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Chewing lice of passerine birds in reed beds in Slovakia, with a special focus on *Panurus biarmicus*

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Abstract

A total of 1185 passerine birds representing five species were examined for chewing lice in reed beds in southwestern Slovakia in spring (April) 2008, 2009 and 2016. Additional collecting focused only on chewing lice from *Panurus biarmicus* (Linnaeus, 1758) (Passeriformes: Panuridae) was carried out in spring (April), summer (July) and autumn (October) 2019. A total of 283 (24%) birds were parasitized by 10 species of chewing lice of four genera: *Penenirmus*, *Menacanthus*, *Philopterus*, and *Brueelia*. Most birds showed only very light (1–10 lice/host; 74%) to light infestations (11–20 lice/host; 16%). The authors found significantly higher prevalences and mean abundances of chewing lice on residents/short-distance migrants, that is, *P. biarmicus*, *Acrocephalus melanopogon* (Temminck, 1823) (Passeriformes: Acrocephalidae), than on long-distance migratory birds, that is, *Acrocephalus scirpaceus* (Hermann, 1804), *Acrocephalus schoenobaenus* (Linnaeus, 1758) (Passeriformes: Acrocephalidae), *Locustella luscinioides* (Savi, 1824) (Passeriformes: Locustellidae). No significant difference was found in the total mean intensity of chewing lice between these two groups of birds. Ischnoceran lice were more prevalent and abundant than amblyceran lice on residents and short-distance migrants, whereas the opposite was found on bird species that migrate long distances. A total of 146 (58%, $n = 251$) *P. biarmicus* were parasitized by 1490 chewing lice. Males of *P. biarmicus* showed higher prevalence and mean abundance than females with gradually descending values of prevalence, mean abundance and mean intensity from spring to autumn. The knowledge of the occurrence and population dynamics of lice on wild passerine birds can be useful in endangered species conservation programs and can also be applied to captive passerine birds, which may be analogous to resident birds in this sense.

KEYWORDS
Acrocephalus, ectoparasites, *Menacanthus*, migration, *Panurus biarmicus*, *Penenirmus*, Phthiraptera, sexual dimorphism

INTRODUCTION

Chewing lice (Phthiraptera) are important ectoparasites of domestic and wild birds (Mullen & Durden, 2018). In small passerine birds, individuals with a large number of chewing lice are not attractive to potential partners, due to reduced fitness and damaged feathers (Møller, 1994). Brown et al. (1995) state that ectoparasites, including chewing lice, can also affect the long-term survival of small migratory passerine birds. Different levels of chewing louse infestation on different birds can be explained by body size, sex, age, or behaviour: ability to preen, solitary versus colonial species, resident versus migratory species, etc. (Piross et al., 2020; Price et al., 2003). Here the authors are focusing on a bird community in a wetland dominated by common reeds (*Phragmites australis* (Cav.) Trin. Ex. Steudel; Poaceae). The local avifauna includes both habitat specialists that are breeding in this environment, that is, *Acrocephalus* spp., *Locustella luscinioides* (Savi, 1824) (Passeriformes: Locustellidae), *Panurus biarmicus* (Linnaeus, 1758) (Passeriformes: Panuridae) as well as bird species that only roost in reed stands during both the breeding season and migration, for example, *Hirundo rustica* Linnaeus, 1758 (Passeriformes: Hirundinidae), *Motacilla alba* Linnaeus, 1758 (Passeriformes: Motacillidae), *Sturnus vulgaris* Linnaeus, 1758 (Passeriformes: Sturnidae) (Trnka et al., 2003). Although some of these bird species are commonly caught during mist netting, that is, *Acrocephalus scirpaceus* (Hermann, 1804), *A. schoenobaenus* (Linnaeus, 1758) (Passeriformes: Acrocephalidae), and their ectoparasites are well-known (Per & Aktaş, 2018; Sychra et al., 2008), others such as *A. melanopogon* (Temminck, 1823) (Passeriformes: Acrocephalidae) or *P. biarmicus* are quite rare within their distribution across Europe (Šťastný & Hudec, 2011) and there are only limited data about their ectoparasites (Najer et al., 2020; Ošlejšková et al., 2021).

Different levels of infestation can also be recognized during different periods of the year. Most studies on the population dynamics of lice on wild birds from temperate zones report a significant increase in their numbers during the spring in connection with the beginning of the breeding period of their hosts (Price et al., 2003). Seasonal dynamics might be species-specific for chewing lice. Nevertheless, the relationship between louse population dynamics and the reproductive cycle of their hosts is most likely affected by a number of different factors. One of these factors could be a simple inability to devote sufficient time to comfort behaviour including preening during the period of courtship and breeding season (Price et al., 2003). In general, whenever a bird cannot adequately care for its feathers, not only during reproduction but also, for example, due to illness, beak or leg deformity, the number of lice can increase significantly (Goodman et al., 2020; Loye & Zuk, 1991).

The five target species in our study, *A. melanopogon*, *A. scirpaceus*, *A. schoenobaenus*, *L. luscinioides* and *P. biarmicus* (belonging to the three different families Acrocephalidae, Locustellidae and Panuridae), represent birds of similar body size, feeding and breeding ecology. However, they exhibit different migration strategies: whereas *A. melanopogon* and *P. biarmicus* are resident or short-distance migrants, *A. scirpaceus*, *A. schoenobaenus* and *L. luscinioides* represent long-distance migrants commonly wintering in sub-Saharan Africa (Cepák et al., 2008), and only *P. biarmicus* displays strong sexual dimorphism in colour (Shirihai & Svensson, 2018). All the above-mentioned species are habitat specialists inhabiting reed beds and all of them belong to the most abundant passerines of the study site (Kloubec & Čapek, 2005; Trnka et al., 2003).

The aims of this paper are: (1) to present data on the species distribution of chewing lice found on passerine birds in reed beds; (2) to include data on their infestation characteristics in relation to their migration behaviour; and (3) to evaluate the impact of sexual dimorphism of *P. biarmicus* on the occurrence of chewing lice during three periods of the year.

MATERIALS AND METHODS

Passerines were captured by mist-netting in reed beds of the National Nature Reserve Parížske močiare Marsh located near the villages of Gbelce and Nová Vieska (47°52′N, 18°30′E) in southwestern Slovakia (for more details on habitat see Kloubec & Čapek, 2005). Birds were examined in spring (April) 2008, 2009 and 2016. Additional collecting focused only on chewing lice from *P. biarmicus* was carried out in spring (April), summer (July) and autumn (October) 2019. Data about lice from *P. biarmicus* from 2019 are not included in the overall evaluation of infestation characteristics concerning birds from the pre-breeding period. On the other hand, for evaluation of the seasonal occurrence of lice on *P. biarmicus*, data from spring 2008, 2009, 2016 and 2019 are pooled together. Lice were collected by the fumigation chamber method, with chloroform as a fumigant (Clayton & Drown, 2001) and accompanied by a visual examination of the head when the authors also noted the presence or absence of louse eggs. Birds were released after examination. Lice were stored in 96% ethanol and subsequently slide-mounted following the technique by Palma (1978).

Infestation characteristics were determined by Sychra et al. (2011). For purposes of statistical analysis, the authors divided the five target passerine species into two groups according to their migration strategy (Cepák et al., 2008): residents/short-distance migrants (R/SDMs—*P. biarmicus*, *A. melanopogon*), and long-distance migrants (LDMs—*A. scirpaceus*, *A. schoenobaenus*, *L. luscinioides*). To designate the infestation on passerine hosts the authors used categories of infestation according to Ošlejšková et al. (2020) (see also Table S2). For statistical analyses, Fisher's exact test (for prevalences) and bootstrap 2-sample t-test (for intensities and abundances) were used. Calculations were made in Quantitative Parasitology 3.0 (Rózsa et al., 2000).

RESULTS

Chewing lice of wild passerines in reed beds

A total of 1185 wild birds representing five species belonging to three families were examined for chewing lice in spring of 2008, 2009 and 2016. A total of 283 (24%) birds were parasitized by six species of chewing lice and four louse taxa identified only to genus level (Table S1). Most birds (90%, $n = 377$ including *P. biarmicus* examined in 2019) showed only very light (1–10 lice/host; 74%) to light infestations (11–20 lice/host; 16%; Table S2). Heavy infestations were found on two *P. biarmicus* parasitized by 71 and 61 individuals of *Penenirmus visendus* (Złotorzycka, 1964) (Phthiraptera: Philopteridae) and one *A. schoenobaenus* parasitized by 64 individuals of *Menacanthus curuccae* (Schrank, 1776) (Phthiraptera: Menoponidae). Some birds that had

TABLE 1 Infestation characteristics of chewing lice collected from resident and migrating birds during the pre-breeding period in spring (April) in reed beds in southwestern Slovakia

	Residents/short-distance migrants (n = 114)[a]			Long-distance migrants (n = 906)[b]		
	Total	Amblycera	Ischnocera	Total	Amblycera	Ischnocera
Prevalence (%) (95% C.I.)	82.5* (74.2–88.7)	2.6 (0.7–7.3)	82.5* (74.2–88.7)	11.5 (9.5–13.7)	10.2* (8.3–12.3)	1.9 (1.1–3.0)
Mean abundance (95% C.I.)	8.0* (6.4–10.5)	0.04 (0.0–0.09)	8.0* (6.3–10.4)	0.8 (0.6–1.1)	0.7* (0.5–1.0)	0.1 (0.04–0.3)
Mean intensity (95% C.I.)	9.8 (7.8–12.5)	1.3 (1.0–1.7)	9.7* (7.9–12.6)	7.1 (5.5–9.4)	7.0 (5.3–9.5)	6.0(2.2–13.2)
Percentage of male lice[c]	50.0 (318)	0 (3)	50.5 (315)	22.4 (192)	21.8 (170)	27.3 (22)
Percentage of adult lice[d]	34.7 (916)	100 (3)	34.5 (913)	20.7 (927)	20.2 (840)	25.3 (87)

Abbreviation: C.I., confidence interval.
*Statistically significantly higher value ($p < 0.05$).
[a]*A. melanopogon*, *P. biarmicus*.
[b]*A. scirpaceus*, *A. schoenobaenus*, *L. luscinioides*.
[c]Number of adult lice is in parenthesis.
[d]Number of lice for which age was assessed is in parenthesis.

been trapped infested had later been retrapped and found to be uninfested and vice versa (Table S3). All examined and infested birds were apparently in good condition, well-coloured, and without visible injury, or deformation of the bill or legs.

On most birds (93%, n = 283), only one species of chewing louse was found. In all 19 cases of co-occurrence of two species of lice, one amblyceran and one ischnoceran louse species were recorded. Dominance among the four genera of lice is ranked as follows: *Penenirmus* (45%, n = 1670), *Menacanthus* (39%), *Philopterus* (10%), and *Brueelia* (6%).

The authors found significantly higher total prevalence and mean abundance of chewing lice on R/SDMs than on LDMs (Table 1). Prevalence and mean abundance on R/SDMs ranged from 65% to 100% and from 3.7 to 10, respectively; whereas on LDMs ranged from 2% to 33% and from 0.08 to 2.6, respectively (Table S1). On the other hand, no significant difference was found in the total mean intensity of chewing lice between these two groups of birds (Table 1). The mean intensity of R/SDMs and LDMs ranged from 4.4 to 14.5 and from 4.0 to 13.3, respectively (Table S1).

Moreover, ischnoceran lice were more prevalent and abundant than amblycerans on the R/SDMs, whereas the opposite was found on LDMs (Table 1). No significant difference was found in the mean intensity of amblyceran and ischnoceran lice on LDMs whereas the mean intensity of ischnoceran lice on R/SDMs was significantly much higher than those of amblycerans and comparable with those of both groups of lice on LDMs (Table 1). The overall sex ratio of lice on five dominant bird species breeding in reed beds was female-biased (male: female = 1:1.5; n = 510; $\chi^2 = 22$, $p < 0.05$). The overall age ratio of lice on these birds was immature-biased (adults:immatures = 1:2.6; n = 1843; $\chi^2 = 367$, $p < 0.05$). The sex ratio of lice was equal for R/SDMs (male:female = 1:1; n = 318; $\chi^2 = 0$, $p > 0.05$) but female-biased for LDMs (male:female = 1:3.5; n = 192; $\chi^2 = 58$, $p < 0.05$). The age ratio of lice was immature-biased in both R/SDMs (adults: immatures = 1:1.9; n = 916; $\chi^2 = 85$, $p < 0.05$) as well as LDMs (adults:immatures = 1:3.8; n = 927; $\chi^2 = 318$, $p < 0.05$; Table 1).

Chewing lice of the P. biarmicus

A total of 146 (58%, n = 251) *P. biarmicus* were parasitized by 1490 chewing lice of two species: 1461 *Penenirmus visendus* and 29 *Menacanthus* sp. (Table S1). Infestation characteristics of the dominant species, *Penenirmus visendus*, are presented in Table 2. *Menacanthus* sp. has been collected from 14 birds, all these hosts harboured a *Penenirmus* as well. Most birds (88%, n = 146) showed only very light (1–10 lice/host; 65.8%) to light infestations (11–20 lice/host; 21.9%; Table S2). Heavy infestations were found on two males, one with 71 and 61 lice in spring and autumn, respectively. These two males were apparently in good condition, coloured like to other males examined without visible injury, or deformation of the bill or legs.

When comparing the infestation characteristics in the individual seasons (spring–summer–autumn), a successively decreasing trend was found for prevalence and mean abundance. A difference in mean intensity was found only between spring and summer (Table 2). The authors found also different prevalences of louse eggs occurrence, with the significantly highest prevalence in summer ($p < 0.05$; Table 2). The authors found no lice on 13 birds with louse eggs in summer. Eggs were located on the head; on the males, eggs were mostly found on the bases of black feathers of the "beard".

Male birds showed a higher overall prevalence and mean abundance of lice than females (Table 2). During different seasons this difference was confirmed only in spring. There were no significant differences between males and females in other infestation characteristics in other seasons, including overall mean intensity and prevalence of louse eggs. The overall sex ratio of *P. visendus* was equal (male:female = 1:1.1; n = 447; $\chi^2 = 1.6$, $p > 0.05$). The overall age ratio of *P. visendus* was immature-biased (adults:immatures = 1:2.3; n = 1461; $\chi^2 = 220$, $p < 0.05$). The sex ratio of *P. visendus* was equal and the age ratio of lice was immature-biased (adults:immatures = 1:2) on both males and females in all evaluated periods (Table 2).

TABLE 2 Occurrence of *Penenirmus visendus* on females and males of *Panurus biarmicus* in different seasons of the year in reed beds in southwestern Slovakia

	Spring (April)	(95% C.I.)	Summer (July)	(95% C.I.)	Autumn (October)	(95% C.I.)	Total	(95% C.I.)
Examined (females/ males)	95 (32/61)[a]		76 (32/44)		80 (37/43)		251 (101/148)[a]	
Parasitized (females/ males)	75 (23/50)[a]		46 (18/28)		25 (10/15)		146 (51/93)[a]	
Number of lice (on females/ males of the host)	906 (199/675)[a]		388 (137/251)		167 (71/96)		1461 (407/1022)[a]	
Prevalence of lice (%)	78.9	(69.6–86.4)	60.5[b]	(48.7–71.2)	31.3[b,c]	(21.8–42.5)	58.2	(51.8–64.2)
Females	71.9	(53.8–84.8)	56.3	(39.0–72.2)	27[b,c]	(14.4–43.2)	50.5	(40.6–60.4)
Males	82.0	(70.1–90.0)	63.6[b]	(48.5–76.6)	34.9[b,c]	(21.9–50.0)	62.8[d]	(54.7–70.3)
Prevalence of louse eggs (%)	14.7[c]	(8.8–23.6)	77.6	(66.5–85.7)	10.0[c]	(4.7–18.6)	32.3	(26.7–38.4)
Females	6.3[c]	(1.1–20.0)	75.0	(57.7–87.8)	5.4[c]	(1.0–18.5)	27.7	(19.7–37.6)
Males	19.7[c]	(11.2–31.8)	79.5	(64.9–89.2)	14.0[c]	(6.3–27.7)	35.8	(28.3–43.9)
Mean abundance	9.5	(7.4–12.6)	5.1[b]	(6.7–10.5)	2.1[b,c]	(0.8–5.3)	5.8	(4.8–7.4)
Females	6.2	(3.8–9.9)	4.3	(2.5–6.5)	1.9[b]	(0.5–6.2)	4.0	(3.0–5.9)
Males	11.1[d]	(8.0–15.4)	5.7[b]	(3.9–7.8)	2.2[b]	(0.6–8.2)	6.9[d]	(5.4–9.2)
Mean intensity	12.1	(9.6–15.7)	8.4[b]	(6.7–10.5)	6.7	(2.6–16.0)	10.0	(8.5–12.4)
Females	8.7	(5.6–13.0)	7.6	(4.9–10.7)	7.1	(2.0–20.7)	8.0	(6.1–10.9)
Males	13.5	(10.0–18.2)	9.0	(6.8–11.6)	6.4	(2.0–19.6)	11.0	(9.0–14.5)
Percentage of male lice (females/ males)	50 (43/51)		44 (51/41)		40 (38/42)		47 (45/47)	
Percentage of adult lice (females/ males)	29 (33/29)		34 (27/37)		30 (37/25)		31 (31/30)	

Abbreviation: C.I., confidence interval.
[a]Sex was not noted for two birds that were infested in total by 32 lice.
[b]Significantly lower value than that from spring ($p < 0.05$).
[c]Significantly lower value than that from summer ($p < 0.05$).
[d]Significant difference between females and males ($p < 0.05$).

DISCUSSION

To our knowledge, this is the first comprehensive study focused on chewing lice on passerines breeding in reed beds. Similarly to Sychra et al. (2011) and Literák et al. (2015), the authors found significantly higher values of prevalence and mean abundance of chewing lice on resident or short-distance migrants compared to those for long-distance migrants. The main factors that could explain these differences are the population cycles of lice and the fact of bird migration. In April, when the spring sampling was conducted, most of the resident or short-distance migratory species of passerine birds in reed beds are already breeding (Šťastný & Hudec, 2011). Sychra et al. (2011) hypothesized that the increase in lice abundance comes earlier in such bird species than in species that migrate long distances because the latter is only arriving at their breeding sites during that time (Cepák et al., 2008; Šťastný & Hudec, 2011). The increase in lice population in spring may be affected by the reproductive hormones of their hosts, deficiency of time needed for effective preening during breeding (Price et al., 2003), or photoperiod, especially in the case of resident temperate birds (Perrins, 1970).

Impact of avian reproductive hormones on the population cycles of lice is assumed mainly in hematophagous lice such as *Menacanthus* (Foster, 1969). On the other hand, hormones, including testosterone, and the seasonal changes in their concentrations are detectable also in feathers (Adámková et al., 2019). Males of *Hirundo rustica* concentrations of feather testosterone were higher in the prebreeding period compared to the postbreeding period. Therefore it is possible that feather-eating lice such as *Penenirmus* could also be affected in some way by these hormones, especially if they feed on feathers that moult at different times of the year, and thus may reflect the dynamics of hormone levels during the annual cycle.

The assumption that birds during the breeding period birds spend more time in epigamic and territorial behaviour and behaviour connected with nesting at the expense of comfort behaviour is widely accepted. The evidence for this assumption is not conclusive in the literature. Cotgreave and Clayton (1994) did not confirm the impact of season on maintenance time. However, they had only limited data from which they reported that six of nine species of birds for which data were available for both breeding and non-breeding seasons spent more time on comfort behaviour during the non-breeding period than during the breeding period. There are probably differences between species and also the sex of particular species. For example, Kopij (1998) found that males of *Geronticus eremita* (Linnaeus, 1758) (Pelecaniformes: Threskiornithidae) spent 23.3% of time preening during the non-breeding season and only 2.5% in the breeding season, whereas females spent equally 4.9% and 8.6% of time by preening in the non-breeding and breeding season, respectively. Conversely, Metzmacher (1990) reported that for females of *Passer hispaniolensis* (Temminck, 1820) (Passeriformes: Passeridae) preening decreased during incubation, whereas for males the length of this activity did not appear to fluctuate during breeding the period. Not only species or sex, but also the personality of a particular individual can play an important role in parasite–host interactions. Clayton (1990) discussed the phenomenon of social facilitation of preening. In his experiment pairs of males of *Columba livia* Gmelin, 1789 (Columbiformes: Columbidae) (one with and one without lice) competed for females. He found no difference in the preening rates of these males, so he concluded that the competition between these males overwhelmed any differences in their preening rates.

Photoperiod is known to significantly affect the timing of insect life cycles (Saunders, 2008; Tauber et al., 1986). There is no apparent reason for photoperiodism in parasitic lice, which are permanently on the body of their hosts and reproduce continuously, having several generations throughout the year. Moreover, Kotwica-Rolinska et al. (2022) found that parasitic lice lost several circadian clock genes involved in insect photoperiodism. On the other hand, the same authors described similar gene losses in *Pyrrhocoris apterus* (Linnaeus, 1758) (Hemiptera: Pyrrhocoridae) in which the clock has remained functional. As suggested by Srivastava et al. (2003), Saxena et al. (2004) and Singh et al. (2009), photoperiod could play some role also for seasonal changes in populations of chewing lice. More research is necessary to resolve the impact of photoperiod on parasitic lice.

Our results suggest that there could be different life strategies or abilities to survive on resident bird species or short-distance migrants and long-distance migrants between ischnoceran and amblyceran lice. This fact can be greatly affected by the host and evolution of host–parasite associations, including the ability to colonize new hosts and also by the environmental conditions not only in the breeding area but also in wintering grounds. The authors found ischnoceran feather lice more prevalent and abundant than amblyceran lice on resident species and short-distance migrants, whereas the opposite was found on long-distance migrants. Amblyceran louse species included in our study represent host generalists. They are agile lice moving quickly across the skin of their hosts, allowing them to easily colonize new hosts (Price et al., 2003). As shown by Martinů et al. (2015), such generalists have lower genetic diversity that is probably maintained by the ability of these lice to disperse among the related and unrelated hosts in both breeding and wintering areas. Literák et al. (2015) confirmed that differences in chewing louse load on resident and migratory birds can also be found within populations of single species of a host with different migration strategies. Closely related taxa with different migration strategies are known also for certain passerines from reed beds (e.g., *A. scirpaceus* vs. *Acropcephalus baeticatus* (Vieillot, 1817) (Passeriformes: Acrocephalidae); del Hoyo et al., 2006). In these cases, migratory birds can meet resident ones on wintering grounds, where these birds can serve as a source of chewing lice. To confirm such a scenario, additional data collected from both resident populations of commonly migrating birds and wintering grounds are needed.

Chewing lice usually occur within the entire range of their hosts (Price et al., 2003). On the other hand, parasite fauna and infestation characteristics can differ between populations of the same host, especially in birds with a large area of distribution (Bush et al., 2009). Differences between chewing lice fauna on different hosts may be due to sorting events such as "missing the boat" "drowning on arrival" (Paterson et al., 1999), or "lost overboard" (MacLeod et al., 2010). A strong impact of ambient humidity and the ability of different louse genera to adapt to different climates are probably responsible for differences in the distribution of louse species on the same host in different parts of its range (Bush et al., 2009; Carrillo et al., 2007; Takano et al., 2018). In general, "humid-adapted" *Guimaraesiella* (Ischnocera) and *Myrsidea* (Amblycera) are abundantly occurring mainly in more humid areas whereas "arid-adapted" *Brueelia* (Ischnocera) and "humidity-indifferent" *Menacanthus* (Amblycera) and *Philopterus* (Ischnocera) can be adapted also to drier areas.

In addition to the local distribution of lice, infestation characteristics can also vary from year to year. The authors documented that some uninfested birds had later been retrapped and found to be infested and vice versa (Table S3). Because not all lice may be captured by the method used (Clayton & Drown, 2001) the authors cannot absolutely eliminate the possibility that some lice had been overlooked during the collection process. On the other hand, the authors found no lice on birds with louse eggs, despite having examined these birds more carefully when the authors the authors found these eggs. In some species of chewing lice, it has been reported that they wait out the period of host migration in the egg stage

(Marshall, 1981). Such an "uninfested" bird can later serve as a "reservoir" and other birds can be colonized by lice from this individual. For example in the case of *P. biarmicus*, horizontal transmission is also possible in the non-breeding period in communal roosting places where individuals cluster in close contact (Cramp & Perrins, 1993). The authors believe that similar parallels can be found not only in other wild birds (Sychra et al., 2011) but also in exotic birds in aviaries, where these parasites can then be easily overlooked and can thus survive for a long time and colonize new hosts (Sychra, 2006).

Focusing on *P. biarmicus*, males showed higher overall prevalence and mean abundance of lice than females with successively descending values of prevalence, mean abundance and mean intensity from spring to autumn. On the other hand, there was almost no significant difference in parasite load between males and females in a particular season of the year. It may be due to only a slightly different size. Males of *P. biarmicus* are only slightly larger than females (Šťastný & Hudec, 2011). These small differences may also be due to the social behaviour of the *P. biarmicus* which breeds mainly in individual pairs or smaller colonies (Šťastný & Hudec, 2011). *Panurus biarmicus* thus differs from other birds, in which males show different types of courtship displays and mate with a larger number of females. In these bird species, a significantly higher parasitization was recorded in males (Price et al., 2003; Sychra et al., 2010). Colour dimorphism may also play a role in the occurrence of lice (Loye & Zuk, 1991; Potti & Merino, 1995), but according to our results in the case of *P. biarmicus*, it is probably not important.

Panurus biarmicus represents a resident bird species moving only on a relatively short distance (Cepák et al., 2008). As shown by Sychra et al. (2011) and Literák et al. (2015), resident birds usually have quite a high prevalence of chewing lice. The higher infestation of *P. biarmicus* may also be due to the social behaviour of this bird species. A higher prevalence of lice is known for social birds that nest in colonies or congregate in larger flocks (Rózsa et al., 1996). *Panurus biarmicus* is socially monogamous, with a large number of pairs often nesting in groups (even up to 3–4 nests 20–30 cm apart; Šťastný & Hudec, 2011). Couples are faithful even for several seasons when the cohesion of the couple was recorded even in the post-breeding period (Griggio & Hoi, 2011). However, extra-pair copulations and intraspecific nest parasitism have also been found in the colonies (Hoi & Hoi-Leitner, 1997). This information also fits the data about the higher prevalence of chewing lice infestation and also about the fact that both sexes are roughly equally parasitized.

CONCLUSION

Bird communities in reed beds include species of similar body size, feeding and breeding ecology, but with different migration strategies. Our study has shown that bird migration can be one of the factors affecting louse abundance. Despite showing higher louse infestation in general, this presence of chewing lice on resident birds probably need not be such a burden in comparison to migrating birds, for whom any handicap could mean a significant loss of energy. A difference in louse abundance can be also affected by the social behaviour of their hosts, which can explain only slight differences found in louse load between males and females of *P. biarmicus*. Due to population dynamics, the louse abundance gradually descended from spring to autumn. Therefore, spring is probably the crucial season for colonization of new hosts by lice. The knowledge of the occurrence and population dynamics of lice on wild passerine birds can be useful in endangered species conservation programs and can also be applied to captive passerine birds, which may be analogous to resident birds in this sense.

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CONFLICT OF INTEREST

The authors declare that they do not have any conflict of interest. The authors confirm that there are no disputes over the ownership of the data presented in the paper and all contributions have been attributed appropriately, via co-authorship.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. List of hosts and their chewing lice for five target species occurring in reed beds in southwestern Slovakia: two residents/short-distance migrants (*Acrocephalus melanopogon*, *Panurus biarmicus*) and three long-distance migrants (*Acrocephalus scirpaceus*, *Acrocephalus schoenobaenus*, *Locustella luscinioides*). A = Amblycera: Menoponidae; I = Ischnocera: Philopteridae.

Table S2. Proportion of birds (%) in reed beds in southwestern Slovakia with a particular category of infestation of all chewing lice species combined on all parasitized birds during pre-breeding spring migration in April ($n = 377$), and also separately for *Penenirmus visendus* on parasitized target species *Panurus biarmicus* ($n = 146$).

Table S3. List of individual retrapped birds examined in reed beds in southwestern Slovakia in two different periods and their chewing lice.

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Supplementary Table S1. List of hosts and their chewing lice for five target species occurring in reed beds in southwestern Slovakia: two residents/short-distance migrants (*Acrocephalus melanopogon*, *Panurus biarmicus*) and three long-distance migrants (*Acrocephalus scirpaceus*, *Acrocephalus schoenobaenus*, *Locustella luscinioides*). A = Amblycera: Menoponidae; I = Ischnocera: Philopteridae.

Bird species **Chewing louse family/species**	prevalence				mean abundance				mean intensity			
	2008	2009	2016	**total**	2008	2009	2016	**total**	2008	2009	2016	**total**
Panurus biarmicus	n=39	n=34	n=13	**n=86**								
A/*Menacanthus* sp.	0	5.9	7.7		0	0.1	0.1		0	1.5	1.0	
I/*Penenirmus visendus*	84.6	64.7	84.6		10.0	9.3	3.6		11.8	14.4	4.3	
Total	84.6	64.7	84.6	**76.7**	10.0	9.4	3.7	**8.8**	11.8	14.5	4.4	**11.5**
Acrocephalus melanopogon	n=11	n=9	n=8	**n=28**								
I/*Philopterus acrocephalus*	100	100	100	**100**	6.0	5.1	5.8	**5.6**	6.0	5.1	5.8	**5.6**
residents/short-distance migrants	88.0	72.1	90.5	**82.5**	9.1	8.5	4.5	**8.0**	10.4	11.8	4.9	**9.8**
Acrocephalus scirpaceus	n=235	n=149	n=49	**n=433**								
A/*Menacanthus curuccae*	7.7	18.1	2.0		0.4	1.0	0.1		5.1	5.6	4.0	
I/*Brueelia* sp.	0.9	2.0	0		0.03	0.03	0		3.0	1.3	0.0	
I/*Philopterus* sp.	0.4	0.7	0		0.004	0.01	0		1.0	1.0	0	
Total	8.9	19.5	2.0	**11.8**	0.4	1.0	0.08	**0.6**	4.7	5.3	4.0	**5.1**
Acrocephalus schoenobaenus	n=284	n=51	n=28	**n=363**								
A/*Menacanthus curuccae*	6.3	17.6	0		0.7	2.3	0		10.5	13.2	0	
I/*Brueelia vaneki*	1.1	3.9	0		0.01	0.3	0		1.0	6.5	0	
I/*Philopterus* sp.	0	2.0	0		0	0.02	0		0	1.0	0	
Total	7.4	19.6	0	**8.5**	0.7	2.6	0	**0.9**	9.1	13.3	0	**10.5**
Locustella luscinioides	n=49	n=52	n=9	**n=110**								
A/*Menacanthus obrteli*	22.4	11.5	22.2		0.7	0.8	1.2		3.2	6.7	5.5	
I/*Brueelia locustellae*	4.1	1.9	11.1		0.8	0.6	0.1		20.5	31.0	1.0	
Total	24.5	13.5	33.3	**20.0**	1.6	1.4	1.3	**1.4**	6.3	10.1	4.0	**7.2**
long-distance migrants	9.5	18.3	4.7	**11.5**	0.6	1.4	0.2	**0.8**	6.8	7.8	4.0	**7.1**

Supplementary Table S2. Proportion of birds (%) in reed beds in southwestern Slovakia with a particular category of infestation of all chewing lice species combined on all parasitized birds during pre-breeding spring migration in April (n = 377), and also separately for *Penenirmus visendus* on parasitized target species *Panurus biarmicus* (n = 146).

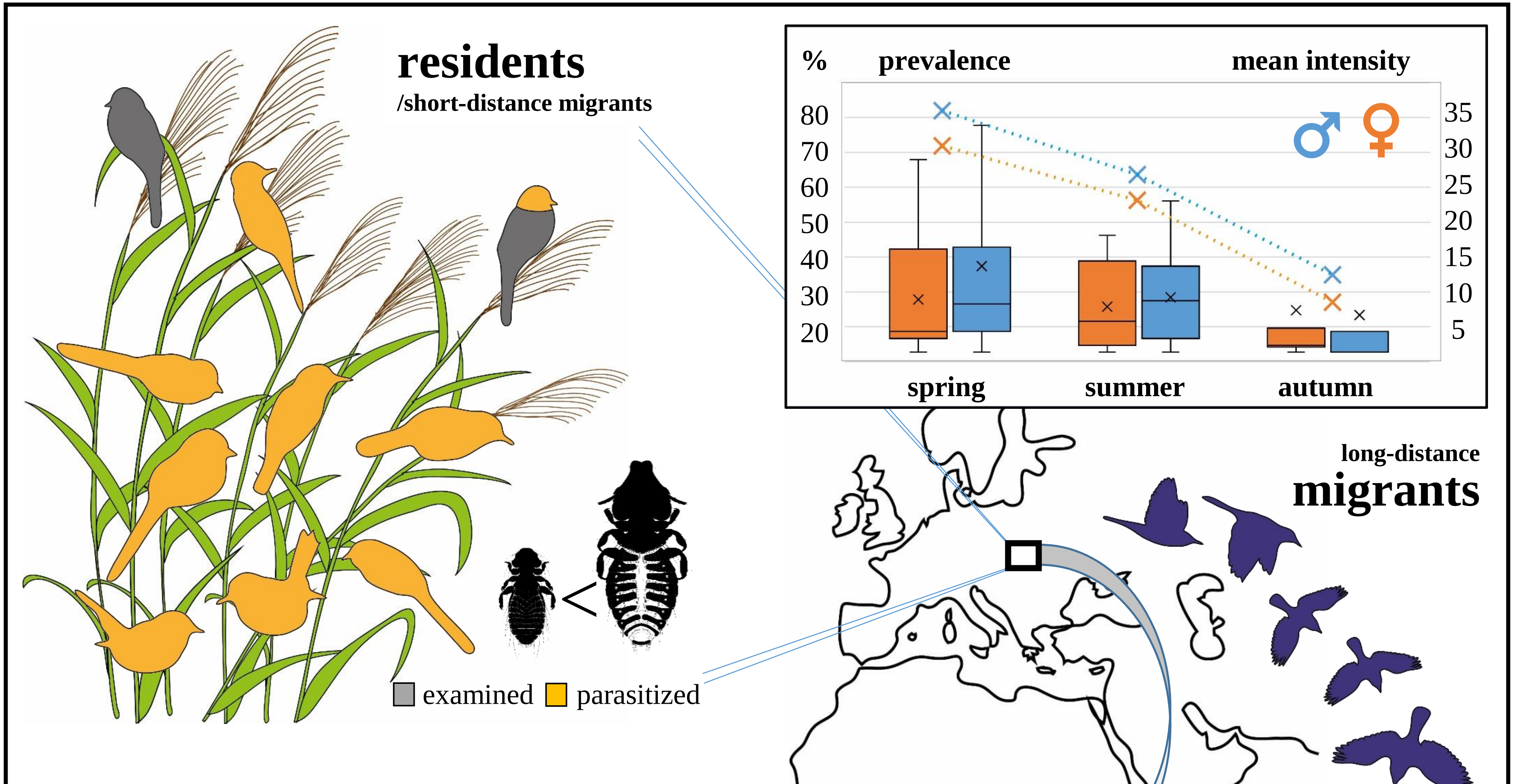
	All chewing louse species on all host species*	*Penenirmus visendus* on *Panurus biarmicus**		
	(n=283)	Total (n=146)	Female (n=51)	Male (n=93)
very light infestation (1–10 lice/host)	74.2	65.8	70.6	64.5
light infestation (11–20 lice/host)	16.3	21.9	19.6	21.5
medium infestation (21–30 lice/host)	4.2	6.2	7.8	5.4
heavy infestation (31–50 lice/host)	4.2	4.8	2.0	6.5
very heavy infestation (51–100 lice/host)	1.1	1.4	–	2.2

* = sex was not noted for two birds

Supplementary Table S3. List of individual retrapped birds examined in reed beds in southwestern Slovakia in two different periods and their chewing lice.

host / ring number	the first trap	chewing louse	retrap	chewing louse
Acrocephalus melanopogon				
S013921	14 April 2008	*Philopterus* (7 ex)	30 April 2009	*Philopterus* (10 ex)
S126012	19 April 2008	*Philopterus* (2 ex)	18 April 2009	*Philopterus* (6 ex)
Acrocephalus scirpaceus				
S068237	12 April 2008	–	20 April 2009	–
S013943	15 April 2008	–	19 April 2009	*Menacanthus* (30 ex)
S034279	15 April 2008	–	20 April 2009	–
S013405	17 April 2008	*Menacanthus* (4 ex)	27 April 2009	–
S126004	18 April 2008	*Menacanthus* (2 ex)	24 April 2009	–
S126040	21 April 2008	–	21 April 2009	–
S126069	22 April 2008	*Menacanthus* (4 ex)	28 April 2009	–
S126121	23 April 2008	–	22 April 2009	–
S126144	23 April 2008	–	29 April 2009	–
S126170	24 April 2008	–	29 April 2009	–
S074228	25 April 2008	–	22 April 2009	*Menacanthus* (1 ex)
S126221	25 April 2008	–	27 April 2009	–
S126307	29 April 2008	*Menacanthus* (2 ex)	22 April 2009	–
S126378	30 April 2008	–	20 April 2009	–
Locustella luscinioides				
S013899	13 April 2008	–	19 April 2009	*Brueelia* (31 ex)
S126209	25 April 2008	*Menacanthus* (6 ex)	21 April 2009	–
S068165	30 April 2008	–	19 April 2009	–
Panurus biarmicus				
S224021	9 July 2019	–	1 October 2019	–
S224036	9 July 2019	–	1 October 2019	*Penenirmus* (4 ex)
S224070	9 July 2019	*Penenirmus* (18 ex)	2 October 2019	–
S224132	10 July 2019	*Penenirmus* (12 ex)	2 October 2019	*Penenirmus* (11 ex)
S224136	10 July 2019	*Penenirmus* (3 ex)	2 October 2019	–
		Menacanthus (1 ex)		
S224154	10 July 2019	–	2 October 2019	–

ex = exemplars



- Significantly higher prevalences of chewing lice was found on residents/short-distance migrants, compared to long-distance migratory birds.
- Ischnoceran lice were more prevalent and abundant than amblyceran lice on residents and short-distance migrants, while the opposite was found on bird species that migrate long distances.
- Males and females of *Panurus biarmicus* showed only slight differences in lice load. Infestation characteristics (prevalence and louse abundance) gradually descended from spring to autumn.