

Chewing lice (Phthiraptera: Amblycera, Ischnocera) species found on birds in Turkey, with new records and a new host association

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Abstract: This study was carried out between 2011 and 2014 to detect chewing louse species found on birds in Turkey. For this purpose, 246 birds were examined for lice. Thirty-three birds (13.4%) were found to be infested by 25 louse species; 17 Ischnoceran species belonging to 15 genera and 8 Amblyceran species belonging to 5 genera were recorded in this study. In this study, usually 1 or 2 louse species were detected on a single bird, and in only 2 cases, 3 louse species were found on the same bird. *Rhynonirmus helvolus* (Burmeister, 1838) and *Saemundssonina* sp. (nymph: N) from the Eurasian Woodcock (*Scolopax rusticola*), *Penenirmus silvicultrix* (Mey, 1982) from the Common Redstart (*Phoenicurus phoenicurus*), *Penenirmus longuliceps* (Blagovestchensky, 1940) from the Cetti's Warbler (*Cettia cetti*), *Brueelia iliaci* (Denny, 1842) from the Redwing (*Turdus iliacus*), *Penenirmus pikulai* (Balát, 1981) from the Barred Warbler (*Sylvia nisoria*), *Cuculoecus latifrons* (Denny, 1842) from the Common Cuckoo (*Cuculus canorus*), and *Brueelia* sp. (N) and *Penenirmus* sp. (N) from the Black-headed Bunting (*Emberiza melanocephala*) were reported for the first time in Turkey. In addition, *Cuclotogaster heterographus* (Nitzsch [In Giebel], 1866) was collected from a turkey (*Meleagris gallopavo*) for the first time anywhere in the world.

Key words: Chewing lice, Amblycera, Ischnocera, Passeriformes, *Cuclotogaster heterographus*, *Cuculoecus*, *Penenirmus*, *Brueelia*, *Rhynonirmus*, host

1. Introduction

Around 10,500 bird species have been identified in the world (Gill and Donsker, 2015), while the number of bird species in Turkey is around 460 (Kirwan et al., 2008). Mites and chewing lice have an important role as bird ectoparasites, and they are frequently found on birds. Chewing lice are permanent parasites which complete their life cycle on the body of the host and feed on feathers, skin or skin debris, and blood (Johnson and Clayton, 2003).

So far, more than 5500 chewing louse species have been described, and around 4000 of them are reported as accepted (Price et al., 2003). Approximately 100 louse species from about 150 bird species have been recorded in Turkey in recent studies (Aksin, 2003; Dik, 2006, 2010; Dik and Uslu, 2006a, 2006b, 2008, 2009; Dik and Aydenizöz Özkayhan, 2007; Aksin, 2010a, 2010b; Dik et al., 2010, 2011a, 2011b, 2013a, 2013b, 2013c; İnci et al., 2010a, 2010b; Açııcı et al., 2011; Girişgin et al., 2013). Most previous studies on louse species in Turkey have been focused only on chickens and pigeons (Dik et al., 1999;

Gıcık, 1999; Köroğlu et al., 1999; Köroğlu and Şimşek, 2001; Okursoy and Yılmaz, 2002; Şenlik et al., 2005), while more recent studies have been carried out on wild birds (Aksin, 2003; Dik, 2006, 2010; Dik and Uslu, 2006b, 2008, 2009; Dik and Aydenizöz Özkayhan, 2007; Aksin, 2010a, 2010b; Dik et al., 2010, 2011a, 2011b, 2013a, 2013b, 2013c; İnci et al., 2010b; Açııcı et al., 2011; Aksin and Oncel, 2011; Girişgin et al., 2013). However, many birds in the Turkish fauna had not been examined for chewing lice yet.

This study was performed to detect chewing louse species occurring on birds in Turkey and to evaluate their host associations.

2. Materials and methods

This study was carried out in the years 2011–2014. A total of 246 birds belonging to 36 species in 28 genera, 23 families, and 13 orders were examined for the presence of chewing lice. Two hundred and eleven of the studied birds belonged to the Passeriformes, followed by 7 samples from Accipitriformes, and 5 samples from Columbiformes.

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Birds from other orders were also examined, which are given in the Table. Chewing lice were collected from 33 of 246 bird specimens examined; 43 birds were found injured or dead on the road, and 203 live birds were sampled at Cernek Ringing Station in the city of Samsun on the Black Sea coast, where bird migration studies are performed and birds are captured with mist-nets for ringing. Three of the sampled bird species (*Meleagris gallopavo*, *Psittacula erithacus*, *Melospittacus undulatus*) are captive birds and are not found in the Turkish avifauna. The location names of all sampled bird species are given in the Table. The birds were identified visually according to the experience of the ornithologist authors; in some cases, *Collins Bird Guide* (Svensson, 2009) and *Identification Guide to European Passerines* (Svensson, 1992) were used for identification. Each bird was kept separately in a cotton bird-holding bag. The feathers of each bird were carefully examined macroscopically and the lice were removed with forceps. The examined birds at the ringing station were released in the same area of capture after treatment. Along with the visual examination, tetramethrin (Avispray, Biyoteknik) was applied to injured and dead birds in the clinic; each treated bird was placed in a white basin, where they were kept for at least 15 min. The lice were made transparent in 10% KOH for 24 h; they were washed in distilled water and passed in 70% ethanol followed by 99% alcohol. The specimens were mounted in Canada balsam as permanent slides by using a stereo-zoom microscope (Olympus SZ60). The slides were dried in an incubator at 50–60 °C for a few weeks. The lice were identified using a light microscope in accordance with the descriptions and illustrations in the papers by Blagoveshtchensky (1940), Balát (1981), Mey (1982), and Mey and Barker (2014). Some of the lice could not be identified at species level because they were in the nymphal stage; these have been shown with (N) throughout the text.

3. Results

Two hundred and forty-six birds were examined and 25 louse species belonging to 20 genera were identified (Table 1). Thirty-three birds (13.4%) were found to be infested by 25 louse species: 17 Ischnoceran species belonging to 15 genera, and 8 Amblyceran species belonging to 5 genera. These numbers do not include the samples that were not determined at species level: *Saemundssonina* sp. (N) from the Eurasian Woodcock (*Scolopax rusticola*), and *Brueelia* sp. (N) and *Penenirmus* sp. (N) from the Black-headed Bunting (*Emberiza melanocephala*). In addition, *Menacanthus* sp. specimens were collected from the Barn Swallow (*Hirundo rustica*) and European Robin (*Erithacus rubecula*),

The Sardinian Warbler (*Sylvia melanocephala*) and Eurasian Blackcap (*Sylvia atricapilla*) are also not included in the given numbers. In this study, 2 turkeys (*Meleagris gallopavo*) were examined in the city of Bartın for the presence of chewing lice; after microscopic evaluation, the chewing lice were identified as *Cuculotogaster heterogarpus*.

Infestation rates for the orders are shown in Figure 1. Infestation rate was highest in the orders Accipitriformes and Charadriiformes (100%), followed by Cuculiformes (66.6%), Galliformes (60%), Coraciiformes (40%), Columbiformes (20%), and Passeriformes (7.5%). No lice were detected on birds belonging to the orders Pelecaniformes, Psittaciformes, Phoenicopteriformes, Gruiformes, or Otidiformes (Table 1). Mean intensity per bird species was highest in the Eurasian Eagle-Owl (*Bubo bubo*) (23), Rock Dove (*Columba livia*) (19), Long-legged Buzzard (*Buteo rufinus*) (16), and Common Buzzard (*Buteo buteo*) (13), and was quite low (approximately 2) in the other bird species.

The high number of examined passerines is due to the samples gathered from the Cernek Ringing Station. The 211 examined passerines belonged to 19 different bird species. Sixteen (7.6%) of these samples were infested, but only 8 lice species could be identified to species level. Not counting lice in their nymphal stages, we collected 8 louse species from 19 bird species belonging to the Passeriformes, 5 louse species from 2 bird species belonging to the Accipitriformes, 4 louse species from 2 bird species belonging to the Galliformes, 2 louse species from 1 bird species belonging to the Charadriiformes, 2 louse species from 3 bird species belonging to the Strigiformes, 2 louse species from 1 bird species belonging to the Cuculiformes, 1 louse species from 1 bird species belonging to the Coraciiformes, and 1 louse species from 1 bird species belonging to the Columbiformes.

Generally, only 1 or 2 louse species were detected on the same infested bird. As an exception, in 2 cases, 3 louse species were found on the same host species.

4. Discussion

So far, more than 5500 chewing louse species have been described, and around 4000 of them are reported as accepted (Price et al., 2003). In recent years, there has been an increase in studies of the louse fauna on birds in Turkey. Consequently, the number of detected louse species is increasing (Dik and Uslu, 2009; Dik et al., 2009, 2010, 2011a, 2011b, 2013a, 2013b, 2013c; Dik, 2010; İnci et al., 2010b; Açııcı et al., 2011; Girişgin et al., 2013). However, only one-quarter of the bird species recorded in Turkey have been examined for lice. As lice have not been found on all bird species examined, and many lice that have been

Table. Detected chewing louse species associated with birds in Turkey between the years 2011 and 2014.

Orders	Families	Species	Sampling site	Number of examined birds	Number of infested birds	Infestation rate (%)	Louse species
Pelecaniformes	Pelecanidae	Great White Pelican <i>Pelecanus onocrotalis</i>	Konya	1	0	0	-
		Greater Flamingo <i>Phoenicopterus roseus</i>	Konya	1	0	0	-
Accipitriformes	Accipitridae	Common Buzzard <i>Buteo buteo</i>	Konya	1	1	100	<i>Craspedorrhynchus platystomus</i> 1 ♀ 2 N <i>Degeeriella fibva</i> 5 ♀ 2 ♂ <i>Kurodaia fulvofasciata</i> 2 ♀ 1 ♂
		Long-legged Buzzard <i>Buteo rufinus</i>	Konya	6	6	100	<i>Colpocephalum nanum</i> 1 ♂ <i>Craspedorrhynchus platystomus</i> 13 ♀ 10 ♂ 10 N <i>Degeeriella fibva</i> 22 ♀ 20 ♂ 6 N <i>Laemobothrion maximum</i> 3 ♀ 2 ♂ 7 N
		Turkey <i>Meleagris gallopavo</i>	Ankara, Bartin, Kastamonu	4	2	50	<i>Cheloptistes meleagridis</i> 2 ♀ 1 N <i>Cuctotogaster heterographus</i> ** 8 ♀ 9 ♂ 4 N
Galliformes	Phasianidae	Chukar Partridge <i>Alectoris chukar</i>	Eskişehir	1	1	100	<i>Goniodes dispar</i> 1 ♂ <i>Gonitocotes pusillus</i> 2 ♀ <i>Cuctotogaster</i> sp. 1 N
		Common Moorhen *** <i>Gallinula chloropus</i>	Konya	1	0	0	-
Otidiformes	Otididae	Macqueen's Bustard*** <i>Chlamydotis macqueenii</i>	Konya	1	0	0	-
Charadriiformes	Scolopacidae	Eurasian Woodcock*** <i>Scolopax rusticola</i>	Eskişehir	1	1	100	<i>Rhyonimimus helvolus*</i> 1 ♀ 1 N <i>Saemundssonina</i> sp.* 1 N
Columbiformes	Columbidae	Rock Dove <i>Columba livia</i>	Konya	5	1	20	<i>Columbicola columbae</i> 10 ♀ 6 ♂ 3 N
		African Grey Parrot <i>Psittacus erithacus</i>	Konya	1	0	0	-
Psittaciformes	Psittacidae	Budgerigar <i>Melopsittacus undulatus</i>	Konya	1	0	0	-
		Common Cuckoo <i>Cuculus canorus</i>	Samsun	3	2	66.6	<i>Cuculicola latirostris</i> 1 ♀ 1 ♂ <i>Cuculococcus latifrons*</i> 2 ♀
Strigiformes	Strigidae	Eurasian Eagle-Owl <i>Bubo bubo</i>	Konya	1	1	100	<i>Strigiphilus strigis</i> 11 ♀ 4 ♂ 2 N <i>Kurodaia longipes</i> 3 ♀ 2 ♂ 1 N
		Tawny Owl*** <i>Strix aluco</i>	Konya	1	0	0	-
Coraciiformes	Meropidae	Long-eared Owl <i>Asio otus</i>	Konya	1	0	0	-
		European Bee-eater <i>Merops apiaster</i>	Samsun	5	2	40	<i>Meropoecus meropis</i> 5 ♀

Table. (Continued).

Hirundinidae	Barn Swallow <i>Hirundo rustica</i>	Samsun	7	2	28.6	<i>Myrsidea rustica</i> 2 ♀ 1 ♂ 1 N <i>Menacanthus</i> sp. 1 N
	European Robin <i>Erithacus rubecula</i>	Samsun	20	1	5	<i>Menacanthus</i> sp. 1 N
Muscicapidae	Common Redstart <i>Phoenicurus phoenicurus</i>	Samsun	3	1	33.3	<i>Penenirmus sibilicaltrix</i> * 2 ♀
	Common Blackbird <i>Turdus merula</i>	Niğde, Samsun	6	0	0	-
Turdidae	Song Thrush <i>Turdus philomelos</i>	Konya, Niğde, Samsun	5	1	20	<i>Braeelia turdimulae</i> 3 ♀ 3 ♂ <i>Menacanthus eurystemus</i> 1 ♀ 1 N
	Redwing *** <i>Turdus iliacus</i>	Niğde	1	1	100	<i>Braeelia iliacti</i> * 4 ♀ 1 ♂
	Cetti's Warbler <i>Cettia cetti</i>	Samsun	22	1	4.5	<i>Penenirmus longuliceps</i> * 1 ♀
Sylviidae	Sardinian Warbler <i>Sylvia melanocephala</i>	Samsun	5	1	20	<i>Menacanthus</i> sp. 1 N
	Barréd Warbler <i>Sylvia nisoria</i>	Samsun	3	1	33.3	<i>Penenirmus pikulai</i> * 1 ♀ <i>Myrsidea</i> sp. 1 ♀ 1 N
	Garden Warbler <i>Sylvia borin</i>	Samsun	40	2	5	<i>Menacanthus currucae</i> 2 ♀ 6 N <i>Myrsidea</i> sp. 2 N
	Eurasian Blackcap <i>Sylvia atricapilla</i>	Samsun	45	1	2.2	<i>Menacanthus</i> sp. 1 N
	Common Whitethroat <i>Sylvia communis</i>	Samsun	22	1	4.5	<i>Myrsidea</i> sp. 1 N
	Common Chiffchaff <i>Phylloscopus collybita</i>	Samsun	10	1	10	<i>Menacanthus agilis</i> 2 ♀
Phylloscopidae	Willow Warbler <i>Phylloscopus trochilus</i>	Samsun	8	0	0	-
	River Warbler <i>Locustella fluviatilis</i>	Samsun	1	0	0	-
Laniidae	Red-backed Shrike <i>Lanius collurio</i>	Bolu, Samsun	3	0	0	-
	Hooded Crow <i>Corvus cornix</i>	Konya	1	0	0	-
Passeridae	House Sparrow <i>Passer domesticus</i>	Adıyaman, Eskişehir, Konya, 8 Sanlıurfa	8	1	12.5	<i>Menacanthus eurystemus</i> 2 ♀ 2 N
	Black-headed Bunting <i>Emberiza melanocephala</i>	Samsun	1	1	100	<i>Braeelia</i> sp. 4 N * <i>Penenirmus</i> sp. 1 N *
Total			246	33	13.4	

* First record from Turkey; ** First record from this host in the world; *** First time this host has been examined for lice in Turkey.

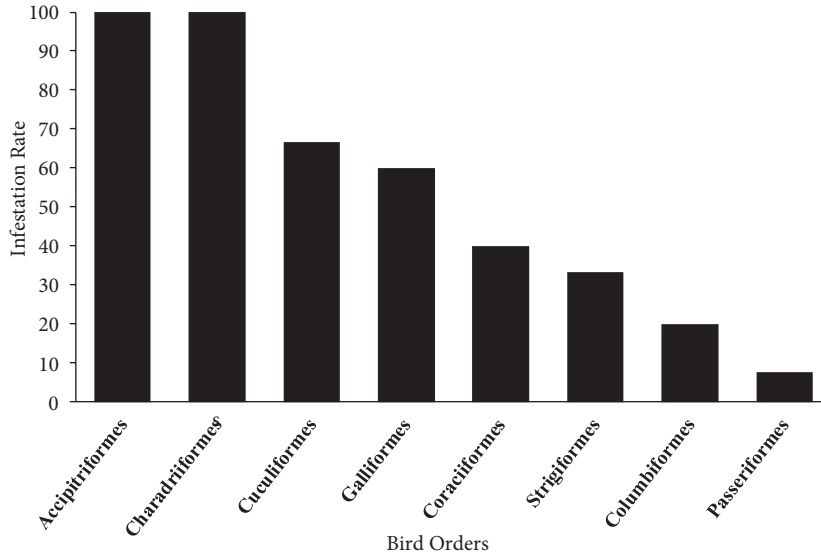


Figure 1. Infestation rates in bird orders.

recorded from the same host species outside Turkey have not been recorded, the Turkish lice fauna is still not fully studied. The first studies focused on chickens and pigeons (Dik et al., 1999; Gıcık, 1999; Köroğlu et al., 1999; Köroğlu and Şimşek, 2001; Okursoy and Yılmaz, 2002; Şenlik et al., 2005). More recently, studies focusing on bird species other than pigeons and chickens have been performed, but these studies have included only a few bird species (Aksın, 2003, 2010a, 2010b; Dik, 2006; Dik and Uslu, 2006a, 2008; Dik and Aydenizöz Özkayhan, 2007; Aksın and Oncel, 2011). In recent studies, the number of studied bird species has increased, and, in parallel, the determined louse species have increased also (Dik and Uslu, 2009; Dik et al., 2009, 2010, 2011a, 2011b, 2013a, 2013b, 2013c; Dik, 2010; İnci et al., 2010b; Açııcı et al., 2011; Girişgin et al., 2013). Some of these studies were performed on dead birds found serendipitously or injured birds brought to veterinary clinics, especially birds belonging to the orders Accipitriformes, Anseriformes, Charadriiformes, and Passeriformes. For this reason, birds belonging to other orders were poorly studied.

It has been stated that large-bodied bird species may harbor more lice than small passerines (Rózsa, 1997; Johnson and Clayton, 2003). Dik et al. (2013a) examined 204 passerines belonging to 29 species in 12 families captured in 7 different localities in Turkey and Lesbos Island (Greece); 5 of them (2.45%) were infested with chewing lice, and 4 chewing louse species were identified. According to a study in Ukraine, the infestation rate in Passeriformes was 58.2%. Sturnidae, Corvidae, Ploceidae, Hirundinidae, and Laniidae families had the highest infestation rates (Fedorenko, 1974). In the present

study, 211 passerines were examined for lice, and the infestation rate was 7.5%, which is lower than the rate found by Fedorenko (1974) and higher than that found by Dik et al. (2013a). Fedorenko (1974) stated that the infestation rate in Passeriformes was lower than that in the Charadriiformes, Anseriformes, Galliformes orders, and the Rallidae family, which is consistent with the present study. No lice were found on some sampled bird families within the Passeriformes; the prevalence of lice was higher on the Barn Swallow (*Hirundo rustica*) than on other bird species in this order. These results are very similar to previous findings (Dik et al., 2010, 2011a, 2013a).

In one study (Dik et al., 2011a), 51 birds belonging to 22 species and 16 genera in 10 families in the order Passeriformes were examined for lice, and 11 of them (21.57%) were found to be infested with at least 1 chewing louse species. In that study (Dik et al., 2011a), the infestation rates had been found to be 100% in *Emberiza schoeniclus*, *Lanius collurio*, and *Hirundo rustica*; 66.7% in *Motacilla flava*; 50% in *Phylloscopus collybita*; and 11.1% in *Anthus spinoletta*. No chewing lice were found in samples from the bird families Sylviidae and Muscicapidae in that study. In a study by Dik et al. (2013a) on chewing lice on passerines, 204 birds belonging to 12 families were evaluated; only 5 birds were infested and only the Sittidae and Turdidae families had infested species. In the present study, 211 birds belonging to 11 families were evaluated; apart from the species in Locustellidae, Laniidae, and Corvidae, the other families had at least 1 species with 1 chewing lice infestation where the infestation rate ranged between 2.2% to 100% (Figure 2). The infestation rate among passerines was highest in Emberizidae, Hirundinidae, and Turdidae.

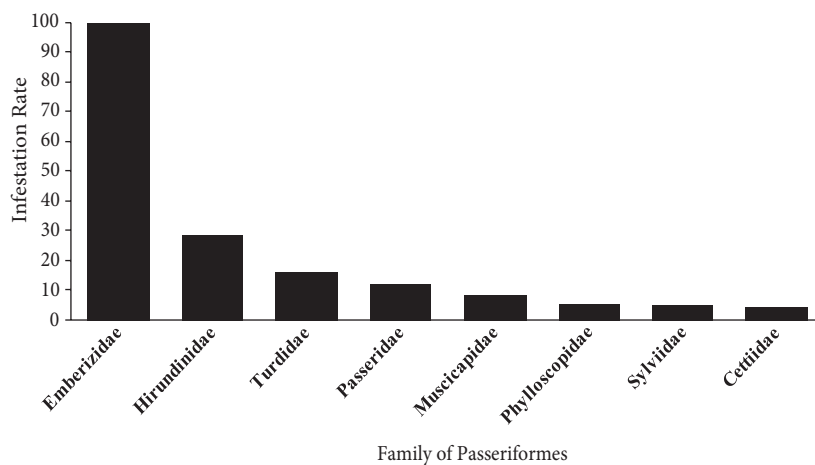


Figure 2. Infestation rates in families of Passeriformes.

As stated before, the bird sample size is not homogeneous in all orders and families, and it is thus hard to form a reasonable discussion of it; however, the infestation in all 3 Lanidae members is similar to the findings of Fedorenko (1974). In examined Sylviidae and Muscicapidae samples, chewing lice were identified; some of them have been described for the first time in Turkey.

In macroscopic examination, the nymphs are difficult to detect; in particular, the chewing lice belonging to Amblycera are very quick and are hard to detect by visual examination only (Johnson and Clayton, 2003). Thus, some chewing lice may not be seen. For this reason, the size of the bird and the feather density play an important role in macroscopic examination and thus harmless synthetic pyrethroid insecticides can be applied to collect chewing lice (Clayton and Walther, 1997). Insecticide was used to collect chewing lice from birds examined at Kuyucuk Ringing Station (Dik et al., 2010, 2011a), and infestation rate was high. However, in another study by Dik et al. (2013a), insecticide was not used, and only macroscopic examination was performed and visually detected chewing lice were collected; as a result, the infestation rate was quite low. In the present study, passerines sampled at Cernek Ringing Station were only examined macroscopically; hence, the infestation rate was low compared to those of other studies and the detected chewing lice species were few.

In previous studies, the infestation rate was high in Accipitriformes (Dik, 2006; Dik and Aydenizöz Özkayhan, 2007; İnci et al., 2010b) and Charadriiformes (Dik et al., 2010), which was also reported by Fedorenko (1974). In the present study, the infestation rate in both orders was 100%, although only 1 bird species (Eurasian Woodcock) was evaluated from Charadriiformes. These results support the results from other studies (Rózsa, 1997; Johnson and Clayton, 2003; Dik, 2006; Dik and Aydenizöz Özkayhan,

2007; Dik et al., 2010; İnci et al., 2010b). On the other hand, in the Pelecaniformes, Phoenicopteriformes, Gruiformes, Otidiformes, Psittaciformes, and Strigiformes orders there was no infestation. Considering that these are large birds without infestation, we can say that the sample size was too low to make any significant evaluation.

Mean intensity per bird species was highest in large birds like the Eurasian Eagle-Owl, Rock Dove, Long-legged Buzzard, and Common Buzzard, and lower in small birds, which is consistent with the findings of other studies (Rózsa, 1997; Johnson and Clayton, 2003; Dik, 2006; Dik and Aydenizöz Özkayhan, 2007; Dik et al., 2010; İnci et al., 2010b).

Generally, only 1–3 louse species were detected on the same infested bird. However, in some cases, there have been more than 10 chewing louse species recorded on a single bird (Price et al., 2003). Ward (1957) reported that he recorded 10 chewing louse species on a single bird from the *Tinamia* subfamily; on the *Crypturellus soui* bird species from the same subfamily, more than 20 chewing louse species have been reported (Johnson and Clayton, 2003; Price et al., 2003). In the present study, a maximum of 3 chewing louse species were detected on a single bird.

Chewing lice spend their entire lives on their host. After the host's death, the chewing lice directly abandon the host within several hours. Ischnoceran chewing lice continue to feed on the skin, while amblyceran chewing lice abandon the host within a relatively short time (Johnson and Clayton, 2003). In the present study, there were no chewing lice detected on examined dead birds, but quite rarely there were found a very few chewing lice on fresh carcasses from ischnoceran species. In our study, while there were no chewing lice collected from 3 living Song Thrushes *Turdus philomelos*, 6 *Brueelia turdinulae* and 2 *Menacanthus eurysternus* were collected from 1 dead

Song Thrush. Birds like the Black-headed Bunting, Rock Dove, and Redwing, which were examined short after their death, were infested by ischnoceran species. These results are consistent with Johnson and Clayton (1997).

Cuclotogaster heterogarpus was previously reported on the Chukar (*Alectoris chukar*), chicken (*Gallus gallus*), and Common Pheasant (*Phasianus colchicus*) (Price et al., 2003). In Turkey, it has been reported from the chicken (Merdivenci, 1965; Dik et al., 1999, Köroğlu et al., 1999, Okursoy and Yilmaz, 2002) and Common Pheasant (Dik and Uslu, 2006a). However, *C. heterogarpus* has not been reported from a Turkey so far throughout the world. In the present study, *C. heterogarpus* (Figures 3–5) collected from young turkeys were wider and larger than those on the Common Pheasant (Dik and Uslu, 2006a), but the male genitalia were the same in both.

In conclusion, 25 lice species were recorded on birds in this study. *R. helvolus* and *Saemundssonina* sp. (N) from



Figure 5. *Cuclotogaster heterogarpus*, male genitalia, original.



Figure 3. *Cuclotogaster heterogarpus*, female, original.



Figure 4. *Cuclotogaster heterogarpus*, male, original.

the Eurasian Woodcock, *P. silvicultrix* from the Common Redstart (*Phoenicurus phoenicurus*), *P. longiceps* from the Cetti's Warbler (*Cettia cetti*), *B. iliaci* from the Redwing, *P. pikulai* from the Barred Warbler (*Sylvia nisoria*), *Brueelia* sp. (N) and *Penenirmus* sp. (N) from the Black-headed Bunting, and *C. latifrons* from the Common Cuckoo (*Cuculus canorus*) are reported for the first time in Turkey. The Common Moorhen (*Gallinula chloropus*), Macqueen's Bustard (*Chlamydotis macqueniei*), Eurasian Woodcock, Redwing (*Turdus iliacus*), and Tawny Owl (*Strix aluco*) were examined for lice for the first time in Turkey in this study. The Eurasian Woodcock had 2 louse species and Redwing had 1 louse species, while the others had no louse infestation. These lice are therefore new records for Turkey. Thus, *C. heterogarpus* was determined for the first time anywhere in the world on turkeys.

In spite of our findings, further investigation is needed not only to complete the list of the phthirapteran fauna in Turkey, but also to provide information about phylogenetic relationships among species and host-parasite associations.

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