

Based on: 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

4.3.1 Introduction

Body size is a fundamental trait of living organisms which influences most aspects of their biology. In sexually reproducing species, body size often differs between sexes. This is referred to as sexual size dimorphism (SSD). Male-biased sexual size dimorphism (MBSSD) refers to taxa the males of which are larger than the females, and female-biased sexual size dimorphism (FBSSD) refers to taxa the females of which are larger. When examining patterns of SSD among closely related animal species, Rensch (1959) observed that the relative male size (as compared to female size) increases with the average size of the species. In cases of taxa characterized by MBSSD, SSD increases as a consequence of the increasing relative male size. In taxa which exhibit FBSSD, the difference between the sexes diminishes with the increasing size of the species. This phenomenon is known as Rensch's rule (RR). RR can be neatly visualised by plotting the male against the female sizes of different species on a logarithmic scale (Fairbairn and Preziosi, 1994). On the resulting graph, a group of species with a constant relative male size is positioned along trend lines of slope 1. When RR applies, the trend can be characterised by a line with a slope >1 , meaning that relative male size increases with the female absolute size. See Figure 7a for further details. The reversed relationship between relative male size and the size of the species is called Converse Rensch's rule (CRR). In this case, relative male size decreases with the average size of the species, resulting in a decreasing SSD among MBSSD species and increasing SSD among FBSSD species. This defines a line with a slope <1 on the same graph. See Figure 7b for further details.

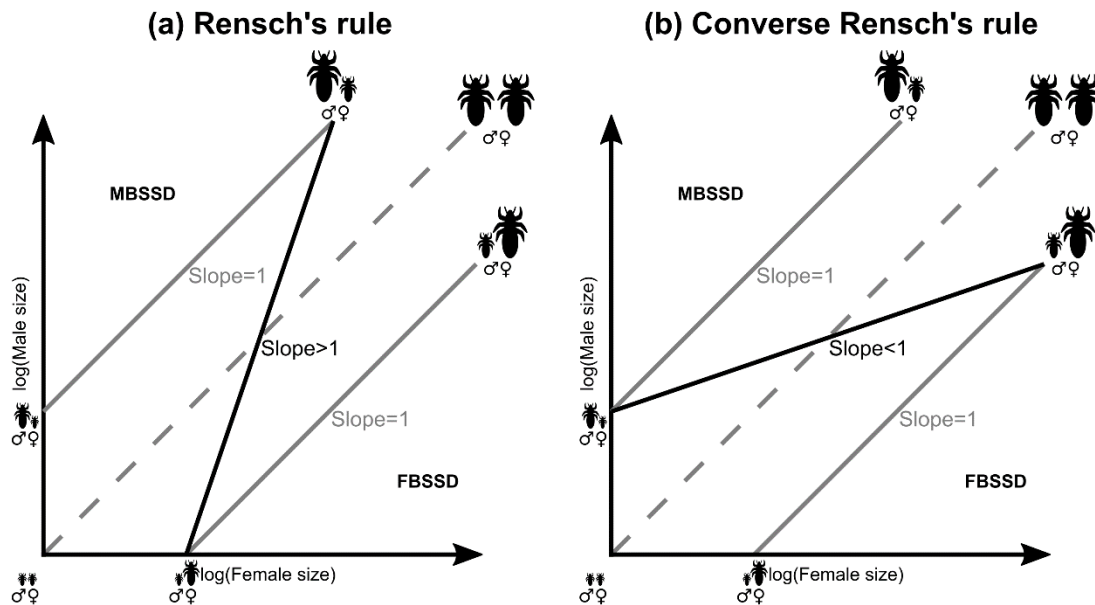


Figure 7 Graphical representation of Rensch's rule and converse Rensch's rule. When the logarithm of male body size is plotted against the logarithm of female body size, species with equal male and female sizes (no sexual size dimorphism: No SSD) are located along a line with a slope of 1 going through the origin (grey dashed line). Species deviating from it show SSD proportional to the distance from this line. Species where the males are larger (male-biased sexual size dimorphism: MBSSD) are located above, and species where females are larger (female-biased sexual size dimorphism: FBSSD) located below it. The slopes of the trend lines indicate whether the relative male size changes with the average size of the species. If relative male size does not change with the average size, the trend has a slope of 1 (grey solid lines). If relative male size increases with the average size, the trend has a slope >1 (a, black solid line). This is called Rensch's rule (a). Among species where the females are smaller (FBSSD), SSD decreases. When the males' size exceeds the females' size (MBSSD), the SSD increases. If relative male size decreases with the average size, the trend has a slope <1 (b, black solid line). This is called converse Rensch's rule (b). In this case, males are getting proportionally smaller with the average size of the species, meaning that SSD decreases in MBSSD species and increases in FBSSD species with size.

Although there have been many studies focusing on RR, there is no general consensus about the causes for the allometry for SSD across closely related species. A thorough review by Fairbairn (1997) gathered a variety of functional hypotheses to explain RR. Dale et al. (2007) organised the existing explanations into three groups. We adopt this categorisation with the difference that we treat the fecundity selection hypothesis separately from the natural selection hypothesis. Note that the following hypotheses are not necessarily exclusive.

First, the evolutionary constraints hypothesis (Fairbairn, 1997) posits that the two sexes react to a different extent to the same selection pressures on body size. One cause

of this may be that one sex has more additive genetic variance on body size, allowing it to respond more rapidly to selection. If the selection pressure varies among species, this can give rise to a pattern consistent with RR when males can respond more strongly and to CRR when females do.

Second, the natural selection hypothesis (Fairbairn, 1997) predicts that if the increase in the species' body size reduces interspecific competition, then it enhances intersexual resource competition, resulting in a niche divergence between the sexes, and this niche divergence finds manifestation in divergences in body size.

Third, the sexual selection hypothesis (Fairbairn, 1997; Fairbairn et al., 1994) assumes correlation — but not a total correspondence — between the body sizes of the sexes. When sexual selection on body size is stronger in one sex than the other, the other sex follows the growth of the first with more sexual selection pressure on it, but it cannot quite keep up, since there is only a correlation between the body sizes of the sexes. If sexual selection acts more heavily on males, RR is expected to turn up, regardless of whether the selection is for larger or smaller body size. When the males are selected to be larger, the female body size does not change as rapidly, resulting in RR. Stronger sexual selection on female body size results in CRR.

The “Fecundity selection” hypothesis (Head, 1995) claims that variation in SSD among species could be caused by a variation in the intensity of fecundity selection acting on female size. In this case, it is hypothesised that males show only a correlated response to changes in female body size. This process results in the emergence of a CRR pattern.

RR seems to hold in many taxa, primarily (but not exclusively) among vertebrates (Abouheif and Fairbairn, 1997; Fairbairn et al., 1994; Smith and Cheverud, 2002; Székely et al., 2004). Dale et al. (2007) showed that polygynous bird species follow RR, while in cases of species with reversed sex roles, the allometry follows CRR. Székely et al. (2004) argued that selection favours larger males in birds, where a larger size is advantageous in competition for females, while FBSSD develops in bird species where females compete with one another for males.

However, there are controversies concerning the applicability of the rule. The evidence for RR in FBSSD taxa is particularly scarce (Webb and Freckleton, 2007). Blanckenhorn et al. (2007) reviewed the validity of RR in insects. Investigating data from seven insect orders, they found that RR applies to only half of the insect orders and, thus, may not be the norm in insects. CRR also occurs in insects (Garcia-Navas et al., 2017; Guillermo-Ferreira et al., 2014).

While parasitism is one of the most common life strategies on earth (Poulin and Morand, 2014), only a handful of papers have investigated RR among parasites. For instance, Poulin determined that RR applies to parasitic copepods (Poulin, 1996), but found no evidence for it among parasitic Nematodes (Poulin, 1997). Recently, Surkova et al. (2018) found RR among fleas, but not among parasitic mites.

Since parasitic lice (Insecta: Phthiraptera) reproduce sexually and exhibit remarkable sexually selected traits, including size dimorphism (Rózsa et al., 2015a), they constitute a suitable taxon to investigate the applicability of RR in parasites. Lice are obligate ectoparasites which complete their entire life cycle in the host plumage or pelage (Johnson et al., 2003). Two suborders of lice are found on avian hosts: Amblycera and Ischnocera. Philopteridae, the only avian lice in the latter suborder, are particularly specialised to move on feathers and hide in plumage (Clayton et al., 2015). Birds mainly counter philopterids by preening.

Menoponidae is the largest family in the suborder Amblycera. Menoponids are less specialized, and they can be found on any body parts of the host, although their oviposition and feeding are more restricted to certain areas. They live on the skin, in the fluffy underlayer of the plumage, and also on feather shafts (Ash, 1960; Baum, 1968; Mey, 2003). They are more agile than ischnocerans, and they use their mobility to escape from preening (Johnson et al., 2003). A few genera are more specialized, for example *Actornithophilus* and *Colpocephalum* species can live inside feather shafts, and *Piagetiella* species can live inside the pouch of pelicans (Galloway et al., 2014).

Ricinid lice — also from the suborder Amblycera — are mostly restricted to small-bodied passerines and hummingbirds (Trochilidae), with a few species parasitizing medium-sized passerines like thrushes (*Turdus* spp.) and orioles (*Oriolus* spp.). They tend to be relatively large-bodied compared to their hosts (Harnos et al., 2017), and the prevalence and intensity of their infestations tend to be low (Nelson, 1972).

As in most other sexually reproducing animals, the males constitute the more competitive sex among lice and, thus, their body size may be more influenced by intrasexual rivalry. Mating time in louse species can range from 10–15 seconds up to 40 hours, although the latter can be interpreted as mate guarding behaviour by the males. The males of several philopterid lice possess modified antennae, which they use to grasp the female's thorax during copulation to ensure attachment to the female. This is important, as it prevents rivals from dislodging them during copulation (Clayton et al., 2015; Rózsa et al., 2015a). Another form of male-male competition among these organisms is sperm competition, which is the most widespread form of sexual

competition in arthropods (Andersson, 1994). Larger males can produce greater quantities of sperm, and, therefore, they are more competitive in this context (Pap et al., 2013; Rózsa et al., 2015a; Tryjanowski et al., 2009).

Generally, females are the larger sex in lice (Johnson et al., 2003). Harnos et al. (2017) showed that females of the Philopteridae, Menoponidae and Ricinidae families follow Harrison's rule (HR; Harrison, 1915). This rule postulates that larger hosts tend to harbour larger parasites. In the case of females of the philopterid lice *Columbicola columbae*, fertility is positively related to body size (Villa et al., 2018). The authors proposed a microevolutionary mechanism to explain the emergence of HR. When *C. columbae* find themselves on relatively smaller hosts, host defences (preening) select them for smaller sizes better able to fit in the interbarb spaces. On relatively larger hosts, fecundity selection selects for larger females.

The purpose of our present study is to test whether RR applies to avian lice. Since the epidemiological and morphological characteristics of different louse taxa exhibit markedly different relationships to host characters (Harnos et al., 2017; Rózsa et al., 2015a), first, we investigate three major families of avian lice; the ischnoceran family Philopteridae and the amblyceran families Menoponidae and Ricinidae. Harnos et al. (2017) also compared host-parasite body size allometries across the four philopterids guilds (called 'wing lice', 'body lice', 'head lice', and 'generalists') formerly outlined by Johnson et al. (2012) Since this categorization is challenged by recent studies on the *Brueelia*-complex, where a species-level categorization is required (Bush et al., 2016; Gustafsson et al., 2017), we prefer to discontinue comparisons between 'ecomorph' categories until a widely accepted new categorization will be published. In the second part of our study, we analyse RR in menoponid and philopterid lice separately from three different host orders. In the hope of gaining more insight into the underlying mechanism behind RR in avian lice, we also provide descriptive statistics linking SSD and the body size of lice to the body mass of their hosts.

4.3.2 Materials and methods

4.3.2.1 Data collection

Data were obtained from species descriptions and are identical with the dataset recently used by Harnos et al. (2017), although that study used only female total body length values. Most of the body length data refer to species, however, when available, data regarding distinct subspecies or distinct populations associated with different host species were included as separate louse lineages. In cases of multiple measurements of the same parasite species (or subspecies, or lineage) from different sources in the

literature, we averaged the values. Louse body size was expressed as the total body length of slide-mounted specimens. Slide-mounting is a well standardized method for preserving and measuring lice (Palma, 1978), thus its potential distorting effects are expected to be similar across samples. Research efforts may differ across host taxa, potentially introducing a certain degree of bias in our data set. Table 8 and Table 9 contain the sample sizes.

To analyse RR separately for different host orders, information on host taxonomy was obtained from IOC World Bird List v 8.2 (Gill and Donsker, 2018). The vast majority of ricinid lice in our dataset are from passeriform birds (97 out of 106 records), therefore, this louse family was excluded. In the cases of philopterids and menoponids, we chose the three most common host orders of the two families. The dataset with references to sources are available online at the publisher's website. <http://doi.org/10.1038/s41598-019-44370-5>

4.3.2.2 Louse phylogeny

The molecular phylogeny of lice is poorly understood; therefore, we adapted the louse tree of Harnos et al. (2017) without any further modifications. This tree is basically a compilation based on published taxonomies (Cicchino and Mey, 2007; Cruickshank et al., 2001; Hughes et al., 2007; Lonc, 1990; Marshall, 2003; Mey, 2004; Nelson, 1972; Price and Johnson, 2007; Rheinwald, 1968; Smith, 2001, 2000) and interpreted as an approximation of the true phylogeny of avian lice. The phylogeny of lice in CAIC format is available online at publisher's website. <http://doi.org/10.1038/s41598-019-44370-5>

4.3.2.3 Statistical analyses

We fitted phylogenetic reduced major axis regression (Clarke, 1980; McArdle, 1988) (pRMA) for log-transformed male vs. female body lengths separately for the three louse families, and for philopterids and menoponids from three different host orders. Deviation from isometry was accepted when the slope of the fitted line significantly (p -value ≤ 0.05) differed from 1. We also estimated phylogenetic signal expressed as Pagel's λ (Pagel, 1999). All analyses were carried out in R 3.4.3 (R Core Team, 2018). We used a jackknife method to investigate the influence of each observation on the slopes of the fitted lines. We refitted all pRMA models by leaving out each observation one at a time, and we recorded the results for each model, calculated the difference in the slope estimates, and observed if the significance of its deviation from isometry changed. We applied the ape 5.0 package (Paradis et al., 2004) to import and handle phylogenetic trees, the phytools 0.6-44 package (Revell, 2012) to fit pRMAs, the RcmdrMisc 1.0-5 package (Fox, 2016) to calculate descriptive statistics, and the ggplot2 2.2.1 package (Wickham, 2009) to

create a visual rendering of the data. The R code we used is available online at publisher's website. <http://doi.org/10.1038/s41598-019-44370-5>.

4.3.3 Results

4.3.3.1 Descriptive statistics

The means and standard deviations of male and female body lengths, the relative male sizes (expressed as the ratio of male to female body length), host body masses, and the sample sizes are reported in Table 8.

As mentioned above, our sample may be biased, i.e. it may not necessarily represent the true distribution of lice across host body size classes. In this sample, the mean host mass is the largest among the philopterids, with a considerable standard deviation. Host masses tend to be lower for menoponid lice, though they still cover a wide range. As expected, ricinids were found only on small-bodied birds. The means of relative male sizes are similar between louse families. Menoponids have a somewhat shorter body length than philopterids, while ricinids are the largest among the three families.

In our sample, the differences between menoponids and philopterids grouped by three different host orders suggest that larger-bodied bird orders (Passeriformes < Charadriiformes < Galliformes) harbour lice with larger mean male and female body length and also a slightly larger mean relative male length. The mean host masses of philopterids and menoponids marginally differ in the three orders, with menoponids found on slightly larger hosts.

Table 9 shows the louse species (or subspecies, or lineage) closest to the 2.5%, 50% (median), and 97.5% quantiles of relative male size (ratio of male to female body length) for each group investigated. Relative male size, male and female body lengths, and host size and species are also reported. On a family level, philopterid and menoponid lice seem to show a pattern consistent with RR; with the increase of female body length, the male body lengths increase faster (thus the relative male size increases), with increasing host body weights. Ricinids, on the other hand, seem to exhibit a CRR pattern. Relative male size decreases as the female size increases, and host body masses also decrease with the increase of relative male size. Grouped by host orders, philopterids and menoponids from Passeriformes also show a trend consistent with RR, while in other groups, these descriptive statistics do not clearly match either RR or CRR.

Table 8 Means and standard deviations of male and female body lengths, relative male sizes (male body length/female body length), and host weights (g) for each investigated group, N is the number of operational taxonomic units (species, populations, or host specific lineages).

		Male body length (μm)		Female body length (μm)		Male body length/Female body length (μm)		Host mass (g)		N
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	
Louse families	Philopteridae	2063	939	2385	919	0.85	0.08	1213	5422	514
	Menoponidae	1764	685	2081	688	0.84	0.1	846	1656	375
	Ricinidae	2999	570	3686	747	0.82	0.06	28	23	100
Philopterid and menoponid lice from different host orders	Philopteridae from Passeriformes	1526	246	1843	255	0.83	0.07	113	148	90
	Menoponidae from Passeriformes	1383	275	1693	300	0.82	0.06	124	211	97
	Philopteridae from Charadriiformes	1673	199	2018	213	0.83	0.04	248	236	90
	Menoponidae from Charadriiformes	1643	330	2037	366	0.81	0.09	262	278	56
	Philopteridae from Galliformes	2229	679	2534	715	0.88	0.09	1051	989	97
	Menoponidae from Galliformes	1788	296	1965	237	0.91	0.12	1189	1000	34

Table 9 Allometric relationships of the louse families Allometric relationship between log-transformed male and female body lengths (μm).

	Quantile	Male body length/ Female body length (μm)	Male body length (μm)	Female body length (μm)	Host weight (g)	Louse species name	Host species name	
Louse families	Philopteridae	2.5%	0.71	1322	1873	66	<i>Brueelia mahrastran</i>	<i>Turdoides striata</i>
		50%	0.85	1560	1830	74	<i>Brueelia straminea</i>	<i>Dendrocopos major</i>
		97.5%	1.03	2800	2720	217	<i>Strongylocotes subconiceps</i>	<i>Crypturellus soui</i>
	Menoponidae	2.5%	0.67	1550	2330	291	<i>Hohorstiella gigantea</i>	<i>Columba oenas</i>
		50%	0.84	1800	2150	634	<i>Colpocephalum leptopygos</i>	<i>Plegadis falcinellus</i>
		97.5%	1.08	2710	2500	2419	<i>Holomenopon goliath</i>	<i>Anseranas semipalmata</i>
	Ricinidae	2.5%	0.72	3400	4700	68	<i>Ricinus elongatus</i>	<i>Turdus philomelos</i>
		50%	0.81	3180	3920	16	<i>Ricinus serratus</i>	<i>Serinus flaviventris</i>
		97.5%	0.92	2930	3190	12	<i>Ricinus dendroicae</i>	<i>Dendroica striata</i>
Philopterid and menoponid lice from different host orders	Philopteridae from Passeriformes	2.5%	0.70	1411	2012	61	<i>Brueelia magnini</i>	<i>Turdoides fulva</i>
		50%	0.83	1429	1716	70	<i>Brueelia addoloratoi</i>	<i>Turdus rufiventris</i>
		97.5%	0.98	2460	2500	570	<i>Philopterus ocellatus</i>	<i>Corvus corone</i>
	Menoponidae from Passeriformes	2.5%	0.70	1190	1700	18	<i>Menacanthus eurysternus</i>	<i>Tichodroma muraria</i>
		50%	0.82	1600	1960	200	<i>Myrsidea bakeri</i>	<i>Corvus kubaryi</i>
		97.5%	0.91	1730	1900	294	<i>Colpocephalum fregili</i>	<i>Corvus splendens</i>
	Philopteridae from Charadriiformes	2.5%	0.74	1680	2280	192	<i>Saemundssonina (Saemundssonina) africana</i>	<i>Vanellus albiceps</i>
		50%	0.83	1630	1960	96	<i>Saemundssonina (Saemundssonina) platygaster theresae</i>	<i>Jacana spinosa</i>
		97.5%	0.92	1520	1660	61	<i>Saemundssonina (Saemundssonina) chathamensis</i>	<i>Thinornis novaeseelandiae</i>
	Menoponidae from Charadriiformes	2.5%	0.66	1150	1750	655	<i>Austromenopon atrofulvum</i>	<i>Sterna caspia</i>
		50%	0.82	1690	2050	53	<i>Actornithophilus ceruleus</i>	<i>Procelsterna cerulea</i>
		97.5%	0.97	1650	1700	136	<i>Actornithophilus pediculoides</i>	<i>Arenaria interpres</i>
	Philopteridae from Galliformes	2.5%	0.71	1875	2640	1135	<i>Lipeurus maculosus</i>	<i>Phasianus colchicus</i>
		50%	0.87	2000	2290	749	<i>Lipeurus sarissa</i>	<i>Rhizothera longirostris</i>
		97.5%	1.05	2770	2650	1330	<i>Lipeurus raymondi</i>	<i>Acryllium vulturinum</i>
Menoponidae from Galliformes	2.5%	0.75	1556	2070	504	<i>Menacanthus lyali</i>	<i>Alectoris chukar</i>	
	50%	0.90	1680	1870	1490	<i>Amyrsidea (Cracimenopon) jacquacu</i>	<i>Penelope jacquacu</i>	
	97.5%	1.19	2090	1750	379	<i>Menacanthus werneri</i>	<i>Polyplectron napoleonis</i>	

4.3.3.2 Results of pRMA models

Results of the pRMA regressions, the estimated phylogenetic signals, and sample sizes are reported in Table 10. For visual representations of the data and the fitted lines, see Figure 8 for families, Figure 9 for philopterids and menoponids from different host orders. On a family level, both philopterid and menoponid lice show male-female allometric relationships consistent with RR. Ricinid lice exhibit a CRR trend (allometric slope < 1), which is surprising. Grouping the lice by host orders, we observed that RR applies to menoponids from Passeriformes and philopterids from both Charadriiformes and Galliformes. In all cases in which allometries consistent with RR were confirmed, the estimated slopes have numerically similar values, ranging from 1.11 to 1.16.

4.3.3.3 Jackknife diagnostics of pRMA models

In each pRMA model where deviation from isometry was confirmed, leaving out any single observation (data point) from the regression model changed neither the significance of the results nor the general direction of the slope (whether it is smaller or larger than 1). The effects of the most influential points on the slope — expressed as a percentage of the slope estimate — are reported in Table 10. In the cases of these models, the maximal effects range from 0.46% to 3.09%.

In some models where the deviation from isometry was not confirmed, certain observations can have a notable influence on the estimated slope. In these cases, leaving out particular observations from the model can result in a significant (p -value ≤ 0.05) deviation from isometry. In the regression model of menoponids from Galliformes 9 out of 34 have this property.

Table 10 Results of the phylogenetic reduced major axis regressions of log(male body length (μm)) on log(female body length (μm)) for the three louse families, and for philopterids and menoponids from three different host orders. The estimated phylogenetic signals (λ) and sample sizes (N , number of operational taxonomic units: species, populations, or host specific lineages) are also reported.

		Intercept	Slope	R ²	t-value	degrees of freedom	p-value (H ₀ : true slope=1)	Phylogenetic signal (λ)	Effect of the most influential point on the slope	N
Louse families	Philopteridae	-1.29	1.15	0.86	8.21	360.47	<0.0001	0.91	0.46%	514
	Menoponidae	-1.14	1.12	0.76	4.47	272.57	<0.0001	0.93	1.51%	375
	Ricinidae	0.60	0.90	0.88	3.07	70.01	0.0030	0.86	0.46%	100
Philopterid and menoponid lice from different host orders	Philopteridae from Passeriformes	-0.94	1.10	0.71	1.67	66.86	0.1004	0.01	1.30%	90
	Menoponidae from Passeriformes	-0.98	1.11	0.86	2.62	68.39	0.0107	0.56	2.58%	97
	Philopteridae from Charadriiformes	-1.14	1.13	0.76	2.29	65.7	0.0255	0.67	2.77%	90
	Menoponidae from Charadriiformes	0.62	0.89	0.64	1.45	42.88	0.1537	0.50	7.07%	56
	Philopteridae from Galliformes	-1.10	1.12	0.87	3.05	68.29	0.0033	0.73	1.39%	97
	Menoponidae from Galliformes	-2.33	1.30	0.44	1.99	28.19	0.0565	0.90	12.06%	34

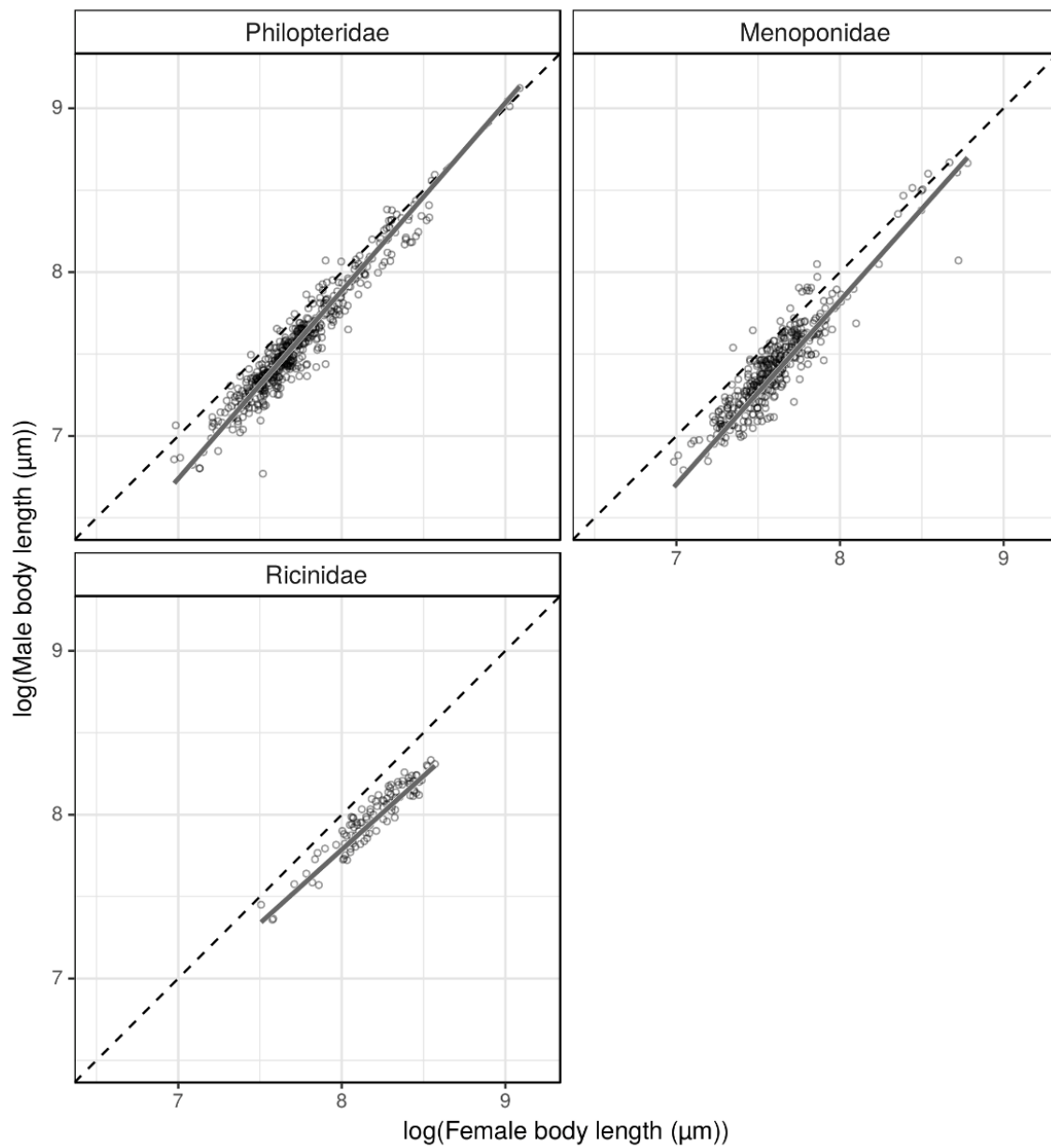


Figure 8 Allometric relationships of the louse families. Allometric relationship between log-transformed male and female body lengths (μm) with isometric slopes (dashed lines) and fitted phylogenetic reduced major axis regression lines (solid lines) by louse families.

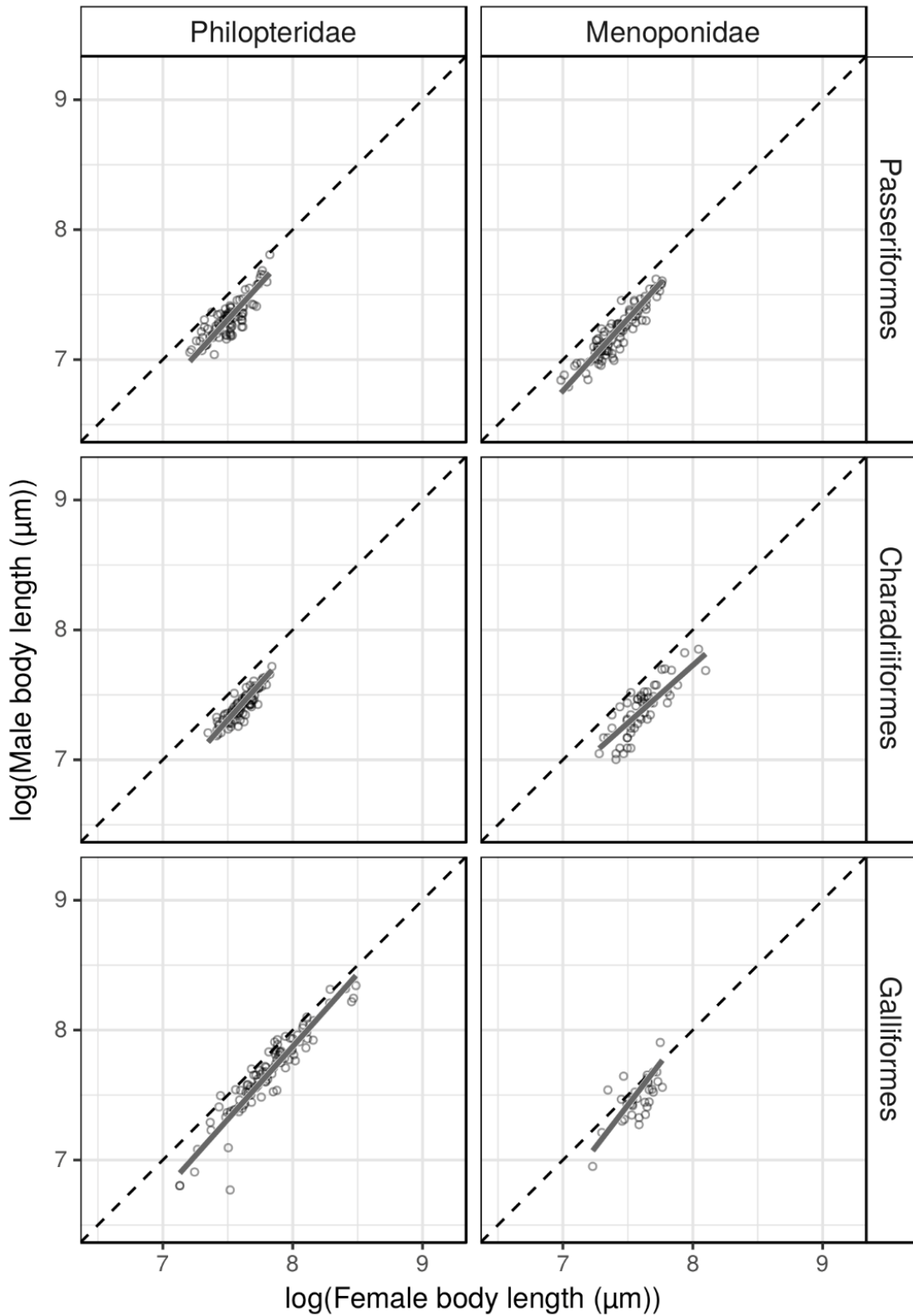


Figure 9 Allometric relationships of philopterid and menoponid lice from passeriform, charadriiform, and galliform birds. Allometric relationship between log-transformed male and female body lengths (μm) with isometric slopes (dashed lines) and fitted phylogenetic reduced major axis regression lines (solid lines) by louse families and host orders.

4.3.4 Discussion

We have shown that two major taxa of avian ectoparasites, philopterid and menoponid lice, clearly obey RR. Host order level analysis in these families also confirmed RR separately in the case of Menoponidae from Passeriformes and Philopteridae from Charadriiformes and Galliformes. In contrast, however, ricinids follow CRR, where males get relatively smaller (as compared to females) with increasing size of the species.

Deviance from isometry was not proven in some cases. Philopterids from Passeriformes show a numerically similar allometric trend compared to menoponids from the same host order. The model explains less variance in the data among philopterids from these birds, perhaps indicating weaker mechanisms behind RR than among menoponids. Although not significant, the steep slope of menoponids from Galliformes is an interesting trend. Also, the slope of Menoponidae from Charadriiformes is consistent with CRR. These results indicate that accounting for host taxonomy and life history traits is a promising direction in investigating the underlying causes for RR.

Although without formal comparison, in all cases where RR was supported, the allometric slopes showed similar values. Based on this, it would be hard to come up with different interpretations of the results. Philopterids altogether show a somewhat steeper, but generally similar allometric trend compared to menoponids.

The non-exclusive alternative hypotheses explaining RR and Converse RR may more or less apply to our findings. Lice can respond quickly to selection pressures on body size (Villa et al., 2018), but the genetics of their body size in relation to sex is not known. Furthermore, we lack knowledge about possible niche divergences between the sexes.

Sexual selection is known to be an influential agent of evolution in several taxa of parasites (Goater et al., 2013; Poulin, 2011b), including parasitic lice (Pap et al., 2013; Rózsa et al., 2015a; Tryjanowski et al., 2009). Given that larger-bodied host species tend to have more prevalent and more abundant infestations of menoponid and philopterid lice (Poiani, 1992; Rothschild and Clay, 1957; Rózsa, 1997), we expect that the males in these populations tend to coexist with more rivals and also face an increased level of outbreeding due to a higher chance of multiple infections. This strengthens intrasexual competition (Eberhard et al., 2018), and it also probably exerts a selection pressure favouring larger males. Our descriptive statistics in Table 9 empirically support this view; in many cases (namely in the Philopteridae and Menoponidae families together and separately from the Passeriformes), relative male size tends to increase with host body size. This probably indicates that in menoponids and philopterids, sexual selection due to male-male rivalry exerts stronger selection pressure on male size than fecundity

selection exerts on female size. Contrarily, CRR observed in ricinid lice may indicate that fecundity selection is stronger on female body size than sexual selection is on male body size.

Based on our findings, it appears that similar selection pressures shape the evolution of SSD across avian lice, except for the family of Ricinidae.

4.4 Conclusions

Rensch (1959) did not explain his rule regarding sexual size allometry. The underlying mechanism is still unclear, but most explanations centre around sexual selection (see 4.3.1 and 4.3.4.; Piross et al., 2019). We discussed that sexual selection pressure is expected to co-vary with host body size. Future analyses could help us better understand the evolutionary trends in sexual size dimorphism in avian lice.

Some studies indicate prevalence is larger in larger-bodied host species than smaller ones (Poiani, 1992; Rothschild et al., 1957; Rózsa, 1997), but this relationship has never been tested. Higher prevalence should, arguably, increase the frequency of multiple infections because — all else being equal — each bodily contact with conspecifics is more likely to come with further parasite transmissions. The local mate competition theory (Hamilton, 1967) predicts that male lice from the more outbred populations of large-bodied host species should be sexually more competitive. We expect to find relatively larger-bodied male lice on larger-bodied host species. The theory also suggests that females should produce fewer male offsprings in more inbred populations to reduce local mate competition. Thus, we expect louse species with low prevalence to show female-biased sex ratios in their infrapopulations and expect their males to be relatively smaller than their females. The hypotheses could be investigated using large louse ecological data sets, using phylogenetic comparative methods (Garamszegi, 2014).

Ricinid lice show the converse Rensch's rule, which is not at all unprecedented in insects (Garcia-Navas et al., 2017; Guillermo-Ferreira et al., 2014). These lice are scarcely collected (Nelson, 1972), and their ecology has never been studied. We speculate that their mating system may differ from that of other louse families due to their low prevalence and abundance. Their host range indicates a preference for small-bodied hosts. Presuming that they are more prevalent and more abundant on smaller-bodied hosts, as we suspect — but never proved —, they may face stronger sexual selection pressure on the smaller host species. This could explain why they face stronger male-to-male rivalry in smaller host species and, therefore, develop a body size allometry pattern consistent with converse RR.

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

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7 Publications in peer-reviewed journals related to the thesis

This dissertation has been partially compiled from the following articles first-authored by me. Some sections were rearranged or edited to make the thesis more cohesive.

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**

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*). *Parasitol Res.*, 2020**

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*). *Parasitol Res.*, 2020**

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**

8 Publications in peer-reviewed journals not related to the thesis

- Mór h,  .; Endr di, A.; Piross, I. S.; Jord n, F., **Topology of additive pairwise effects in food webs.** *Ecological Modelling.*, 440, 109414., 2021
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10 Appendices

10.1 Appendix 1

Appendix to 3.4 Sex-dependent changes in the louse abundance of Red-footed Falcons (*Falco vespertinus*)

The following tables contain information on each generalized linear model, for each dataset used. The fix effects can be separated by the following operators: “+”: no interaction between the variables, “:”: the interaction term of two variables, “*”: the variables and their interaction variable.

Abbreviations:

d.f: The model's degree of freedom

AIC: Akaike's Information Criterion

BIC: Bayesian Information Criterion

χ^2 : Chi-squared value

χ^2 d.f.: Chi-squared distribution's degree of freedom

C. subzerafae: *Colpocephalum subzerafae* Tendeiro, 1988b

D. rufa: *Degeeriella rufa* Burmeister, 1838

Data	Fix effects	d.f.	AIC	BIC	χ^2	χ^2 d.f.	p-value
C. subzerfae, nestlings 2012	Without fix effects	3	232.990	238.280			
	Sex	4	231.360	238.400	3.640	1	0.0565
	Sex + Wing length	5	233.030	241.840	0.330	1	0.5684
	Sex * Wing length	6	234.960	245.520	0.080	1	0.7811
	Sex * Wing length + Number of siblings (categorical)	8	236.890	250.980	2.070	2	0.3561
D. rufa, nestlings 2012	Without fix effects	3	167.310	172.600			
	Wing length	4	165.410	172.450	3.900	1	0.0482
	Sex + Wing length	5	167.290	176.100	0.120	1	0.7297
	Sex * Wing length	6	169.150	179.720	0.140	1	0.7094
	Sex * Wing length + Number of siblings (categorical)	8	172.670	186.760	0.480	2	0.7869
C. subzerfae, nestlings 2014	Without fix effects	3	167.390	174.130			
	Wing length	4	169.030	178.030	0.360	1	0.551
	Sex + Wing length	5	171.000	182.250	0.030	1	0.8641
	Sex * Wing length	6	172.910	186.410	0.090	1	0.7634
	Sex * Wing length + Number of siblings (categorical)	8	175.660	193.650	1.250	2	0.5348
D. rufa, nestlings 2014	Without fix effects	3	251.330	258.080			
	Wing length	4	252.340	261.330	0.990	1	0.3186
	Sex + Wing length	5	254.290	265.540	0.040	1	0.8397
	Sex * Wing length	6	252.020	265.510	4.270	1	0.0387
	Sex * Wing length + Number of siblings (categorical)	8	255.350	273.340	0.670	2	0.7157
	Without fix effects	3	94.860	100.830			

Data	Fix effects	d.f.	AIC	BIC	χ^2	χ^2 d.f.	p-value
C. <i>subzerfae</i>, adults 2014	Sex * days after first egg laid	6	92.320	104.260	8.540	3	0.0361
	Sex * days after first egg laid + Wing length	7	92.730	106.650	1.590	1	0.2068
	Sex * days after first egg laid + Sex : Wing length	8	93.340	109.250	1.390	1	0.2385
<i>D. rufa</i>, adults 2014	Without fix effects	3	234.860	240.820			
	Sex * days after first egg laid	6	207.200	219.130	33.660	3	<0.0001
	Sex * days after first egg laid + Wing length	7	206.560	220.480	2.640	1	0.1042
	Sex * days after first egg laid + Sex : Wing length	8	207.830	223.740	0.720	1	0.3951

10.2 Appendix 2

Appendix to 3.5 Sex interacts with age-dependent change in the abundance of lice infesting Amur Falcons (*Falco amurensis*)

See Appendix 1 for the explanation.

Louse species	Terms	d.f.	AIC	BIC	χ^2	χ^2 d.f.	p-value
<i>C. subzerfae</i>	Without fix effects	2	273.090	276.910			
	Age	3	263.380	269.120	11.710	1	6×10 ⁻⁴
	Age + Wing length	4	264.680	272.330	0.700	1	0.4014
	Sex + Age + Wing length	5	265.050	274.610	1.630	1	0.2017
	Sex * Age + Wing length	6	266.360	277.830	0.690	1	0.4075
	Sex * Age + Wing length + Sex:Wing length	7	268.350	281.740	0.010	1	0.9176
<i>D. rufa</i>	Without fix effects	2	304.920	308.740			
	Sex * Age	5	282.570	292.130	28.340	3	<0.0001
	Sex * Age + Wing length	6	284.330	295.800	0.240	1	0.6212
	Sex * Age + Wing length + Sex:Wing length	7	285.910	299.290	0.420	1	0.5176