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SEX RATIO AND SEXUAL DIMORPHISM OF THREE LICE SPECIES WITH CONTRASTING PREVALENCE PARASITIZING THE HOUSE SPARROW

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ABSTRACT: Female-biased sex ratio is a common phenomenon in parasites; however, the cause and consequence of the skewed sex ratio is less well known. Here, we studied the difference in sex ratio, a possible mechanism responsible for the development of unbalanced proportion of sexes and its consequences on sexual size dimorphism, between 3 louse species parasitizing the house sparrow *Passer domesticus*. *Philopterus fringillae* was more prevalent than *Sturnidoecus refractarius* and *Brueelia cyclothorax*. As expected, the most common species, which was probably least affected by isolation and, hence, inbreeding, was characterized by a balanced sex ratio, whereas the 2 other species with low prevalence were significantly more female biased than expected on the basis of the local mate competition hypothesis. Further, in support of this notion, we found that *P. fringillae* infrapopulation size significantly, and positively, correlated with the sex ratio. Finally, we found significant differences in sexual dimorphism among the 3 louse species and, as expected, the relative size of males was smallest in species with a more female-biased sex ratio.

Sex allocation and sex-ratio theories are central to evolutionary biology (Charnov, 1982; Hardy, 2002; West, 2009). A first impetus was given by Fisher (1930), who demonstrated how frequency-dependent selection can promote equality in sexes under panmixia. The sex-ratio theory predicts an equal investment in production of male and female offspring (Fisher, 1930), which may deviate from equality if the relative cost of producing sons differs from that of daughters. A marked deviation of sex ratio from equality is frequent in parasites that have patchy distributions on “host islands” forming infrapopulations and thus precluding panmictic reproduction (Hamilton, 1967; Marshall, 1981; Poulin, 2007). The variation in sex ratio may be substantial even between closely related parasite species or between those with similar ecological traits (Dick and Patterson, 2008; Krasnov et al., 2008).

Parasites are ideal for studying the causes and consequences of sex allocation theory, because species with different life histories, sexual size dimorphism, dispersal ecology, mean infrapopulation size, and degree of isolation, e.g., due to the behavior of the host, vary in sex ratio (Poulin, 2007). These life history and demographic traits seem to interplay in a complex fashion, resulting in an unbalanced sex ratio. However, the mechanism driving the unbalanced sex ratio is largely unexplored. For example, low prevalence, i.e., many parasite-free islands, and small infrapopulation size of parasites may increase the level of inbreeding because of the reduced chance of multiple infections and, therefore, outbreeding. As a result, species with low transmission capacity, e.g., wingless flies or lice, and low prevalence are prone to inbreeding, which may favor the evolution of the unbalanced sex ratio. Hamilton (1967) demonstrated that when a small number of “foundresses” produce offspring that are to mate with each other, a female-biased offspring sex ratio is often favored by natural selection. This situation is called local mate competition (LMC), which evolves through a female-biased sex ratio, reducing competition among brothers for mates and, by this mechanism, all adults can

contribute to reproduction (see Macke et al., 2011). However, large parasite infrapopulations are generally the result of multiple infections (Read et al., 1995; West and Herre, 1998; Karvonen et al., 2011), which may increase the number of nonkin rivals. Inbreeding was invoked by Marshall (1981) to explain why most ectoparasitic insects exhibited female-biased sex ratios, i.e., parasites live in divided, isolated infrapopulations, where the offspring of 1, or a few, mother(s) mate in a patch. In line with the LMC hypothesis, parasite species with small prevalence(s) are expected to have a more pronounced female-biased sex ratio because lower prevalences are likely to be the result of single infections, which were found to be supported in studies on different parasitic (Poulin, 1997a; Pickering et al., 2000; West et al., 2001; Karvonen et al., 2011) and free-living (West and Herre, 1998) species. Finally, the proportion of sexes affects the level of sexual competition for mates, and thus influences sexual dimorphism.

Ectoparasitic lice (Phthiraptera) constitute an ideal group for studying the demographic and behavioral correlates of sex ratios and their consequence on sexual dimorphism. The distribution of louse populations among different individual hosts is significantly patchy, revealing a substantial level of inbreeding (Nadler et al., 1990). Lice are obligate, and primarily vertically, transmitted parasites with a simple life cycle and often exhibit female-biased sex ratios (Marshall, 1981; Clayton et al., 1992). In an analysis of published data, Marshall (1981) reported 31 of 50 species of lice with significantly female-biased sex ratios. Apparently, louse sex ratio is affected by the level of inbreeding, as expressed by infrapopulation size (Rózsa et al., 1996; Rózsa, 1997; Tryjanowski et al., 2009); however, the results are contradictory. Infrapopulation size is known to covary positively with sex ratio, as measured by the proportion of males in Anopluran (Rózsa, 1997) and Ischnoceran lice (Rózsa et al., 1996). In contrast, Tryjanowski et al. (2009) observed a weak negative relationship between infrapopulation size and the proportion of males in an ischnoceran species. One explanation for the difference in the relationship between sex ratio and infrapopulation size may be related to the variance in the prevalence between lice species, because the proportion of infested hosts may determine the degree of isolation and, therefore, the level of inbreeding. Accordingly, in case of low prevalence, we expect a more pronounced effect of infrapopulation size on louse sex ratios.

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FIGURE 1. Geographical distribution of sites in Romania for study of the 3 louse species parasitizing the house sparrow.

Our goal was to study the demographic correlates of sex ratio, degree of isolation (prevalence and infrapopulation size), and sexual dimorphism of 3 ischnoceran lice species infesting the house sparrow *Passer domesticus* (L., 1758), which differ in their prevalence, abundance, and sexual dimorphism. Among the louse species parasitizing the house sparrow populations studied by us, *Philopterus fringillae* (Scopoli, 1772) and *Sturnidoecus refractariolus* (Złotorzycka, 1964) are characterized by low mobility and highly localized occurrence on the head. The strategy of these species is based on tight attachment to the feathers of those parts of the host where the probability of preening by their host is the lowest. In contrast to the above-mentioned 2 louse species, the *Brueelia cyclothorax* (Burmeister, 1838) is an agile species that inhabits downy body feathers, where they have to evade frequent

host preening activities efficiently. Based on the effect of prevalence on the extent of inbreeding, we predicted that the proportion of males between species increases with prevalence. Sex ratio is a good measure to assess the intensity of sexual rivalry and, given that males are generally the more-competitive sex in most animal species, we predict that sexual selection favors relatively larger body sizes in males in the case of more male-biased species.

MATERIALS AND METHODS

The field study was performed between May 2007 and June 2008 on 16 house sparrow populations situated across Romania (see Fig. 1; Table I), where the birds were breeding in barns. The minimum distance between 2 populations was 22 km, which seemed to be a sufficient geographic barrier to prevent the birds moving between the breeding sites (see Pap et al., 2010). During the fieldwork in May and June, we captured approximately 15 adult male and 15 adult female house sparrows in each colony; in total, 492 birds were inspected for lice. Previous research (Jovani and Tella, 2006) established that a sample size of approximately 30 birds was sufficient to provide statistically acceptable data to estimate the actual prevalence of lice within a population. In addition to adult birds, we also inspected 36 juvenile house sparrows from 12 of the 16 study populations to determine the infestation data for these birds in the examination of louse dispersal behavior. Lice are known to disperse vertically (e.g., Lee and Clayton, 1995; Harbison et al., 2008) from parents to offspring; therefore, the colonization of the newly fledged birds by male and female adult lice could reflect the difference in dispersal capacity between sexes.

Following capture and measurements of standard biometric traits (wing length, tarsus length, and body mass), we quantified the abundance of lice on birds by visual examination and, in the case of infested birds by dust ruffling, using a pyrethrin-based fumigant (see Clayton and Drown, 2001). One of us (CA) carefully inspected birds by gently ruffling contour feathers throughout the body and collecting all nymph and adult lice for later examination. Lice were preserved in 75% ethanol, and their species and developmental stage (adult and nymph) were determined in the laboratory. The sex of adults was established with the use of external morphological traits (see Johnson and Clayton, 2003). The sexual differences between males and females begin to develop during the third nymphal stage; however, because of the individual differences in sexual maturation, sexes can be determined with certainty only in adults. Two

TABLE I. Prevalence, mean intensity, and index of discrepancy (*D*) of the 3 lice species on adult house sparrows during the breeding season across the 16 Romanian populations. Note that the sample size refers to the number of hosts examined.

Sampling site	Latitude and longitude	n	<i>Philopterus fringillae</i>			<i>Sturnidoecus refractariolus</i>			<i>Brueelia cyclothorax</i>		
			Prevalence (%)	Mean intensity $\pm$ SD	<i>D</i>	Prevalence (%)	Mean intensity $\pm$ SD	<i>D</i>	Prevalence (%)	Mean intensity $\pm$ SD	<i>D</i>
Cluj Napoca	46°46'N, 23°33'E	30	6.7	4.0 $\pm$ 4.2	0.93	0.0	—	—	0.0	—	—
Cojocna	46°44'N, 23°50'E	34	73.5	4.6 $\pm$ 3.3	0.52	2.9	1.0 $\pm$ 0.0	0.94	0.0	—	—
Vama Seacă	46°35'N, 23°93'E	30	13.3	2.5 $\pm$ 3.0	0.90	0.0	—	—	0.0	—	—
Bălcăciu	46°10'N, 24°03'E	30	46.7	3.4 $\pm$ 3.1	0.72	0.0	—	—	0.0	—	—
Agnita	45°58'N, 24°38'E	30	6.7	3.0 $\pm$ 1.4	0.91	0.0	—	—	10.0	12.7 $\pm$ 8.1	0.90
Făgăraș	45°50'N, 25°00'E	30	10.0	2.7 $\pm$ 1.5	0.90	16.7	3.8 $\pm$ 3.1	0.87	10.0	4.3 $\pm$ 1.2	0.88
Independența	44°16'N, 27°09'E	30	0.0	—	—	0.0	—	—	30.0	6.4 $\pm$ 7.5	0.83
Văcăreni	45°19'N, 28°11'E	30	0.0	—	—	13.3	2.8 $\pm$ 1.7	0.88	20.0	9.3 $\pm$ 10.0	0.86
Broșteni	44°40'N, 26°44'E	30	0.0	—	—	0.0	—	—	10.0	3.3 $\pm$ 1.5	0.89
Cornești	44°47'N, 25°52'E	30	0.0	—	—	3.3	2.0 $\pm$ 0.0	0.94	13.3	9.8 $\pm$ 13.5	0.91
Jucu de Jos	46°51'N, 23°46'E	29	96.6	5.4 $\pm$ 4.3	0.40	24.1	8.0 $\pm$ 12.3	0.88	0.0	—	—
Balda	46°44'N, 24°08'E	31	87.1	7.5 $\pm$ 5.8	0.46	12.9	1.8 $\pm$ 1.5	0.88	25.8	3.6 $\pm$ 2.5	0.81
Pinticu	46°57'N, 24°32'E	34	82.4	4.8 $\pm$ 2.1	0.35	17.7	2.0 $\pm$ 1.3	0.85	5.9	1.5 $\pm$ 0.7	0.92
Lechința	47°00'N, 24°19'E	30	0.0	—	—	6.7	6.0 $\pm$ 4.2	0.92	3.3	2.0 $\pm$ 0.0	0.94
Turulung	47°55'N, 23°05'E	32	25.0	7.4 $\pm$ 11.7	0.87	3.1	2.0 $\pm$ 0.0	0.94	3.1	2.0 $\pm$ 0.0	0.94
Petrești	47°60'N, 22°37'E	32	59.4	4.0 $\pm$ 5.3	0.71	12.5	7.0 $\pm$ 7.4	0.91	6.3	1.5 $\pm$ 0.7	0.92

morphological traits were measured to study sexual dimorphism, i.e., total body length and head width (taken at the widest region). For measurements, louse specimens were mounted on a dry microscope slide and a scaled metric background under $\times 80$ magnification. All measurements were taken by the same person (ZB) to reduce error or unintentional, but possible, bias. For measurements, we took digital photographs of the lice, which were transferred into the ImageJ v. 1.37 software (URL: <http://rsb.info.nih.gov/ij/> with Java 1.5.0_09). Sex ratio was expressed as proportion of males, i.e., males/(males + females), and the sexual dimorphism was calculated as the male/female trait value. Note that male lice are usually smaller than females, and thus values less than 1 indicate a smaller relative male size. To analyze the reproductive success of lice, we calculated the number of females in relation to nymphs as females/(females + nymphs).

Prevalence (the proportion of infested hosts among those examined) and mean intensity (the mean number of parasites living on infested hosts) were used to quantify parasite infestations (Bush et al., 1997). Further, we calculated the index of discrepancy (D), which is a measure of parasite aggregation (Poulin, 1993), of the 3 lice species and for each host population. This index varies between 0 and 1, and the value increases with the degree of parasite aggregation. The morphological differentiation of lice between infrapopulations was analyzed by 1-way ANOVA on birds that were infested by at least 2 adult lice of the same species and sex, where the morphological trait was entered as dependent factor, and the infrapopulation (host's identity) was entered as explanatory factor. We used generalized linear mixed effect models (GLMM) with binomial distribution for the prevalence, and Gaussian analysis for sex ratio and sexual dimorphism to analyze factors explaining the variation of these traits. The identity of the host and population was included in the models as random factors, and host sex, lice species, and lice sex as fixed factors. At first, we constructed a full model to which all models with 1 explanatory variable excluded were compared. We evaluated the importance of each variable by pairwise likelihood-ratio-based model comparison. All χ^2 and related P values originate from the likelihood ratio test between the full model and another where the candidate predictor was removed. The higher the χ^2 , the worse the model fit is without the investigated predictor. A χ^2 close to 0 indicates a minor, or no, decrease in model fit, with the removal of the candidate predictor compared to the full model. In the analyses regarding the effect of infrapopulation size on sex ratio of the lice, we used the mean values of the infrapopulations of the same size (see Rózsa et al., 1996) in order to reduce the large variance in sex ratio of small infrapopulations. Note that in case of infrapopulations with only 1 individual, the proportion of males is 0 or 1; however, the mean value can vary between 0 and 1.

All statistical analysis was carried out using the R statistical environment version 2.14.1 (R Development Core Team, 2011), package lme4 (Bates et al., 2011). All graphs are based on uncorrected data for population, host sex, and host identity in order to show the raw values.

RESULTS

General pattern in feather lice distribution and morphological differentiation of infrapopulations

The prevalence of *P. fringillae*, *S. refractariolus*, and *B. cyclothorax* parasitizing the adult house sparrows from the 16 inspected populations was 32.5, 7.1, and 8.5 ($n = 492$), respectively, whereas the mean intensity (95% confidence interval) was 5.1 (4.4–5.9), 4.3 (2.1–6.5), and 6.0 (3.8–8.3) (Table I), respectively. Prevalence significantly differed between lice species (GLMM with binomial distribution; full model: $\ln \text{Lik} = -501.0$, $\text{df} = 6$, lice species: $\ln \text{Lik} = -583.2$, $\chi^2 = 164.4$, $\text{df} = 4$, $P < 0.0001$), whereas male and female house sparrows had similar prevalence ($\ln \text{Lik} = -501.4$, $\chi^2 = 0.7$, $\text{df} = 5$, $P = 0.39$) in a model comparison where the effect of population and host's identity was controlled. The prevalence of *P. fringillae* was significantly higher compared to the 2 other species (*S. refractariolus*: $z = 9.97$, $P < 0.0001$; *B. cyclothorax*: $z = 9.49$, $P < 0.0001$), whereas *S. refractariolus* and *B. cyclothorax* did not differ between each other

($z = 0.87$, $P = 0.39$). The intensity of infestation was also significantly different between lice species (GLMM with Poisson distribution; full model: $\ln \text{Lik} = -260.8$, $\text{df} = 6$, lice species: $\ln \text{Lik} = -264.5$, $\chi^2 = 7.4$, $\text{df} = 4$, $P = 0.02$); a marginally significant difference was found between lice intensities for female and male house sparrows ($\ln \text{Lik} = -262.6$, $\chi^2 = 3.7$, $\text{df} = 5$, $P = 0.06$). The intensity of infestation of the *P. fringillae* was significantly higher compared to *S. refractariolus* ($z = 2.32$, $P = 0.02$), whereas *B. cyclothorax* was similar to the other 2 species (*P. fringillae*: $z = 1.71$, $P = 0.09$; *S. refractariolus*: $z = 0.42$, $P = 0.67$). The mean ($\pm \text{SD}$) of D values of *P. fringillae*, *S. refractariolus*, and *B. cyclothorax* parasitizing the adult house sparrows from the 16 inspected populations were $0.89 (\pm 0.04)$, $0.90 (\pm 0.03)$, and $0.70 (\pm 0.22)$, respectively (Table I). D value differed significantly between the 3 lice species ($F = 7.45$, $\text{df} = 2, 28$, $P < 0.01$); *P. fringillae* and *S. refractariolus* had similar values (Tukey post hoc test: $P = 0.98$), whereas *B. cyclothorax* was significantly more uniformly distributed (had lower D values) than the first 2 species (in both cases $P < 0.01$).

Individual lice were generally more dissimilar between, than within, infrapopulations in the cases of *P. fringillae*, *S. refractariolus*, and *B. cyclothorax* (Table II).

Sex ratio, sexual dimorphism and reproductive success

The number of male and female lice was similar for adult house sparrows infested by *P. fringillae* (Wilcoxon test; $Z = 0.32$, $n = 149$, $P = 0.75$), but with marginally significant female bias in *S. refractariolus* ($Z = 1.94$, $n = 28$, $P = 0.053$) and highly significant female bias in *B. cyclothorax* ($Z = 3.64$, $n = 33$, $P < 0.001$). The sex ratios for the 3 louse species differed significantly and, as expected, the number of males in relation to females was balanced in *P. fringillae*, whereas the proportion of females was the highest in *B. cyclothorax* and intermediate between the 2 species in *S. refractariolus* (Fig. 2; Table III). The sex ratios of the lice did not differ significantly between host populations or host genders.

The sexual dimorphism of the 3 louse species differed significantly (Fig. 3; Table III): male-to-female ratio in total body length was close to equal in *P. fringillae*, and intermediate for *S. refractariolus*, whereas males were smallest compared to females of *B. cyclothorax*. The sexual dimorphism in the head width was similar between the 3 lice species (Table III). The relationship between sex ratio and dimorphism, after controlling for the effect of population and host's sex, was not significant in *P. fringillae* (total length: $F = 0.53$, $\text{df} = 1, 61$, $P = 0.47$; head width: $F = 0.01$, $\text{df} = 1, 61$, $P = 0.91$), *S. refractariolus* (total length: $F = 1.02$, $\text{df} = 1, 3$, $P = 0.39$; head width: $F = 0.45$, $\text{df} = 1, 3$, $P = 0.55$), and *B. cyclothorax* (total length: $F = 5.08$, $\text{df} = 1, 3$, $P = 0.11$; head width: $F = 4.31$, $\text{df} = 1, 3$, $P = 0.13$).

The reproductive rate, measured as the number of nymphs related to the number of females, was similar between the 3 louse species, even after we controlled for the effect of confounding factors (Table III).

Sex ratio, infrapopulation size, and dispersal

The sex ratio of the 3 louse species was similar between host populations (*P. fringillae*: $F = 1.07$, $\text{df} = 10, 144$, $P = 0.39$; *S. refractariolus*: $F = 0.45$, $\text{df} = 8, 20$, $P = 0.87$; *B. cyclothorax*: $F = 1.26$, $\text{df} = 8, 24$, $P = 0.31$; Table III). Therefore, in the subsequent analysis, we pooled the data from different host populations. We

TABLE II. Morphological differentiation of lice between intrapopulations. The statistical values show the results of the 1-way ANOVA analysis on birds, which were infested by at least 2 adult lice of the same species and sex. The values in the first row are mean (mm) $\pm$ SD.

	<i>Philopterus fringillae</i>	<i>Sturnidoecus refractariolus</i>	<i>Brueelia cyclothorax</i>
Male			
Total length	1.47 $\pm$ 0.06, $F = 2.03$, $df = 56,126$, $P < 0.001$	1.14 $\pm$ 0.05, $F = 1.94$, $df = 5,11$, $P = 0.17$	1.30 $\pm$ 0.05, $F = 0.59$, $df = 4,13$, $P = 0.68$
Head width	0.51 $\pm$ 0.03, $F = 1.96$, $df = 56,126$, $P < 0.01$	0.41 $\pm$ 0.02, $F = 0.76$, $df = 5,11$, $P = 0.59$	0.24 $\pm$ 0.01, $F = 0.10$, $df = 4,13$, $P = 0.98$
Female			
Total length	1.70 $\pm$ 0.11, $F = 1.69$, $df = 69,128$, $P < 0.01$	1.44 $\pm$ 0.08, $F = 3.02$, $df = 8,21$, $P < 0.05$	1.63 $\pm$ 0.08, $F = 2.91$, $df = 13,39$, $P < 0.01$
Head width	0.56 $\pm$ 0.03, $F = 1.75$, $df = 69,128$, $P < 0.01$	0.46 $\pm$ 0.02, $F = 5.75$, $df = 8,21$, $P < 0.001$	0.27 $\pm$ 0.01, $F = 2.36$, $df = 13,39$, $P < 0.05$

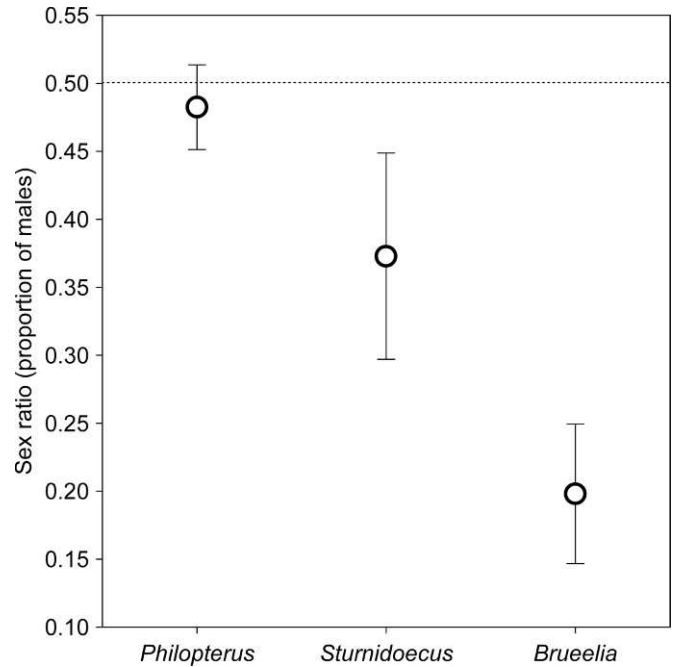


FIGURE 2. The difference between the 3 louse species in sex ratio across populations. For statistical analyses see Table I. Mean $\pm$ SE are shown.

analyzed the relationship between intrapopulation size (averaged for the same-sized intrapopulations; see Rózsa et al. 1996) and sex ratio separately for the 3 louse species. The significant positive association in the case of *P. fringillae* indicates that the larger the size of the intrapopulation, the proportion of males increases (Spearman rank correlation: $r = 0.57$, $n = 19$ intrapopulations of different sizes varying between 1 and 36 individual lice belonging in total to 155 intrapopulations, $P < 0.05$; Fig. 4). This relationship remained significant ($r = 0.72$, $n = 18$, $P < 0.001$) even after the intrapopulation with the lowest sex ratio was omitted from the analysis. We found no significant relationship between intrapopulation size and sex ratio for *S. refractariolus* ($r = 0.09$, $n = 10$ intrapopulations of different sizes varying between 1 to 35 individual lice belonging in total to 29 intrapopulations, $P = 0.80$) and *B. cyclothorax* ($r = 0.29$, $N = 13$ intrapopulations of different sizes varying between 1 and 30 individual lice belonging in total to 33 intrapopulations, $P = 0.34$), which can be explained, however, by the low sample size and the high variance within intrapopulations of similar sizes.

The sex ratio of *P. fringillae* differed between juvenile and adult house sparrows (juvenile: 0.20 ± 0.26 , adult: 0.48 ± 0.37 ; $F = 4.73$, $df = 1,99$, $P < 0.05$), with the relative number of female lice higher on juvenile than adult hosts. The sex ratio of *S. refractariolus* and *B. cyclothorax* on house sparrows belonging to different age classes could not be calculated due to the low sample size of juvenile birds.

DISCUSSION

Here, we showed that the lice intrapopulations parasitizing the house sparrow differed significantly in their size within the 3 ischnoceran species. The sex ratio of lice varied significantly and, as expected, the proportion of sexes was more balanced in *P.*

TABLE III. Likelihood-ratio statistics for models explaining sex ratio, sexual dimorphism and reproductive rate (female-to-nymph ratio) of the 3 lice species parasitizing the house sparrow. The full model is shown in the first row and all other models excluding 1 of the explanatory factors are compared to this. Variables in brackets indicate random factors; all others are fixed. Note that all χ^2 and related P values originate from the likelihood-ratio test between the full model and another where the candidate predictor was removed. The higher the χ^2 , the worse the model fit is without the investigated predictor.

Model	df	Log Lik	χ^2	P
Sex ratio [Model: lice species + host sex + (population) + (host identity)]				
Model	6	-90.3		
Lice species	5	-94.2	7.8	<0.01
Host sex	5	-90.6	0.6	0.44
(Population)	5	-90.3	0.0	1.00
(Host identity)	5	-91.0	1.4	0.23
Total body length dimorphism [model: lice species + host sex + (population) + (host identity)]				
Model	7	97.2		
Lice species	5	91.9	10.6	< 0.01
Host sex	5	97.1	0.2	0.68
(Population)	6	97.2	0.0	1.00
(Host identity)	6	97.2	0.0	1.00
Head width dimorphism [model: lice species + host sex + (population) + (host identity)]				
Model	7	188.2		
Lice species	5	188.1	0.2	0.92
Host sex	5	187.1	2.2	0.13
(Population)	6	188.2	0.0	1.00
(Host identity)	6	188.2	0.0	1.00
Female-to-nymph ratio [model: lice species + host sex + (population) + (host identity)]				
Model	7	-83.1		
Lice species	5	-83.8	1.5	0.48
Host sex	6	-83.4	0.6	0.43
(Population)	6	-83.6	1.0	0.32
(Host identity)	6	-83.4	0.7	0.39

fringillae with the highest prevalence as compared to the less common *S. refractariolus* and *B. cyclothorax*. The balanced sex ratio in the most common species can be explained by the positive effect of high prevalence on outbreeding, which may promote the evolution of an equal sex ratio (Poulin, 1997a; West and Herre, 1998; Pickering et al., 2000; Karvonen et al., 2011; Macke et al., 2011). However, the prevalence of *S. refractariolus* and *B. cyclothorax* was similar, suggesting that factors other than inbreeding through isolation may affect the evolution of the unbalanced sex ratio in lice. The distribution of *B. cyclothorax* between host individuals was more uniform (low index of discrepancy) than in case of *P. fringillae* and *S. refractariolus*, which supports the high mobility-related transmission of the first species and its effect on the homogenous distribution. Because the aggregated distribution of lice may directly affect the mating opportunity (Poulin, 2007), it remains to be tested in future studies if the sex ratio of lice is further affected by the disparity between observed and uniform distribution of these parasites.

Our results show that, at least in the case of *P. fringillae*, the competition for mates can skew the sex ratios between infrapo-

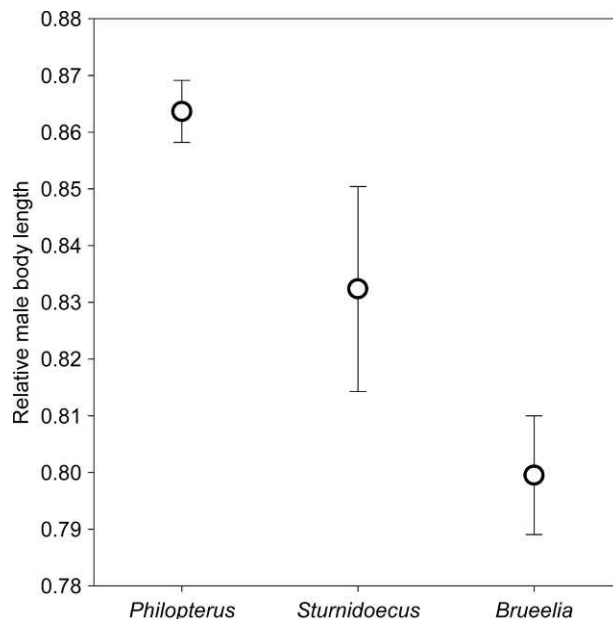


FIGURE 3. The difference between the 3 louse species in sexual dimorphism in the total body length across populations. For statistical analyses see Table I. Mean $\pm$ SE are shown.

pulations, as indicated by the significant positive association between infrapopulation size and the proportion of males. This finding is in line with Hamilton's (1967) local mate competition hypothesis and strongly supports the effect of inbreeding on sex ratio difference between lice species. Our results strengthen the findings of Rózsa (1997) and Rózsa et al. (1996) on the significant positive relationship between the infrapopulation sizes and sex ratios of lice, but contradict data provided by Tryjanowski et al.

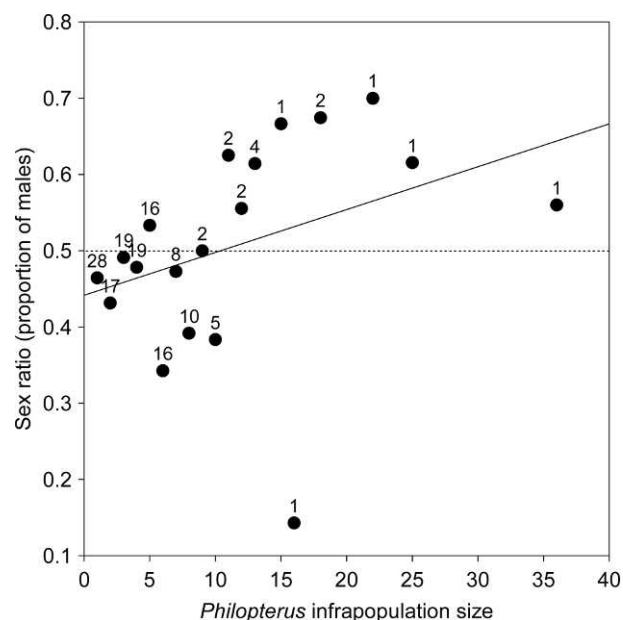


FIGURE 4. The relationship between infrapopulation size and sex ratio in *Philopterus fringillae*. Louse infrapopulations of equal size (the same number of adult lice) were pooled. The values above circles show the number of infrapopulations of the same size which were pooled.

(2009). Further, the increased dispersal of females compared to males, as indicated by the significantly more female biased sex ratio on newly colonized fledged birds compared to adult house sparrows, suggests that the differential dispersal of sexes may further distort the relative number of males on adult birds. It is worth mentioning, however, that we still lack the information regarding the preadult sex ratios, which would further elucidate the mechanism of development of sex ratio in lice, e.g., whether the unbalanced sex ratio develops at egg laying or later during nymphal stages or after maturation. This is a general problem for lice, since the morphological differentiation between sexes develops only in sexually mature adults and the use of molecular techniques for sex determination in this group of parasite is still missing.

The sex ratio of lice varied significantly between species and the sexual dimorphism was decreased in species with unbiased sex ratio. Females are larger than males in most parasite taxa (Poulin, 2007), a phenomenon believed to result from directional positive fecundity selection pressures exerted on female body size. Male–male competition, which can increase male body size, is thought to play an important role in the evolution of sexual size dimorphism; however, our information on parasites is limited (Poulin, 1997b; Dittmar et al., 2011). In case of fewer female-biased species, an intensive sperm competition is likely to select for a larger male body size. This is exactly what we have found in our study, which is consistent with a role for male–male competition in explaining specific deviations from the average ratio of male-to-female body size, suggesting a significant role for sexual selection. The unbalanced sex ratio and sexual dimorphism is a well-known phenomenon in lice (Marshall, 1981; Rózsa et al., 1996; Johnson and Clayton, 2003; Tryjanowski et al., 2007, 2009); however, to our best knowledge, the present study is the first to explore the potential relationship between sex ratio and sexual dimorphism in this group of parasites (but see Tryjanowski et al., 2009).

In conclusion, our results shows that the relative number of males differ between the 3 lice species parasitizing the house sparrow and the sex ratio was more balanced in the most prevalent *P. fringillae* relative to the less common *S. refractariolus* and *B. cyclothorax*. Accordingly, the sexual dimorphism was decreased in species with more intensive sexual competition. Finally, the unbalanced sex ratio in lice can be related to the infrapopulation size, as indicated by the significant positive correlation between the infrapopulation size of *P. fringillae* and the relative number of males. Our results provide a framework for further experimental studies that could further clarify the association between demography, life history, sex ratio, and sexual dimorphism in lice.

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