

DEMOGRAPHIC CORRELATES OF SEXUAL SIZE DIMORPHISM AND MALE GENITAL SIZE IN THE LICE *PHILOPTERUS COARCTATUS*

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ABSTRACT: Sexual selection is an influential agent of evolution, often shaping the sex ratio, sexual size dimorphism (SSD), and genital size in animals. To explore its effects in ectoparasites, we quantified SSD and male genital size in relation to intensity and sex ratio across subpopulations of *Philopterus coarctatus*, a philopterid louse of the great grey shrike. SSD was calculated separately for the width and length of the head and abdomen. Presuming that sexual selection affects the evolution of avian lice, we would expect that infestation intensities should covary with sex ratio, relative male size, and relative male genital size, either positively or negatively depending upon presumptions. Contrary to former studies, there was a weak negative relationship between infestation intensity and sex ratio. The relative width of male abdomens exhibited a highly significant negative interaction with the intensity of infestations. In contrast, sex ratio did not predict any of the dimorphism measures. Similarly, male genital size did not covary with the intensity of infestations or sex ratios. These findings may indicate that intensity covaries positively with levels of inbreeding in this species, suggesting that more-inbred subpopulations, wasting less energy for sexual rivalry, can multiply more intensively. Thus, small subpopulations have more frequent males which also possess larger abdomens. Alternatively, however, the same pattern may also arise due to male-biased starvation in overcrowded habitats; thus, males are rarer and have smaller abdomens in larger infrapopulations.

Most animals reproduce sexually, and the emergent rivalry for more or better sexual partners inherently gives rise to sexual selection (Darwin, 1871). Sexual multiplication, which may effectively shape the evolution of their behavior, sex ratios, and body structures, is also a major event in the life cycle of most parasitic animal species. The surprisingly large testes characteristic of many parasitic taxa (Poulin and Morand, 2000), and the use of copulatory plugs by males to block their partners' subsequent copulation with rivals in some taxa (Dezfuli et al., 1991), provide indirect evidence to suggest that sperm competition is a widespread mechanism of sexual selection in many parasitic animals.

In the case of sperm competition, females copulate with several males, sequentially, and then store the sperm. Males are selected to produce as many sperm as possible, which dilute the sperm of their rivals. Larger males can grow larger testes to produce more sperm and, thus, male body size tends to increase under heavier selection pressure (Andersson, 1994). Not surprisingly, sexual size dimorphism (SSD) has often been considered as a simple measure of the intensity of sexual selection in parasites that are not known to exhibit direct physical contests during male–male rivalry (Poulin, 1997). Copulation that is prolonged so as to increase fertilization success, relative to rivals, is a well-known response to high population density or male-biased sex ratios in several insect species (Wang et al., 2008). In the case of avian lice (Phthiraptera), copulation time varies from a few seconds up to 2 days

(Mey, 2003). Male genital size in insects is also likely to covary positively with levels of sexual selection (Hosken and Stockley, 2003). We assume that long copulation time in avian lice may not be needed for fertilization itself, but may act as a simple form of mate-guarding. In this case, larger male genitals may enhance mate-guarding capabilities in more competitive environments. Female lice can store sperm (Lang, 1975); thus, mate-guarding can be an effective male strategy to monopolize a female.

Animal parasites appear to be suitable subjects for studying sexual selection because they inhabit host bodies as well-isolated habitat patches. Provided that the infection originates from a single source, parasites sharing a single host are likely to be genetic kin and, thus, form an inbred infrapopulation. Sexual rivalry is predicted to be maladaptive in such inbred infrapopulations due to local mate competition (Hamilton, 1967). On the contrary, multiple infections result in parasite infrapopulations consisting of non-kin rivals.

Here, we attempted to study demographic correlates of SSD and male genital size in a species of avian lice in order to explore morphological adaptations in relation to different levels of sexual selection or crowding.

Unfortunately, we cannot easily assess the inbred–outbred nature of louse infrapopulations. Presuming that multiple infections are more likely to yield heavier infections, one can predict that intensity should covary positively with outbreeding. Accordingly, intensity of infestation is already known to covary positively with sex ratio in an anopluran (Rózsa, 1997) and in some philopterid lice (Rózsa et al., 1996). On the contrary, however, one can also presume an opposite trend when considering that more-inbred infrapopulations are predicted to allocate less time and energy for sexual rivalry and, therefore, reproduce more intensively. In this latter case, we predict that levels of infestation intensity covary negatively with levels of outbreeding. In a former study exploring the relationship between infection intensity and louse body size, Tryjanowski et al. (2007) did not find significant sexual differences in this relationship. Here, we use the same sample of lice, but formulate more-specific questions regarding sexually selected morphologies using several different measures of SSD.

Sex ratio is a simple demographic measure to assess the intensity of sexual rivalry. Males are the more-competitive sex in most animal species; thus, sex ratio, i.e., the proportion of males

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within the population (Wilson and Hardy, 2002), is a useful measure to characterize the sexual environment of individuals. We predict that sexual selection favors relatively larger male body sizes and larger male genitals in cases of more outbred and more male-biased infestations.

As an alternative hypothesis, we propose that high levels of crowding, i.e., intensity from the viewpoint of individuals parasites (Reiczigel et al., 2005), should increase rivalry for nutrient resources. Bush and Malenke (2008) have recently shown the interspecific competition for nutrient resources between 2 species of philopterid lice, and we cannot exclude the possibility that intraspecific rivalry for food resources plays a similar role. More specifically, the *Philopterus* spp. lice used in the present study belong to the so-called ‘head lice’ of birds, as their habitat is quite strictly restricted to the host’s head, the nape in particular, and to the dorsal side of its neck (Mey, 2004). Given that their habitat is rather strictly confined to an area of host body surface covered by a relatively narrow layer of plumage, they appear to be suitable subjects for studying the effects of intraspecific competition for nutrient resources.

Philopterid lice graze the downy layer of the plumage. They typically consume the finest barbules first and then go on chewing the thicker and stronger barbs as well (see e.g., Bush and Malenke, 2008). Because males tend to be smaller than females, we predict that males are the first to face nutrient limitations when their mandibles become too weak to chew what has been left. Thus, provided that nutrient shortage influences louse morphologies at high levels of crowding, we predict that males should be subjected to starvation more than are females.

Philopterids are insects that live as permanent ectoparasites of birds and mammals (Price et al., 2003). As the most species-rich group of avian lice, they inhabit the plumage of birds, feed mainly by grazing non-living parts of the plumage, and have little if any direct interaction with the host immune system (Møller and Rózsa, 2005). Their population size and distribution is mostly limited by host behavioral defenses such as preening by the bill or grooming by the legs (Clayton, 1991). The ‘predation pressure’ exerted by these defenses is highly size-specific and selects against large body size (Clayton et al., 1999). Consequently, we expect natural selection to prefer small males, contrary to the sexual selection that favors large males. In general, philopterid lice exhibit fine-tuned body size adaptations to fit host morphologies (Bush and Clayton, 2006); however, their body size is also evidently sex-specific. They are less agile and, therefore, more closely restricted to individual hosts than are most other avian ectoparasites. Consequently, their population genetic structures are rather strictly influenced by host demographic processes such as parent–offspring infestation lineages and host sociality (Darolová et al., 2001; Valera et al., 2003; Whiteman and Parker, 2004; Kristofik et al., 2007; Whiteman et al., 2007).

MATERIALS AND METHODS

Philopterus coarctatus (Scopoli, 1763) (= *P. fuscicollis* (Burmeister, 1838), = *Docophorus coarctatus fuscicollis* (Eichler, 1953)) is the most prevalent (>90%) louse species found on the great grey shrike (Szczykutowicz et al., 2006).

Lice were collected from freshly killed birds by a direct visual inspection of the plumage for ectoparasites. Collections were carried out between 1962 and 1974 in Slovakia in accordance with contemporary legislation on nature conservation. All lice were preserved in 75% ethyl alcohol. After

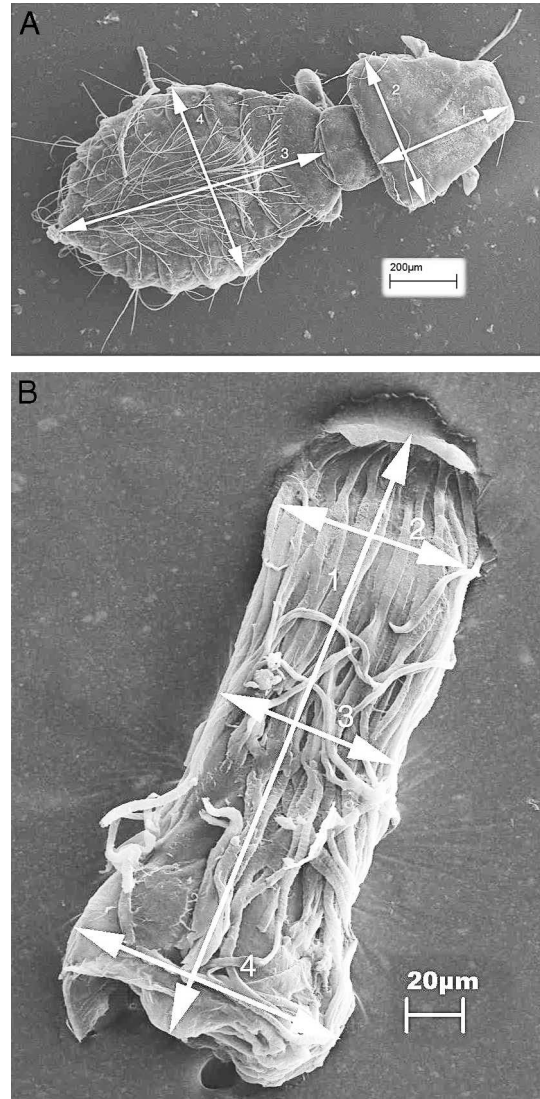


FIGURE 1. The head louse *Philopterus coarctatus* (Scopoli, 1763) of the great grey shrike *Lanius excubitor* L. Male individual (A) showing head length (1) and width (2) and abdomen length (3) and width (4) measures. Male genitalia (B) showing length (1), anterior-end width (2), mid-length width (3), and posterior-end width (4) measures.

removal from alcohol, lice were cleaned and mounted on microscope slides for measurement (see more details in Szczykutowicz et al., 2006).

Only well-preserved adult lice were used to obtain morphological measurements with a scanning electron microscope Zeiss Evo 40 (SEM; Carl Zeiss SMT AG, Oberkochen, Germany). A total of 470 lice from 49 shrikes was measured. From each individual host, all male and female lice were measured in cases of weak infestations; a minimum of 5 males and 5 females were measured in cases of heavy infestations (see details in Tryjanowski and Adamski, 2007; Tryjanowski et al., 2007). The following 4 measurements (in μm) were taken from each parasite, i.e., head width, head length, abdomen width, and abdomen length (Fig. 1A). These measures were used to calculate SSD.

In a subsequent effort, 35 male lice from 29 birds were dissected and their genitalia measured. Four measurements of the male genitalia were taken, i.e., length, anterior end width, mid-length width, and posterior end width (Fig. 1B). The set of birds involved in these measurements only partially overlapped with the birds that yielded the lice for SSD measures, as lice mounted on microscope slides for body size measurements are not suitable for obtaining genital preparations. There were only 19 birds that yielded both louse body size and louse genital size measures.

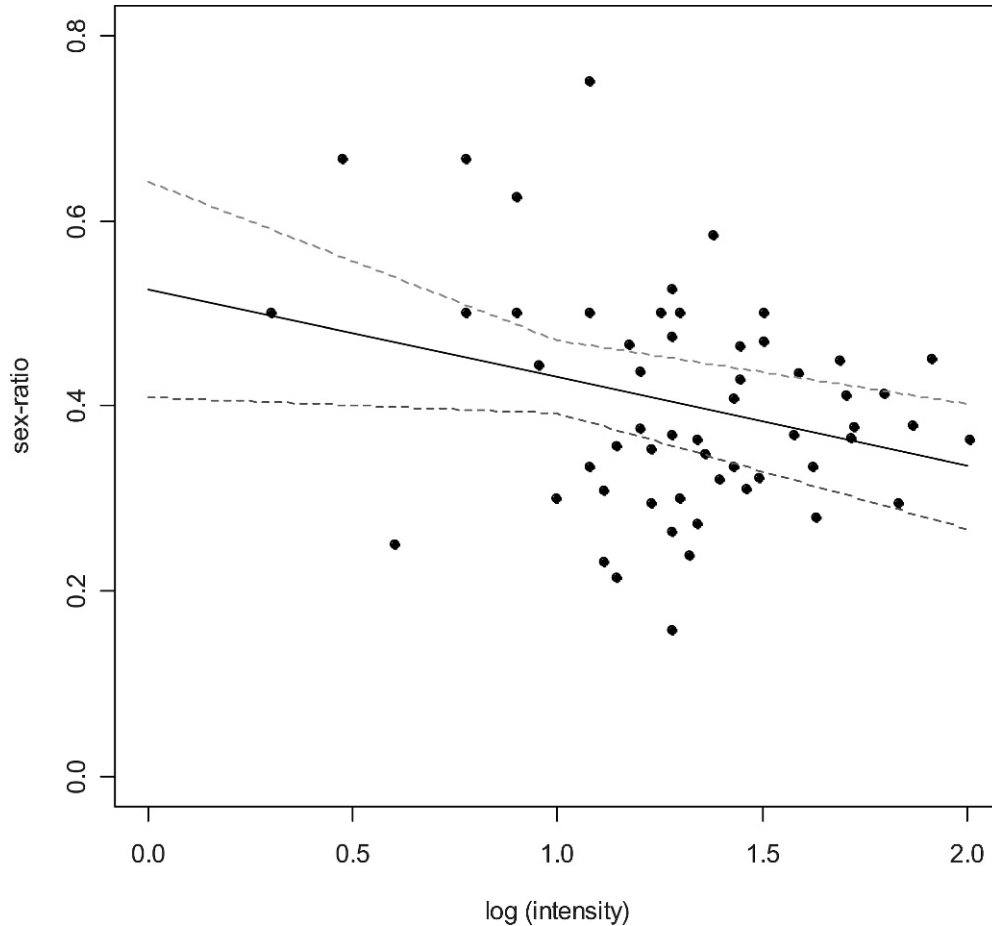


FIGURE 2. Interaction between the intensity of infestation and sex-ratio across infrapopulations of *Philopterus coarctatus* living on the great grey shrike (ordinary least square regression, 95% CI).

The dataset appeared to contain outlier values. First, male lice from one particular bird (No. 98/65) were unusually large, even after repeating the measures. Males from this shrike were significantly larger (data not shown) than females, challenging even the taxon descriptions (Eichler, 1953; Zlotorzycska, 1964). Consequently, this infrapopulation was entirely excluded. Second, to exclude mistyping errors, we calculated mean and SD for all measurements of males and females separately and deleted all measurements outside the range of the mean ± 3 SD (Zar, 1999). We also excluded all individuals from the body size dataset, if at least 1 body size data was absent, and excluded individuals from the genital size dataset if at least 1 genital size datum was lacking. To avoid pseudo-replication, all louse size measurements were averaged above each individual bird. Thus, all morphological data included below represent mean values to characterize louse infrapopulations obtained from separate shrikes.

Louse SSD was quantified separately for the 4 different measures in the following way. Mean male head length was regressed over mean female head length. The residuals from this regression line were interpreted as relative male head length. Note that male lice are usually smaller than females, and thus relatively larger measures, in fact, indicate a smaller degree of dimorphism. To avoid misleading terminology, we will refer to the relative male size as compared to the hypothetical male size predicted by the mean female size on a particular bird. A similar method was applied to generate measures of relative male head width and relative male abdomen length and width. Naturally, these dimorphism measures covaried positively with each other and, thus, they yielded redundant information about SSD.

To analyze potential interactions between genital size measures and ecological variables, we first used non-adjusted genital size data. Second, we also calculated relative genital sizes in the following manner: male genital length was regressed over average male head length from the same bird (not that of the same louse individual). The residuals from this

regression were interpreted as a measure of relative genital size. Male head width was used in a similar way to calculate relative genital width measures. These relative measures were available for only relatively few subpopulations ($n = 19$).

Intensity, i.e., the number of lice sharing the same bird (N), was meant as the log-transformed number of adults found on a host. Sex ratios were expressed as males/(males+females) and there was no need for arc-sin transformation because the values were all within the range of 0.15–0.75. Statistical calculations were carried out using R (Reiczigel et al., 2007; R Development Core Team, 2008).

RESULTS

Contrary to the results of a few former louse studies (Rózsa et al., 1996; Rózsa, 1997), there was a negative interaction between log (intensity) and sex ratio (linear regression, ordinary least square method: adjusted R^2 : 0.0627, df: 1, 57, $P = 0.0313$) (Fig. 2).

We analyzed louse SSD measures (head length and width, abdomen length and width) in relation to log (intensity) and sex ratio as predictor variables in the context of a canonical correlation. The correlation coefficient of the first canonical variates was $r = 0.644$. Log (intensity) appeared to have a stronger effect than sex ratio. Head-length dimorphism and abdomen-width dimorphism had a relatively stronger contribution to the model, positive and negative, respectively. Indeed, a multiple linear regression between these 4 dimorphism measures

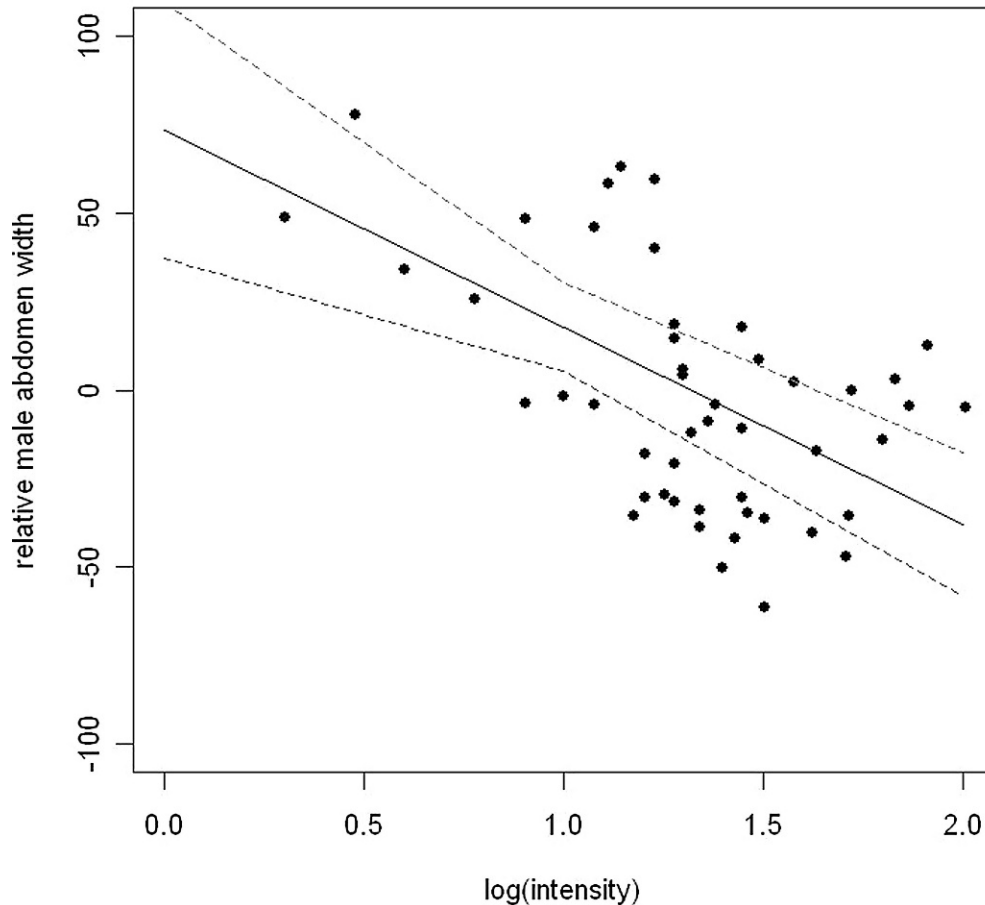


FIGURE 3. Interaction between intensity of infestation and relative male abdomen size across subpopulations of the lice *Phlopterus coarctatus* (ordinary least square regression, 95% CI).

as dependent variables, and $\log(\text{intensity})$ as a predictor variable, indicated a highly significant relationship (adjusted R^2 : 0.3533, df: 4, 44, $P = 0.0001$). Within this model, abdomen-width dimorphism exhibits the strongest effect and is, again, negative. Head-length dimorphism also has a strong positive effect. More specifically, the abdomen-width dimorphism $\sim \log(\text{intensity})$ interaction proved to be highly significant when examined separately (linear regression, ordinary least square method, adjusted R^2 : 0.2604, df: 1, 47, $P = 0.0001$) (Fig. 3). However, the head-length dimorphism $\sim \log(\text{intensity})$ interaction, when examined separately, was not significant at all (data not shown).

The above-mentioned canonical correlation had already indicated that sex ratio had little if any influence on SSD measures. Accordingly, a multiple linear regression using sex ratio as a predictor, and dimorphism measures as dependent variables, showed no significant interaction (data not shown). Repeating the same analysis while weighting sex ratio by $N^{0.5}$ as a dependent variable gave no significant results either.

The second canonical correlation analysis was conducted to describe potential interactions among male genital measures (1 length and 3 width measures) as dependent variables and $\log(\text{intensity})$ and sex ratio as predictor variables. The correlation coefficient of the first canonical variate was weaker than in the former case ($r = 0.522$). Sex ratio appeared to have a much stronger effect than $\log(\text{intensity})$. However, a multiple linear

regression between the 4 genital measures as dependent variables, and the sex ratio as a predictor variable, yielded only marginally significant results (data not shown). We repeated the same analysis while weighting by $N^{0.5}$; however, this interaction was not significant at all (data not shown). Moreover, we repeated these calculations using relative male genital sizes (see Materials and Methods). This effort also provided no significant results (data not shown).

DISCUSSION

Contrary to our expectations, sex ratio did not covary significantly with sexually selected morphological measures. Similarly, genital size measures (either as absolute or relative measures) did not covary with demographic correlates. This lack of interaction may have been partly caused by the relatively low sample size (29 and 19 infrapopulations represented, respectively).

However, we have documented significant interactions between infrapopulation intensity and sex ratio and also between intensity and male relative abdomen width. There are at least 2 alternative explanations that can plausibly interpret these findings.

First, we documented a negative interaction between infestation intensity and subpopulation sex ratios. This may indicate that more-outbred infrapopulations allocated more time, energy, and nutrients into sexual rivalry and, thus, multiplied less intensively

than the more-inbred infrapopulations. Accordingly, males in smaller infrapopulations developed relatively larger abdomens so as to incorporate larger testes. However, the size of the male genitals, the only sexual organs that we measured, did not covary with intensity or sex ratio across infrapopulations.

Second, we cannot exclude an alternative interpretation based on a food limitation scenario. One can argue that overcrowded host individuals do not yield nutrients in appropriate quantities and qualities; thus, sex-biased starvation arising at high intensities may influence the sex ratio and morphology of lice. Males, being smaller than females, may be more vulnerable to starvation, and this effect may also explain their being scarcer and having smaller abdomens at high intensities.

To our best knowledge, the present study is the first to explore potential demographic correlates of SSD and male genital size in lice (Phthiraptera). In view of the absence of any parallel studies, our results are presently difficult to interpret or generalize. We cannot exclude the possibility that the relevancy of the above findings is confined to the 'head lice' guild of avian ectoparasites, i.e., *Philopterus* spp.-complex and *Saemundsson* spp.-complex in the sense of Smith (2001). These lice, as compared to avian 'body lice' and 'wing lice,' inhabit a particularly nutrient-poor and preening-free microhabitat within the avian plumage. We need further studies to elucidate selective pressures shaping the population size, sex ratio, and morphologies of avian lice.

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