Parasitology International 66 (2017) 699–706

Contents lists available at ScienceDirect

Parasitology International

journal homepage: www.elsevier.com/locate/parint

Chewing lice from wild birds in northern Greece

Anastasia Diakou[a,1], José Bernardo Pedroso Couto Soares[b,1], Haralambos Alivizatos[c], Maria Panagiotopoulou[d], Savas Kazantzidis[e], Ivan Literák[b], Oldřich Sychra[b,*]

[a] Laboratory of Parasitology and Parasitic Diseases, School of Veterinary Medicine, Faculty of Health Sciences, Aristotle University of Thessaloniki, Thessaloniki, Greece
[b] Department of Biology and Wildlife Diseases, Faculty of Veterinary Hygiene and Ecology, University of Veterinary and Pharmaceutical Sciences Brno, Czech Republic
[c] Hellenic Bird Ringing Center, Athens, Greece
[d] Frangini Str. 9, Thessaloniki, Greece
[e] Forest Research Institute, Hellenic Agricultural Organization "DEMETER", Thessaloniki, Greece

A R T I C L E I N F O

Keywords:
Chewing lice
Phthiraptera
Amblycera
Ischnocera
Wild passerine birds
Greece
Mediterranean area

A B S T R A C T

Greece represents an important area for wild birds due to its geographical position and habitat diversity. Although the bird species in Greece are well recorded, the information about the chewing lice that infest them is practically non-existent. Thus, the aim of the present study was to record the species of lice infesting wild birds in northern Greece and furthermore, to associate the infestation prevalence with factors such as the age, sex, migration and social behaviour of the host as well as the time of the year. In total 729 birds, (belonging to 9 orders, 32 families and 68 species) were examined in 7 localities of northern Greece, during 9 ringing sessions from June 2013 until October 2015. Eighty (11%) of the birds were found to be infested with lice. In 31 different bird species, 560 specimens of lice, belonging to 33 species were recorded. Mixed infestations were recorded in 11 cases where birds were infested with 2–3 different lice species. Four new host-parasite associations were recorded *i.e. Menacanthus curuccae* from *Acrocephalus melanopogon*, *Menacanthus agilis* from *Cettia cetti*, *Myrsidea* sp. from *Acrocephalus schoenobaenus*, and *Philopretus citrinellae* from *Spinus spinus*. Moreover, *Menacanthus sinuatus* was detected on *Poecile lugubris,* rendering this report the first record of louse infestation in this bird species. The statistical analysis of the data collected showed no association between parasitological parameters (prevalence, mean and median intensity and mean abundance) in two different periods of the year (breeding *vs* post-breeding season). However, there was a statistically significant difference in the prevalence of infestation between a) migrating and sedentary passerine birds (7.4% *vs* 13.2%), b) colonial and territorial birds (54.5% *vs* 9.6%), and c) female and male birds in breeding period (2.6% *vs* 15.6%).

1. Introduction

Chewing lice are ectoparasites of birds and mammals, belonging to three suborders (Amblycera, Ischnocera and Rhynchophthirina) of the order Phthiraptera. They are obligate, permanent parasites, having all of their life cycle stages (egg, three nymphal stages and adult) adapted on a single host [1]. Although chewing lice are generally considered parasites of minor pathogenicity, under certain circumstances they can severely affect their host. Bird chewing lice feed on feathers, skin, or blood and can eventually cause irritation, pruritus and lesions on the feathers with adverse effects on the fitness, life span and reproductive success of the bird [2,3]. Moreover, chewing lice may transmit other parasites to the birds, such as certain species of filarial nematodes, and can also act as vectors for some bacterial diseases [4,5].

The study of bird lice is of particular scientific interest, not only because of the potential pathogenicity to the host, but also as it may lighten the paths of host-parasite coevolution and interaction, the status of population robustness in a particular area and the possible routes of pathogen transmission to birds [6–8]. However, the literature concerning screening of lice species distribution and abundance in birds in Europe is limited [9–13].

Greece, within the eastern Mediterranean area is situated in an important geographical position both for local and migratory birds, being located on the intersection of three continents and providing habitats of great diversity [14]. There are 442 bird species recorded in Greece, of which 242 breed locally, while the rest are migratory birds that spend the winter in, or fly over the country during migration, or are randomly found in Greece [15]. Although internationally, > 900 species of lice have been identified from these 442 bird species occurring in Greece (with almost 1800 host-louse associations) [1], data on

* Corresponding author.
E-mail address: sychrao@vfu.cz (O. Sychra).
[1] These authors contributed equally to this work.

http://dx.doi.org/10.1016/j.parint.2017.07.003
Received 24 March 2017; Received in revised form 6 July 2017; Accepted 12 July 2017
Available online 12 July 2017
1383-5769/

the louse fauna of birds living in Greece are essentially lacking. Indeed, only singleton specimens are reported in the literature, mainly from Natural History Museums' collections. More precisely, *Myrsidea subcoracis* from *Corvus corax* [16] *Philopterus ocellatus* from *Corvus corone* [17], *Philopterus vernus* from *Turdus viscivorus* [18], *Quadraceps similis* from *Tringa nebulari* [19], *Halipeurus abnormis* from *Calonectris diomedea* [20], and *Saemundssonia lobaticeps* from *Chlidonias niger* [21] have been identified. Moreover, an unknown, but presumably very small number of birds from the Greek Island Lesvos (Aegean Sea) have been examined for lice, in a broader survey of 204 birds in total, that also included birds from seven areas of Turkey [18]. In order to fill, at least partially, the gap in the understanding of these ectoparasites in both sedentary and migrating birds in this area of Europe, the aim of the present study was to record for the first time on a wider scale, the species of lice infesting wild birds (mainly passerines) in northern Greece and furthermore, to associate the burden of infestation with factors such as age, sex, migration and the social behaviour of the host as well as the season of the year.

2. Materials and methods

2.1. Study area and sampling periods

The present study was conducted in seven localities of three areas of northern Greece, characterised as protected both at national and international level (National Parks). These areas are also characterised as important biotopes for birds both by the Hellenic Ornithological Society (http://www.ornithologiki.gr/ sites 032, 028 and 011 respectively) and Bird Life International (http://www.birdlife.org/). Chewing lice were collected from birds in these locations, during 9 ornithological ringing sessions, from June 2013 until October 2015. The sites and periods of sampling were a) Loutra Appolonias (40.65′ N, 23.41′ E, 53 m a.s.l.) 4-6/6/2013, b) Platia Volvis (40.62′ N, 23.34′ E, 517 m a.s.l.) 6-7/6/2013, c) Nea Agathoupoli Pierias (40.46′ N, 22.58′ E, 2 m a.s.l.) 26-31/7/2013 and 11-14/12/2013, d) Dasos Apollonias (40.65′ N, 23.49′ E, 43 m a.s.l.) 26-29/9/2013, 6-9/9/2014, 9-10/6/2015 and 15-18/10/2015) e) East Cost of Koronia Lake (40.67′ N, 23.21′ E, 54 m a.s.l.) 15-16/4/015, f) Varvara (40.54′ N, 23.38′ E, 516 m a.s.l.) 10-13/6/2015 g) Porto Lagos (41.00′ N, 25.02′ E, 0 m a.s.l) 23-27/4/2014 (Fig. 1).

2.2. Capture and examination of birds

Wild birds (mostly small passerines) were trapped using mist nets. Birds were identified according to Svensson, Mullarney and Zetterström [22]. The taxonomy of the birds adheres to that in Clements et al. [23]. Chewing lice were collected from each bird applying the fumigation chamber method in combination with visual examination of the head [24]. Fumigation was performed with chloroform for 10 min, resulting in the death of ectoparasites. Manipulation of the birds was performed in a way that ensured minor stress and prompt release to their habitat. The chewing lice of each bird were conserved separately in 70% ethanol, until examination. For every bird examined, approximate age (juvenile or adult) and sex were recorded. Beak or other malformations, if occurring were also recorded.

2.3. Identification of lice

Lice were mounted in Canada balsam as permanent slides, according the method described by Palma [25]. Identification of the lice was based on their morphological characteristics, according to corresponding identification keys [26–35], and the nomenclature provided by Price et al. [1].

2.4. Statistical analysis

For statistical analyses, Quantitative Parasitology 3.0 was used [36]. The Chi-square and Fisher's exact tests were applied for comparing prevalence, and sex and age ratios, Bootstrap 2-sample *t*-test was applied for comparing mean abundance and mean intensity and Mood's median test was applied for comparing median intensity. All statistical analyses were evaluated with the level of significance set to $p < 0.05$. The parameters that were analysed were the sex and the age of the birds, the timing of sampling in relation to the breeding season (April–July as breeding *vs* September–December as post-breeding) and the classification of birds as migratory *vs* sedentary, and colonial *vs* territorial.

3. Results

A total of 729 birds, belonging to 9 orders, 32 families and 68 species were examined. Eighty (11%) of these birds were found to be infested with lice. In total, 33 species of lice were identified in 31 different bird species. In 6 additional cases, identification was achieved only to the genus level as the lice were at the nymphal stage. A total of 45 host-louse associations were found with five (11%) of them being new: *Menacanthus agilis* from *Cettia cetti*, *Menacanthus curuccae* from *Acrocephalus melanopogon*, *Menacanthus sinuatus* from *Poecile lugubris*, *Myrsidea* sp. from *Acrocephalus schoenobaenus*, *Philopretus citrinellae* from *Spinus spinus*. Mixed infestations were recorded in 11 cases where birds were infested with 2 − 3 different lice species. The most common infestation intensity was one louse, recorded in 26 of the infested birds, followed by 2 lice (14 birds), 3 lice (9 birds), 6 lice (7 birds), 5 lice (4 birds), 9 lice (3 birds), 4, 7 or 8 lice (2 birds), and finally the totals of 11, 14, 15, 16, 18, 20, 22, 24, 45, 66 and 101 lice were recorded in one bird each.

In total 560 specimens of lice were examined. Four lice species were found in more than one bird species, *i.e.* *Menacanthus agilis* in *Phylloscopus collybita* and *Cettia cetti*, *Menacanthus curuccae* in

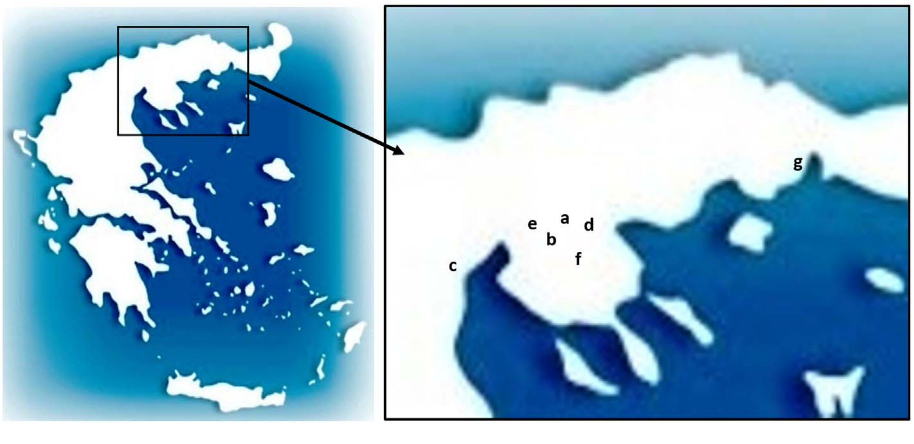

Fig. 1. Sites of sampling in Northern Greece and number of birds examined.
a: Loutra Volvis (n = 69), b: Platia Volvis (32), Nea Agathoupoli Pierias (169), d: Dasos Apollonias (358), e: East Cost of Koronia Lake (47), f: Varvara (32), g: Porto Lagos (22).

Table 1
List of wild birds as hosts of chewing lice found in Greece. Following abbreviations of locations are used: breeding period (April–July): DAI = Dasos Apollonias, KE = East Cost of Koronia Lake, LV = Loutra Volvis, NAPI = Nea Agathoupoli Pierias, PL = Porto Lagos, PV = Platia Volvis, Va = Varvara; post-breeding period (September–December): DAII = Dasos Apollonias; NAPII = Nea Agathoupoli Pierias.

Bird species	I	E	Louse species	M	F	N	Location
Charadriiformes							
Charadriidae							
Charadrius alexandrinus Linnaeus, 1758	1	1	*Quadraceps macrocephalus* (Waterston, 1914)	2			PL
Scolopacidae							
Calidris alpina (Linnaeus, 1758)	1	1	*Actornithophilus umbrinus* (Burmeister, 1838)		1	1	PL
Calidris minuta (Leisler, 1812)	1	2	*Carduiceps zonarius* (Nitzsch, 1866)		4	1	PL
Columbiformes							
Columbidae							
Streptopelia turtur (Linnaeus, 1758)	2	2	*Columbicola bacillus* (Giebel, 1866)	2			LV
Coraciiformes							
Alcedinidae							
Alcedo atthis (Linnaeus, 1758)	4	15	*Alcedoffula alcedinis* (Denny, 1842)		4	5	DAII
	0	1	–	–	–	–	NAPI
Meropidae							
Merops apiaster Linnaeus, 1758[a]	3	7	*Meropoecus meropis* (Denny, 1842)	1	2		NAPI
	2	7	*Meropsiella apiastri* (Denny, 1842)	1	1		NAPI
	5	7	*Meromenopon meropis* Clay and Meinertzhagen, 1941	5	5	11	NAPI
Apodiformes							
Apodidae							
Apus apus (Linnaeus, 1758)	1	1	*Dennyus hirundinis* (Linnaeus, 1761)		1		DAI
Piciformes							
Picidae							
Dendrocopos syriacus (Ehrenberg, 1833)	1	1	*Penenirmus auritus* (Scopoli, 1763)		1	8	DAI
	0	1	–	–	–	–	NAPI
Passeriformes							
Acrocephalidae							
Acrocephalus melanopogon (Temminck, 1823)	1	10	*Menacanthus curuccae* (Schrank, 1776)*		1		NAPI
	2	10	*Philopterus* sp.	1	1	1	NAPI
Acrocephalus palustris (Bechstein, 1798)	1	1	*Menacanthus* sp.			24	LV
	0	3	–	–	–	–	DAII
Acrocephalus scirpaceus (Hermann, 1804)	1	19	*Menacanthus curuccae* (Schrank, 1776)	16	13	37	NAPI
	1	18	*Menacanthus curuccae* (Schrank, 1776)	1	7	8	DAII
	0	1	–	–	–	–	DAI
	0	7	–	–	–	–	KE
	0	1	–	–	–	–	PL
Acrocephalus schoenobaenus (Linnaeus, 1758)	2[b]	24	*Menacanthus curuccae* (Schrank, 1776)		2	5	NAPI
	1	11	*Menacanthus curuccae* (Schrank, 1776)				DAII
	1	24	*Myrsidea* sp.*			1	NAPI
	0	2	–	–	–	–	KE
Cettiidae							
Cettia cetti (Temminck, 1820)	1		*Menacanthus agilis* (Nitzsch, 1866)*		1		DAII
	3	5	*Penenirmus longuliceps* (Blagoveshtchensky, 1940)			33	DAI
	4	39	*Penenirmus longuliceps* (Blagoveshtchensky, 1940)	1	6	5	DAII
	0	1	–	–	–	–	NAPI
	0	1	–	–	–	–	NAPII
	0	4	–	–	–	–	PL
	0	2	–	–	–	–	KE
Emberizidae							
Emberiza schoeniclus (Linnaeus, 1758)	1	10	*Menacanthus chrysophaeus* (Kellogg, 1896)	2	2	2	NAPII
Fringillidae							
Fringilla coelebs Linnaeus, 1758	1	4	*Brueelia* sp.			2	Va
	1[c]	3	*Menacanthus eurysternus* (Burmeister, 1838)		2	10	NAPII
	1	3	*Ricinus fringillae* De Geer, 1778		2		NAPII
	1	3	*Philopterus fortunatus* (Zlotorzycka, 1964)		3	3	NAPII
	1	4	*Philopterus fortunatus* (Zlotorzycka, 1964)	2	3	9	Va
	0	2	–	–	–	–	DAII
Spinus spinus (Linnaeus, 1758)	1	1	*Philopterus citrinellae* (Schrank, 1776)*		1	2	NAPII
Hirundinidae							
Delichon urbicum (Linnaeus, 1758)	1	1	*Brueelia gracilis* (Burmeister, 1838)	1	3	1	PV
Hirundo rustica Linnaeus, 1758	1	6	*Myrsidea rustica* (Giebel, 1874)			1	NAPI
	1	3	*Myrsidea rustica* (Giebel, 1874)	2	3		PL
	1	1	*Myrsidea rustica* (Giebel, 1874)	1			DAI
	1	3	*Brueelia domestica* (Kellogg and Chapman, 1899)		1		PL
Laniidae							
Lanius collurio Linnaeus, 1758	1	4	*Menacanthus camelinus* (Nitzsch, 1874)		2	1	DAII
	0	2	–	–	–	–	NAPI
	0	1	–	–	–	–	PV
Paridae							
Parus major Linnaeus, 1758	1	31	*Menacanthus sinuatus* (Burmeister, 1838)		1		DAII
	0	6	–	–	–	–	DAI
	0	6	–	–	–	–	LV
	0	1	–	–	–	–	PV

(continued on next page)

Table 1 *(continued)*

Bird species	I	E	Louse species	M	F	N	Location
	0	1	–	–	–	–	Va
Poecile lugubris (Temminck, 1820)**	1	2	*Menacanthus sinuatus* (Burmeister, 1838)*	1			Va
Passeridae							
Passer domesticus (Linnaeus, 1758)	1	22	*Menacanthus eurysternus* (Burmeister, 1838)		2		LV
	9	22	*Philopterus fringillae* (Scopoli, 1772)	5	4	19	LV
	0	7	–	–	–	–	NAPI
	0	3	–	–	–	–	PL
Passer hispaniolensis (Temminck, 1820)	1	2	*Sturnidoecus boeevi* (Balát, 1958)		1	2	LV
	0	1	–	–	–	–	DAII
Phylloscopidae							
Phylloscopus collybita (Vieillot, 1817)	1	2	*Menacanthus agilis* (Nitzsch, 1866)		1	1	NAPII
	1	1	*Menacanthus agilis* (Nitzsch, 1866)		1		KE
	1	4	*Menacanthus* sp.			1	DAII
Phylloscopus trochilus (Linnaeus, 1758)	3	40	*Menacanthus curuccae* (Schrank, 1776)		2	2	DAII
Sittidae							
Sitta europaea Linnaeus, 1758	1	2	*Brueelia conocephalus* (Blagoveshtchensky, 1940)		4		Va
Sturnidae							
Sturnus vulgaris Linnaeus, 1758	4[d]	5	*Brueelia nebulosa* (Burmeister, 1838)	10	4	5	LV
	4	5	*Myrsidea cucullaris* (Nitzsch, 1818)	2	2	14	LV
	1	5	*Sturnidoecus sturni* (Schrank, 1776)	1			LV
Sylviidae							
Sylvia atricapilla (Linnaeus, 1758)	3	68	*Menacanthus curuccae* (Schrank, 1776)		3		DAII
	0	1	–	–	–	–	PL
	0	10	–	–	–	–	KE
Sylvia borin (Boddaert, 1783)	3	17	*Menacanthus curuccae* (Schrank, 1776)		5	10	DAII
Sylvia curruca (Linnaeus, 1758)	1	4	*Brueelia currucae* Bechet, 1961	15	13	17	DAII
	0	1	–	–	–	–	NAPI
	0	8	–	–	–	–	KE
Turdidae							
Turdus merula Linnaeus, 1758	1	3	*Menacanthus eurysternus* (Burmeister, 1838)		1		PV
	2[e]	3	*Brueelia amsel* (Eichler, 1951)	5	10	4	PV
	1	3	*Brueelia amsel* (Eichler, 1951)	2	5	2	DAII
	1	1	*Brueelia merulensis* (Denny, 1842)	30	29	42	DAI
	1	3	*Brueelia merulensis* (Denny, 1842)	1			NAPII

I = infected birds, E = examined birds.
[a] One bird harboured all three specie of lice, one bird harboured *Meromenopon* + *Meropsiella*, two birds harboured *Meromenopon* + *Meropoecus*.
[b] One bird harboured also *Myrsidea* sp.
[c] This brid harboured also *Philopterus* and *Ricinus*.
[d] Three birds harboured *Brueelia* + *Myrsidea*, and one bird harboured *Brueelia* + *Myrsidea* + *Sturnidoecus*.
[e] One bird harboured also *Menacanthus eurysternus*.
* New louse-host association.
** First record of any louse from this host.

Acrocephalus scirpaceus, *A. schoenobaenus*, *A. melanopogon*, *Sylvia borin*, *Sylvia atricapila*, and *Phylloscopus trochilus*, *Menacanthus eurysternus* in *Turdus merula, Passer domesticus* and *Fringilla coelebs*, and *Menacanthus sinuatus* in *Parus major* and *Parus lugubris* (Table 1).

The majority of the birds examined ($n = 689$) belonged to the order Passeriformes (21 families and 53 species). Of these birds 64 (9.3%) were found positive for infestation with lice belonging to the following suborders and genera: Amblycera: *Menacanthus* (dominance was 33%), *Myrsidea* (5%), *Ricinus* (0.4%); Ischnocera: *Brueelia s.l.* (41%), *Penenirmus* (9%), *Philopterus* (11%), *Sturnidoecus* (0.8%) (Table 1).

No chewing lice were found on (in alphabetical order): *Accipiter brevipes* ($n = 1$), *Acrocephalus arundinaceus* (30), *Athena noctua* (1), *Caprimulgus europaeus* (1), *Cecropis daurica* (1), *Certhia brachydactyla* (5), *Chloris chloris* (2), *Cyanistes caeruleus* (14), *Dendrocopos major* (1), *Dendrocopos medius* (1), *Emberiza cirlus* (8), *Emberiza hortulana* (1), *Emberiza calandra* (1), *Emberiza schoeniclus intermedia* (2), *Erithacus rubecula* (19), *Garrulus glandarius* (3), *Haematopus ostralegus* (1), *Hippolais icterina* (3), *Iduna pallida* ($n = 36$), *Lanius senator* (1), *Locustella luscinioides* (4), *Luscinia luscinia* (1), *Luscinia megarhynchos* (31), *Motacilla flava flava* (1), *Muscicapa striata* (2), *Passer montanus* (1), *Phylloscopus sibilatrix* (1), *Picus viridis* (2), *Poecile palustris* (2), *Prunella modularis* (3), *Remiz pendulinus* (9), *Saxicola rubetra* (1), *Sylvia cantillans* (12), *Sylvia communis* (37), *Sylvia crassirostris* (2), *Sylvia melanocephala* (7), *Troglodytes troglodytes* (2), and *Turdus philomelos* (5).

The statistical analysis was applied to all the examined birds and also to subgroups such as the passerines, as these constituted the vast majority of examined birds (689 birds of 53 species and 21 families), and also separately to some of the groups with the highest number of examined individuals, *i.e.* the family Acrocephalidae and the species *Cettia cetti*. No association was found between the observed parasitological parameters and the infestation prevalence in the two different periods of the year (breeding *vs* post-breeding) in any of the groups. However, statistically significant difference in the prevalence of infestation was found between the following groups: a) migrating and sedentary passerine birds (7.4% *vs* 13.2%); b) colonial and territorial birds (54.5% *vs* 9.6%); and c) female and male birds in the breeding period (2.6% *vs* 15.6%).

The overall sex-ratio of lice was female-biased (male: female = 1: 1.5; $n = 270$; $\chi^2 = 9.3$, $p < 0.01$) (Table 2). In the case of passerine birds sex-ratio of lice was equal in the breeding period (1: 1.1; $n = 158$; $\chi^2 = 0.2$, $p > 0.05$), while it was strongly female-biased in the post-breeding period (1: 2.6; $n = 82$; $\chi^2 = 15.8$, $p < 0.001$). The overall age ratio of lice was immature-biased in the breeding period (adults: immatures = 1: 1.3; $n = 357$; $\chi^2 = 4.7$, $p < 0.05$), while it was equal in the post-breeding period (1: 0.8; $n = 147$; $\chi^2 = 2.0$, $p > 0.05$) (Table 3).

4. Discussion

This is the first extensive survey on chewing lice infestation of wild birds in Greece: a relatively large number of individuals (729 birds) and bird species (68) was examined, in repeated sessions ($n = 9$) and over a

Table 2
Parasitological parameters of chewing lice collected from wild birds in Greece.

	All examined birds			Passeriformes
	Total	Colonial	Territorial	Total
	(68 spp.)	(5 spp.)	(63 spp.)	(53 spp.)
Examined birds	729	22	707	689
Prevalence (%)	11.0	54.5[a]	9.6	9.3
Mean intensity	7.0	3.6	7.6	7.9
Median intensity	1.0	3.0	2.0	2.0
Mean abundance	0.8	2.0	0.7	0.7
Range	1–101	1–11	1–101	1–101
Percentage males	40.7[b]	39.3	40.9[b]	41.3[b]
No. of adult lice	270	28	242	240
Percentage adults	48.2	65.1[c]	46.8	47.6
Total no. of lice	560	43	517	504

[a] Significantly higher prevalence on the level $p < 0.05$.
[b] Significantly female-biased sex ratio.
[c] Significantly adult-biased age ratio.

period of nearly 2.5 years. Thus, it can be claimed that the present study provides a representative image of the avian louse fauna in the examined area.

According to the results of the present study, the overall prevalence (11%) of chewing lice infestation in wild birds in Greece is analogous with relevant studies in other European countries. In a similar study in Czech Republic, about 15% of the 262 passerine birds examined bore at least one louse [10], a result comparable to that reported here, as the same method of ectoparasite collection (fumigation chamber) was applied.

The only previous survey conducted in southern Europe was in Portugal, where 21.3% of the 122 birds examined were found positive for lice infestation [11]. However, its findings are not easily comparable to those of the present survey, because there are important differences between the two studies: the survey in Portugal included different families of birds, most of them being water and shore birds, admitted to a Wildlife Rehabilitation Centre (thus presumably ill or injured) and the lice were detected only by visual examination, without the usage of fumigation chamber or any kind of insecticide.

Higher overall prevalence (80 out of 226 birds, 35%) of lice infestation, compared to that reported in the present study was found recently in Romania, where the collection of lice was performed with the aid of an ectoparasiticide spray [12]. However, in Romania, the birds of the order Passeriformes (*i.e.* the main category of birds examined in the present study) were the least often infested, compared to the rest of the orders of birds examined [12].

A similar prevalence of infestation was reported in the most recent faunistic survey from Bulgaria, where 76 (10.8%) of the 705 examined birds were infested [9]. Most of those birds were captured during the migration period and were examined by the same method as in the present study (visual examination and fumigation chamber).

In general, it is expected that birds with bigger body mass have a higher number of lice when infested, compared to birds of smaller body mass, when no other underlying conditions exist [12,37]. This is mainly attributed to the hypothesis that larger birds have more surfaces where greater numbers of ectoparasites could be harboured [38]. For example, Adam et al. [12] found 211 lice on a *Buteo rufinus* and 186 on a *Ciconia ciconia*, while on the smaller birds, including the passerines, the infestation intensity was 1 louse on each bird. In the present study, with the exclusion of the highest number of lice (101) found in one individual of the species *T. merula*, which can be considered a relatively large bird compared to the majority of the examined passerines species, the highest numbers of lice were found in typical sized passerine birds *i.e. Acrocephalus scirpaceus* (66 lice) and *Sylvia curruca* (45 lice). This suggests that other reasons, *e.g.* general health status, fitness condition *etc.* may have contributed to this relatively high intensity of infestation. Indeed, *A. scirpaceus,* from which 66 lice were collected, showed a heavy beak malformation that most likely contributed to its high infestation rate because of preening disability.

The prevalence of infestation (3.8%) of *Sylvia atricapilla*, the most numerous species examined in the present survey ($n = 79$), was relatively low and almost identical to that reported in the Czech Republic (3.3%) in a recent survey [39]. In contrast, the prevalence of lice infestation of the same bird species in the Azores, was striking, with infestation percentages reaching up to 82.4% on one of the islands of the archipelago [39], supporting the so called "parasite island syndrome" theory and emphasising the dramatic influence of territorial isolation pressure on the occurrence of parasitic infestations.

Among the bird species found free of lice, despite the relatively large number (37) of individuals examined, was *Sylvia communis*, in which *Menacanthus curuccae* is commonly reported in international literature [1,40]. Moreover, a louse of the genus *Sturnidoecus* has

Table 3
Parasitological parameters of chewing lice collected from wild passerine birds in Greece.

	Passeriformes (53 spp.)													
	Total		Breeding		Post-breeding		Breeding		Post-breeding		Breeding		Post-breeding	
	Breeding	Post-breeding	Migratory	Sedentary	Migratory	Sedentary	Adults	Juveniles	Adults	Juveniles	Females	Males	Females	Males
	41 spp.	34 spp.	24 spp.	17 spp.	24 spp.	10 spp.	30 spp.	24 spp.	13 spp.	28 spp.	17 spp.	22 spp.	14 spp.	8 spp.
Examined birds	341	348	231	110	245	103	158	145	65	217	39	64	78	92
Prevalence (%)	10.3	8.3	4.8	21.8[a]	8.2	8.7	8.2	12.4	10.8	6.9	2.6	15.6[a]	9.0	7.6
Mean intensity	10.2	5.1	10.4	10.1	5.2	4.9	11.5	3.4	4.7	6.1	–[1]	6.0	2.9	4.1
Median intensity	4.0	2.0	3.0	4.5	2.0	2.0	4.0	2.0	2.0	2.0	–[1]	3.5	2.0	1.0
Mean abundance	1.0	0.4	0.5	2.2	0.4	0.4	0.9	0.4	0.5	0.4	0.6	0.9	0.3	0.3
Range	1–101	1–45	1–66	1–101	1–45	1–20	1–66	1–9	1–20	1–45	22	1–18	1–6	1–20
Percentage males	48.1	28.0[b]	46.5	48.7	32.8[b]	16.7[b]	40.3	47.8	13.3[b]	32.7[b]	–[2]	28.1[b]	30.8	–[3]
No. of adult lice	158	82	43	115	58	24	62	23	15	55	–[2]	32	13	13
Percentage adults	44.3[c]	55.8	37.7[c]	47.3	56.3	54.5	41.6[c]	37.1[c]	45.5	59.8	–[2]	53.3	65.0	44.8
Total no. of lice	357	147	114	243	103	44	149	62	33	92	22	60	20	29

[a] Significantly higher prevalence on the level $p < 0.05$.
[b] Significantly female-biased sex ratio.
[c] Significantly immature-biased age ratio.
[1] Only one bird was parasitized.
[2] Only nymphs were found.
[3] Only adult females were found.

previously been found on the single representative of this bird species examined by Moodi, Aliabadian, Moshaverinia and Kakhki [41] in Iran and *Myrsidea* sp. was found on one of the 22 birds examined by Dik et al. [42] in Turkey.

Similarly, *I. pallida* (36 birds examined) was also found to be free of lice. Indeed, it seems that this species is rarely infested as only one case of infestation by *Philopterus* sp. has ever been reported [40]. Also, no lice were detected on *L. megarhynchos* in the present study (31 birds examined), as well as in similar surveys in the Czech Republic and Romania [12,13]. Nevertheless, the louse species *Bruelia lais* has been recorded on this host [1,43]. Finally, no lice were found on *A. arundinaceus* despite the relatively high number of birds examined (30), distributed in 5 different sampling sessions and in 3 consecutive years. This absence of louse infestation was also recorded by Sychra et al. [10] on *A. arundinaceus*. However, three louse species *M. curuccae*, *Penenirmus* sp. and *Philopterus fedorenkoae* are occasionally found on this host [1,40].

Interestingly, very low prevalence of infestation was found in Paridae. Only 2 birds (*P. major* and *P. lugubris*) of the 63 examined in total (45 of them being *P. major*) were found to be infested. Similarly, no lice were found in 15 birds of this family in the Czech Republic during the post breeding season [10]. In contrast, Sychra et al. [13] found 11 of the 28 *P. major,* examined in pre-breeding season, infested. It is worth noting, that the examination of these birds in the present study varied in both pre- and post-breeding periods. Generally, the information found in international literature consents that lice are not a rare finding in Paridae [12]. Thus, the low prevalence of infestation in the present study could be attributed to factors related to the local environment and need further investigation.

An interesting result of the present study was the high infestation prevalence of *Sturnus vulgaris* (4 out of 5 birds). Similar results have been reported from Turkey and Romania where 4/4 and 11/11 of the birds were found to be infested, respectively [12,44]. A possible explanation of the high prevalence that is repeatedly recorded could be the colonial way of life of this bird species [45]. It is likely that the same applies to the results for *Merops apiaster* (5 out of 7 birds infested). This hypothesis proposed for colonial birds has been confirmed recently in Portugal [11]. The results of Rékási et al. [46] were also in accordance, revealing lower abundance and rather equal distribution of lice among colonial compared to territorial birds, thus suggesting lower selection pressure applied by these parasites upon such host populations. Other species that were found to be highly infested in the present study were *F. coelebs* (5 out of 11 birds) and *T. merula* (6 out of 11 birds).

It has been postulated that there is higher occurrence of chewing lice on adult birds during the breeding period [47]. A possible explanation for this fact is that moulting after the breeding period may play a determinant role in the decreasing lice populations on passerines [48]. Also, during the period when parents are with their nestlings, the lice can be transmitted from the adults to the juvenile birds. This fact is linked to the synchronisation of life cycles between some species of chewing lice and their hosts, a feature of successful adaptation to parasitism that ensures lice dispersion [49], and it is also a possible explanation for the decrease in lice prevalence on adults in the same period [1]. Moreover, the climatic conditions that occur after the breeding season, *i.e.* high temperatures in combination with low humidity and precipitation are adverse factors for the abundance of lice [50]. However, in the present study a statistically significant difference in the parasitological parameters was not observed, neither between the breeding and post-breeding period nor between adult and juvenile birds. This result is in agreement with the findings of a relevant survey in the Czech Republic, where the comparison between the prevalence of infestation in the pre-breeding *vs* the post-breeding season in different species of wild birds also showed no statistically significant difference [13]. There are obviously many factors that influence the prevalence of infestation in different seasons of the year and different physiological states of the hosts and these controversial results warrant further investigations regarding these factors.

On the other hand, there was a significant difference in the prevalence of infestation between resident and migrating birds, with the latter having a lower prevalence of infestation at the time when they arrived at their breeding sites (pre-breeding period). This finding is in agreement with a previous study in the Czech Republic [13], where the authors suggest two facts as possible explanations for this observation: a) the phenomenon of migration itself, in the sense that heavily infested birds are more likely to fail to reach their breeding sites [51,52] and b) the delay of the peak of infestation in migratory compared to resident birds, because for the latter, the breeding season begins earlier and, as mentioned above, there is generally higher occurrence of lice on birds during the breeding period. This hypothesis corresponds well with the finding of the present study, where migrating birds had similar infestation prevalence as the sedentary ones, after the breeding period (Table 2). This could be attributed to the fact that the factors contributing to lower infestation were buffered during the breeding period. Nevertheless, in Portugal, the results were contradictory from this point of view: migratory birds were significantly more infested than sedentary birds [11]. However, it must be taken into consideration that the bird population examined in Portugal consisted mainly of different bird families and species than in the present study, and that the examined birds were admitted to a wildlife rehabilitation centre, which implies that they were not in good general condition, a fact that may have influenced the occurrence of lice infestation.

In the case of passerine birds, sex-ratio of lice was equal in the breeding period, while it was strongly female-biased in the post-breeding period. This is an observation that is not easily justified. Similar number of lice on both sexes correlates with large and stable populations of lice on their hosts. Rozsa et al. [53], found that colonial birds usually have higher prevalence and intensity of infestation followed by equal sex-ratio of lice, attributed to higher probability of lice migration between particular hosts in the colony. Conversely, territorial birds with limited possibility of contact with other conspecific individuals harbour smaller populations of lice usually with female-biased sex-ratio. It seems that in the case of passerine birds, a decrease in population of lice during the post-breeding period is followed by change of sex-ratio. Differences in age-ratio recorded in this study corresponded with Fowler and Williams [54] and Chandra et al. [55], who found that populations of lice are immature-biased mainly during the population growth in the breeding period. In fact, although it is well documented that factors such as sex, body size and age bias the intensity of infestation [56], there are contradictory findings regarding each of these factors [37].

It is known that chewing lice do not show strict host specificity [1] and although their distribution usually follows their host distribution, there are cases where this does not apply, a fact that can be ascribed to a variety of possible reasons [1]. In our study, four different lice species were found to infest more than one bird species in the area examined. All four species belonged to the genus *Menacanthus*, which is known to include many multihost species [57]. As in other reports in the past, here also, new hosts for several *Menacanthus* species were revealed and to the best of the authors' knowledge, the finding of *M. curuccae* in *A. melanopogon* and *M. agilis* in *C. cetti* constitute new host-parasite associations. Moreover, the species *M. sinuatus* in *P. lugubris* represents not only a new host-parasite report but also, and most importantly, the first record of any louse from this bird species. Two of these three new host-parasite associations are not surprising: *M. curuccae* is reported from a wide range of hosts of the former family Sylviidae *sensu lato* that include six species of *Acrocephalus* and *M. sinuatus* is a common parasite of eight species of the family Paridae [1]. On the other hand, the Genus *Myrsidea* includes the most strictly host-specific lice species [10]. In the present study, 1 nymph, identified as *Myrsidea* sp., was found in *A. schoenobaenus,* which also, to the best of the authors' knowledge, represents new host-parasite association. Similarly, the genus *Philopterus* is traditionally considered strictly host specific [1,27]. In the present study we identified for the first time on *S. spinus* the louse *Philopterus citrinellae*, a species with a wide range of hosts, from the families Emberizidae and Fringillidae [1]. However, undetermined *Philopterus* sp. has been reported from *S. spinus* in Czechoslovakia (rev. in Hudec [58]), the Faroe Islands [59] and Hungary [43].

Such new parasite-host associations and geographical records are of great interest, as they may bring unknown interactions and evolutionary relations of the organisms to light. It is not surprising that most of the surveys studying organisms that belong to such vast taxonomical entities, such as birds and lice, include some reports of new host-parasite associations in their results [9,60–62].

The results of the present study are generally in accordance with other reports on bird chewing lice from Europe. In a degrading environment, on a national and international level, the monitoring of factors which can indicate the overall fitness and robustness of wildlife is essential. The degradation of important biotopes, such as the ones included in the present survey, and caused by human activities, can result in the accumulation of large bird populations in limited areas which remain suitable habitats. This pressure of population density can lead to a higher risk of pathogen transmission and consequently threaten the fitness, migration and reproductive success of the birds.

It is common knowledge that birds in good fitness and health status are generally capable of keeping parasitism under control [1,63]. On the contrary, energy consumptive situations such as migration, can lead to higher abundance of lice on birds, mainly due to restricted preening [1,38]. Similarly, and in relation to the above-mentioned deterioration of habitats, it could be suggested that the energetic cost of struggling for territory, maintaining dominance hierarchies and feeding resources in crowded biotopes may have analogous results. Subsequently, the prevalence and the intensity of infestation by these ectoparasites could be considered a sentinel of the overall ecological status of the biotope.

Moreover, the study of specific characteristics of parasitism such as association with age, sex, ecology and behaviour can contribute to the better knowledge of the complex parasite-host systems and provide tools for designing successful measures for wildlife and environment conservation. Finally, new host-parasite associations are common in the study of such diverse organisms as birds and chewing-lice. The great number of geographical areas, bird species and strands of birds' ecological/biological features that have never been investigated through the spectrum of interaction with parasites, allows for a wide range of further investigations in this field.

Acknowledgments

The authors would like to express their acknowledgments to the personnel of Koronia-Volvi Lakes Management Authority, Axios–Loudias–Aliakmonas Management Authority, and especially to Ms. Lila Karta, for their valuable help during the field work. Also, many thanks to G. Vlachaki, E. Shogolev and S. Shogolev for their help with the catching of birds. Finally, the authors express their thanks to Ms. Anne Beavan for editing the English language.

References

[1] R.D. Price, R.A. Hellenthal, R.L. Palma, K.P. Johnson, D.H. Clayton, The Chewing Lice: World Checklist and Biological Overview, Illinois Natural History Survey Special Publication, Illinois, 2003.
[2] D.H. Clayton, The influence of parasites on host sexual selection, Parasitol. Today 7 (1991) 329–334.
[3] D.T. Booth, D.H. Clayton, B.B.A., Experimental demonstration of the energetic cost of parasitism in free-ranging hosts, Proc. R. Soc. Lond. B Biol. Sci. 253 (1993) 125–129.
[4] S. Cohen, M.T. Greenwood, J.A. Fowler, The louse *Trinoton anserinum* (Amblycera, Phthiraptera), an intermediate host of *Sarconema eurycerca* (Filarioidea, Nematoda), a heartworm of swans, Med. Vet. Entomol. 5 (1991) 101–110.
[5] J.M. Perez, A.L. Extremera, I. Ruiz, Bacteriological study of the feathers and lice of captive common buzzards (*Buteo buteo*), Avian Pathol. 23 (1994) 163–168.
[6] K.P. Johnson, S.E. Bush, D.H. Clayton, Correlated evolution of host and parasite body size: tests of Harrison's rule using birds and lice, Evolution 59 (2005) 1744–1753.
[7] D.H. Clayton, B.A. Walther, Influence of host ecology and morphology on the diversity of Neotropical bird lice, Oikos 94 (2001) 455–467.
[8] N.K. Whiteman, Lice help illuminate the recent evolutionary history of an Australian bird, Heredity 101 (2008) 105–106.
[9] M.N. Ilieva, New data on chewing lice (Insecta: Phthiraptera) from wild birds in Bulgaria, Acta Zool. Bulgarica 57 (2005) 37–48.
[10] O. Sychra, I. Literak, P. Podzemny, V. Benedikt, Insect ectoparasites from wild passerine birds in the Czech Republic, Parasite 15 (2008) 599–604.
[11] A. Tomas, R.L. Palma, M.T. Rebelo, I.P. da Fonseca, Chewing lice (Phthiraptera) from wild birds in southern Portugal, Parasitol. Int. 65 (2016) 295–301.
[12] C. Adam, G. Chsamera, S.J. Daróczi, A.D. Sándor, M. Gogu-Bogdan, Data on the chewing louse fauna (Phthiraptera: Amblycera, Ischnocera) from some wild and domestic birds of Romania, Trav. Mus. Natl. Hist. Nat. 52 (2009) 177–232.
[13] O. Sychra, I. Literak, P. Podzemny, P. Harmat, R. Hrabak, Insect ectoparasites on wild birds in the Czech Republic during the pre-breeding period, Parasite 18 (2011) 13–19.
[14] M. Papazahariadou, A. Diakou, E. Papadopoulos, I. Georgopoulou, A. Komnenou, K. Antoniadou-Sotiriadou, Parasites of the digestive tract in free-ranging birds in Greece, J. Nat. Hist. 42 (2008) 381–398.
[15] G. Handrinos, Birds, in: A. Legakis, P. Maragou (Eds.), The Red Data Book of Threatened Animals of Greece, Hellenic Zoological Society, Athens, 2009, pp. 213–353.
[16] H.F. Klockenhoff, G. Schirmers, Zur Taxonomie der Myrsideen (Myrsidea Waterston, 1915; Menoponidae: Phthiraptera) von *Corvus corax* und *Corvus ruftcollis*, Bonn. Zool. Beitr. 27 (1976) 300–335.
[17] T. Clay, G.H.E. Hopkins, The early literature on Mallophaga. Part II, 1763–1775, Bull. Br. Mus. Nat. Hist. Entomol. 2 (1951) 1–36.
[18] B. Dik, T. Albayrak, R. Adanir, U. Uslu, Chewing lice (Phthiraptera; Ischnocera, Amblycera) species found on some songbirds (Aves: Passeriformes), Kafkas Univ. Vet. Fak. Derg. 19 (2013) 755–760 (in Turkish).
[19] G.H.E. Hopkins, G. Timmermann, A revision of the species *Quadraceps* (Mallophaga) parasitic on the Tringinae, Trans. R. Entomol. Soc. London 105 (1954) 131–150.
[20] R.L. Edwards, Studies of the Philopteridae (Mallophaga) from birds of the order Procellariformes. 1. The Genus *Halipeurus* Thompson, J. Parasitol. 47 (1961) 125–157.
[21] T. Clay, Species of the genus *Saemundssonia* (Mallophaga) from the Sterninae, Am. Mus. Novit. 1409 (1949) 1–25.
[22] L. Svensson, K. Mullarney, D. Zetterström, Collins Bird Guide, 2nd ed, British Birds vol. 103, (2010), pp. 248–252.
[23] J.F. Clements, T.S. Schulenberg, M.J. Iliff, D. Roberson, F.T.A., B.L. Sullivan, C.L. Wood, The eBird/Clements checklist of birds of the world: v2016, Downloaded from http://www.birds.cornell.edu/clementschecklist/download/2016.
[24] D.H. Clayton, D.M. Drown, Critical evaluation of five methods for quantifying chewing lice (Insecta: Phthiraptera), J. Parasitol. 87 (2001) 1291–1300.
[25] R.L. Palma, Slide-mounting of lice: a detailed description of the Canada balsam technique, N. Z. Entomol. 6 (1978) 432–436.
[26] J. Zlotorzycka, Chewing Lice – Mallophaga 2. Superfamily Menoponoidea, Klucze do Oznaczania Owadów Polski 15, Polskie Towarzystwo Entomologiczne, Warszava, 1976 (in Polish).
[27] J. Zlotorzycka, Chewing Lice - Mallophaga 4. Superfamily Philopteroidea, Family Philopteridae, Klucze do Oznaczania Owadów Polski 15, Polskie Towarzystwo Entomologiczne, Warszava, 1977 (in Polish).
[28] R.D. Price, The *Menacanthus* (Mallophaga: Menoponidae) of the Passeriformes (Aves), J. M. Entomol. 14 (1977) 207–220.
[29] D.I. Blagoveshtchensky, Mallophaga from birds of the Talysh Mts (in Russian), Parazitol. Sbornik 8 (1940) 25–90.
[30] T. Clay, A key to the species of *Actornithophilus ferris* with notes and descriptions of new species, Bull. Br. Mus. Nat. Hist. Entomol. 11 (1962) 189–244.
[31] G. Rheinwald, Die Mallophagengattung Ricinus De Geer, Revision der ausseramerikanischen Arten, Mitt. aus dem Hambg. Zooloichen Mus. Inst. 65 (1968) (1778) 181–326.
[32] R.C. Dalgleish, The *Penenirmus* (Mallophaga: Ischnocera) of the Picidae (Aves: Piciformes), J. N. Y. Entomol. Soc. 80 (1972) 83–104.
[33] R. Adams, R.D. Price, D.H. Clayton, Taxonomic revision of Old World members of the feather louse genus *Columbicola* (Phthiraptera: Ischnocera), including descriptions of eight new species, J. Nat. Hist. 39 (2005) 3545–3618.
[34] J. Zlotorzycka, Chewing Lice - Mallophaga 5, Superfamily Philopteroidea, Family Rallicolidae (In Polish), Polskie Towarzystwo Entomologiczne, Warszava, 1978.
[35] J. Zlotorzycka, Chewing Lice - Mallophaga 6, Superfamily Philopteroidea, Families Meinertzhageniellidae, Lipeuridae, Degeeriellidae, Pseudonirmidae, Giebeliidae, Esthiopteridae and Acidoproctidae (In Polish), Polskie Towarzystwo Entomologiczne, Warszava, 1980.
[36] L. Rózsa, J. Reiczigel, G. Majoros, Quantifying parasites in samples of hosts, J. Parasitol. 86 (2000) 228–232.
[37] E.S. Durkin, L.T. Luong, J. Bird, Mechanisms underlying parasite infection: influence of host body mass and age on chewing louse distribution among brown-headed cowbirds, Parasitol. Res. 114 (2015) 4169–4174.
[38] L. Rozsa, Patterns in the abundance of avian lice (Phthiraptera: Amblycera, Ischnocera), J. Avian Biol. (1997) 249–254.
[39] I. Literak, O. Sychra, R. Resendes, P. Rodrigues, Chewing lice in Azorean blackcaps (*Sylvia atricapilla*): A contribution to parasite island syndromes, J. Parasitol. 101 (2015) 252–254.
[40] M. Ilieva, Checklist of the chewing lice (Insecta: Phthiraptera) from wild birds in Bulgaria, Zootaxa (2009) 1–66.

[41] B. Moodi, M. Aliabadian, A. Moshaverinia, O.M. Kakhki, New data on the chewing lice (Phthiraptera) of passerine birds in East of Iran, Sci. Parasitol. 14 (2013) 63–68.
[42] B. Dik, E. Per, K.E. Yavuz, E. Yamac, Chewing lice (Phthiraptera: Amblycera, Ischnocera) species found on birds in Turkey, with new records and a new host association, Turk. J. Zool. 39 (2015) 790–798.
[43] Z. Vas, J. Rékási, L. Rózsa, A checklist of lice of Hungary (Insecta: Phthiraptera), Annls. Hist.-Nat. Mus. Natn. Hung 104 (2012) 5–109.
[44] B. Dik, E. Yamac, U. Uslu, Studies on chewing lice (Phthiraptera: Amblycera, Ischnocera) species from domestic and wild birds in Turkey, Kafkas Univ. Vet. Fak. 19 (2013) 553–560.
[45] G.J. Davis, Seasonal changes in flocking behaviour of starlings as correlated with gonadal development, Wilson Bull. (1970) 391–399.
[46] J. Rékási, L. Rozsa, B.J. Kiss, Patterns in the distribution of avian lice (Phthiraptera: Amblycera, Ischnocera), J. Avian Biol. (1997) 150–156.
[47] M.S. Forster, Synchronized life cycles in the orange-crowned warbler and its mallophagan parasites, Ecology 50 (1969) 315–323.
[48] P. Kettle, The seasonal incidence of parasitism by Phthiraptera on starlings (*Sturnus vulgaris*) in England, N. Z. Entomol. 7 (1983) 403–408.
[49] K.P. Johnson, D.H. Clayton, The biology, ecology, and evolution of chewing lice, in: R.D. Price, R.A. Hellenthal, R.L. Palma, K.P. Johnson, D.H. Clayton (Eds.), The Chewing Lice: World Checklist and Biological Overview, Illinois Natural History Survey Special Publication, Illinois, 2003, pp. 449–476.
[50] A. Derylo, Investigation on economic disadvantage of Mallophaga IV. The influence of ecological and physiological factors on the intensity of Mallophaga infestation, Prz. Zool. 19 (1975) 181–187.
[51] C.R. Brown, M.B. Brown, B. Rannala, Ectoparasites reduce long-term survival of their avian host, Proc. R. Soc. Lond. B Biol. Sci. 262 (1995) 313–319.
[52] S.C. Cork, T. Csörgö, S. Scebba, G. Lövei, The prevalence of nematodes parasites in transcontinental songbirds, Association of Veterinary Teachers and Research, Workers Current Topics in Veterinary Science, 55th Annual Conference, Scarborough, UK, (2001).
[53] L. Rozsa, J. Rekasi, J. Reiczigel, Relationship of host coloniality to the population ecology of avian lice (Insecta: Phthiraptera), J. Anim. Ecol. 65 (1996) 242–248.
[54] J.A. Fowler, L.R. Williams, Population dynamics of Mallophaga and Acari on reed buntings occupying a communal winter roost, Ecol. Entomol. 10 (1985) 377–383.
[55] S. Chandra, G.P. Agarwal, S.P.N. Singh, A.K. Saxena, Seasonal changes in a population of *Menacanthus eurysternus* (Mallophaga, Amblycera) on the common myna *Acridotheres tristis*, Int. J. Parasitol. 20 (1990) 1063–1065.
[56] O. Sychra, T. Najer, F. Kounek, M. Capek, I. Literak, Chewing lice (Phthiraptera) on manakins (Passeriformes: Pipridae) from Costa Rica, with description of a new species of the genus *Tyranniphilopterus* (Phthiraptera: Philopteridae), Parasitol. Res. 106 (2010) 925–931.
[57] J. Martinu, O. Sychra, I. Literak, M. Capek, D.L. Gustafsson, J. Stefka, Host generalists and specialists emerging side by side: an analysis of evolutionary patterns in the cosmopolitan chewing louse genus *Menacanthus*, Int. J. Parasitol. 45 (2015) 63–73.
[58] K. Hudec, Birds 3 - I & II, Fauna ČSSR 23, 24, Academia, Praha, 1983 (in Czech).
[59] R.L. Palma, J.K. Jensen, Lice (Insecta: Phthiraptera) and their host associations in the Faroe Islands, Steenstrupia 29 (2005) 49–73.
[60] M.G. Nasser, A. Alahmed, M. Shobrak, New host/parasite record for very rare chewing louse *Cuculotogaster arabicus* (Clay, 1938) (Phthiraptera: Ischnocera) on endemic mountain partridges of Arabian Peninsula, Parasitol. Res. 115 (2016) 4433–4436.
[61] M. Shobrak, A. Alahmed, R. Palma, M. Almalki, M.G. Nasser, New records of species of *Saemundssonia* (Insecta: Phthiraptera: Philopteridae) infesting breeding terns in the Arabian Peninsula, with notes on their phylogeny and ecology, Parasitol. Res. 114 (2015) 2587–2597.
[62] O. Sychra, S. Naz, S.A. Rizvi, New record of *Afrimenopon waar* (Eichler) (Phthiraptera: Menoponidae) from budgerigar *Melopsittacus undulatus* (Psittaciformes: Psittacidae) from Karachi, Pakistan, Parasitol. Res. 101 (2007) 505–509.
[63] A.G. Marshall, The Ecology of Ectoparasitic Insects, Academic Press, London, 1981.