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The environment and host effects on chewing lice prevalence, richness, and abundance on birds in Turkey

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Abstract

The prevalence, number of species, and individual numbers of chewing lice found on birds may vary depending on different biotic and abiotic factors. Studies detecting the effects of different conditions on chewing lice were carried out generally on bird species belonging to one order or family. In addition, there can be conflict concerning the ecological effects on chewing lice. In this study, 2101 individuals of fifty-nine different bird species were evaluated to identify the habitat, food guild, migration behavior, weight, wingspan, and length effects on chewing lice prevalence, species richness, and abundance. The highest prevalence was detected in urban-dwelling bird species. The highest lice richness was recorded on migratory bird species living in wetlands. Furthermore, there was a positive correlation between wingspan and lice species. The most abundant lice were detected on resident wetland-dwelling bird species. It is thought that detailed studies should be carried out to explain not only host habitat effect on prevalence and abundance but also host body length and wingspan on the abundance and richness.

Keywords Birds · Ectoparasites · Migration · Urban area · Wetland

Introduction

Parasitism is a long-term relationship between the parasites which cause severe effects on hosts and the hosts which supply food and habitat for parasites (Vas 2013). Bird species host many different parasitic groups, including lice species (Marshall 1981). About 4500 obligate ectoparasite chewing lice species are known and about 85% of them infest birds (Price et al. 2003).

It is known that chewing lice negatively affect bird species in different ways. They have effects on flight behavior (Barbosa et al. 2002), thermoregulation (Booth et al. 1993), or mate selection (Clayton 1990) by causing damage to feathers. Brown et al. (1995) report that lice may cause a decrease in the *Hirundo pyrrhonota* population by affecting individual survival. A high infestation rate may lead to pathological effects on hosts (Shanta et al. 2006). For example, *Piagetiella titan* colonizes in the oral cavity of white pelicans (*Pelecanus onocrotalus*) and may cause stomatitis (Dik 2006a).

Prevalence, the number of chewing lice species (richness), and abundance can be affected by numerous biotic factors, such as taxon, body mass, sex, age, feeding, and migration of the bird. Many studies have shown that body mass of the host positively correlates with lice abundance (Clayton et al. 2001; Dik et al. 2010, 2011a, b, 2015, 2017a, b; Galloway and Lamb 2017; Chu et al. 2019; Lamb and Galloway 2019). Lice abundance may also co-vary with sex and age (Durkin et al. 2015).

On the other hand, according to the literature, there is conflict on the findings regarding the biotic and abiotic effects on lice prevalence (Moyer et al. 2002a; Sychra et al. 2011; da Cunha Amaral et al. 2017; Sajid and Ehsan

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2017; Bush and Clayton 2018; Chu et al. 2019; Galloway and Lamb 2021). For example, migratory behavior reduces prevalence (Bush and Clayton 2018). However, contrary to Bush and Clayton (2018), high chewing lice prevalence has been reported in migratory species (Sajid and Ehsan 2017).

A number of studies have indicated that lice prevalence can be affected by the feeding type of the bird. Chu et al. (2019) report that host food guild has an effect on lice prevalence and that the lowest prevalence was recorded in insectivore species. On the other hand, it has been found that the host's beak shape rather than its food guild plays an important role in lice density in *Aphelocoma californica* (Moyer et al. 2002a).

Also, there is no general consensus on the effect of ecological factors on lice. It has been reported that lice species richness and prevalence increase in *Columba livia* in the warmest season (da Cunha Amaral et al. 2017). On the other hand, harsh conditions during the winter and gathering in flocks may lead to a higher prevalence in birds (Sychra et al. 2011). There are different findings on the humidity effects on the abundance of lice. According to Moyer et al. (2002b), birds host fewer lice in arid regions, but Carrillo et al. (2007) determine a high abundance of lice in arid environments.

Furthermore, although there is a correlation between a host's body mass and lice abundance, the host's wingspan and body size effects on the prevalence of chewing lice have not been evaluated sufficiently (Hughes and Page 2007). The aim of this study is to reveal the factors affecting the prevalence, richness, and abundance of chewing lice reported in Turkey on bird species.

Materials and methods

This study was carried out to detect the relationship between chewing lice and their bird hosts. Data on the chewing lice and their hosts consists of published (Dik 2006a, b, 2009, 2010a, b; Dik and Aydenizöz Özkayhan 2007; Dik and Dinçer 2012; Dik and Uslu 2006a, b, c, 2007, 2008, 2009; Dik and Yamaç 2008; Dik et al. 2009, 2010, 2011a, b, 2013a,b, 2015, 2017a, b; Inci et al. 2010; Girişgin et al. 2013; Göz et al. 2015; Karatepe et al. 2017) and unpublished findings in twenty-three different regions of Turkey between 1999 and 2019. In total, 2514 birds from 207 species (22 orders) were examined, from which 762 were infested. A total of 13,034 lice from 200 species were found. We removed all small samples (< 10 individual birds), as species richness may be affected by sample size effects (Cavus et al. 2021). In the end, a total of 2101 individuals from 59 different species were evaluated to understand the effect of habitat, food guild, migratory behavior, weight, wingspan, and length on the prevalence, richness, and abundance of chewing lice. Chewing lice species collected from birds were presented in S1 (Supplementary Material). Data on the morphological and ecological characteristics of birds were obtained from literature (Svensson et al. 2010; BirdLife International 2023). According to the habitat characteristics, birds were considered under five habitat types: those living in wetlands (W), forest areas (F), open areas (O), and urban areas (U) and in more than one different habitat (M). The individuals were grouped under four food guilds: carnivore (C), insectivore (I), herbivore (H), and omnivore (OM), according to their feeding type. In terms of migration behavior, they were evaluated under three groups: resident (R), migrant (MI), and mixed group (D), where both local and migrant individuals are present in the region.

Bird individuals caught using mist nets have been examined for ectoparasites macroscopically since 1999. The chewing lice found on the birds were collected with forceps, and the birds were released back into nature after examination. In a number of cases, birds shot by hunters or injured in traffic accidents were brought to veterinary faculties for treatment. In both cases, a few of the birds were treated with an insecticide with synthetic pyrethroid, such as tetramethrin or permethrin, and kept in a cardboard box for approximately for half an hour. Later, the birds were examined for ectoparasites, after which they released back into nature if they could fly, or kept for further treatment at the clinics. After treatment, the paper at the bottom of the box was examined macroscopically and the ectoparasites, if present, were collected. After this, the contents of the box were emptied into petri dishes and examined under a stereo zoom microscope (Nikon SMZ745) for ectoparasites.

In a number of cases, the birds were found dead on roads or in gardens. They were brought to the parasitology laboratory and washed under tap water in a plastic cuvette, with the contents of the cuvette dish being transferred to petri dishes in small portions. The petri dishes were examined using a stereo zoom microscope for ectoparasites, with any ectoparasites found being collected by forceps and preserved in 70% ethanol in tubes until preparation.

As a result of these studies, a few thousand lice samples were collected. Several of them were cleared in 10% KOH for 24–48 h. Certain samples belonging to the same species were preserved in 70% ethanol for other studies. Cleared chewing lice were rinsed in distilled water and left for a few hours, before being transferred again to ethanol 70%. Later, they were kept in ethanol 99% for a few hours before being mounted in Canada balsam on slides. They were kept in an incubator at 50–60 °C for 2–3 weeks for drying. After drying, the chewing lice specimens were examined under a binocular light microscope (Leica DM 750) and identified to genera and species. In the identification of the genera, the methods of Price et al. (2003) were followed. In the identification of the species, original descriptions of the species were used, if this was possible, or by certain identification keys (Clay 1940, 1958, 1959, 1962, 1969; Hopkins and Timmermann 1954; Price and Beer 1963, 1965; Nelson and Price 1965; Price and Clay 1972; Price et al. 2003; Gustafsson and Bush 2017; Gustafsson et al. 2018).

Statistical analyses

To model the non-normal data with the extreme number of zeros, zero-inflated (ZI) regression models are used, such as zero-inflated Poisson (ZIP) (Lambert 1992), zero-inflated negative binomial (ZINB) (Greene 1994), negative binomial hurdle (NBH), and Poisson hurdle (PH) models. In practice, it is frequently seen that count data with an extreme number of zero values is often over-dispersed. The parameter estimations of the second part in the model may be biased when the ZIP model is directly used to fit data if the frequency of zero values is higher than its expected frequency. Otherwise, the observed over-dispersion parameter has modeled with the negative binomial part in the ZINB model. Therefore, the ZINB model is used instead of the ZIP model to overcome the over-dispersion in the ZI data (Zeileis et al. 2008). The hurdle model can be expressed as in the following equation.

$$P\left(Y_i = y_i \middle| x_i, z_i, \beta, \gamma\right) = \begin{cases} f_{zero}\left(0;z_i;\gamma\right), y_i = 0 \\ \left(1 - f_{zero}\left(0;z_i;\gamma\right)\right)\frac{f_{count}(y_i;x_i;\beta)}{1-f_{count}(0;x_i;\beta)}, y_i > 0 \end{cases}$$

where y_i is the value of the response variable for the observation i, z_i is a vector of the predictor variables in the zero part, x_i represents a vector of predictors in the hurdle part, γ is a vector of coefficients belonging to z, and β denotes a vector of coefficients related to x. f_{zero} is a probability density function on $\{0, 1\}$, and f_{count} is a probability density on $\{1, 2, 3, \ldots\}$ (Hofstetter et al. 2016).

The Poisson Generalized Linear Model (PGLM), the Negative-Binomial Generalized Linear Model (NBGLM), ZIP, ZINB, NBH, and PH models are fitted into the data to assess the impact of habitat, food guild, migratory behavior, weight, wingspan, and length on the number of chewing lice, as well as the chewing lice species in the birds using MASS (Venables and Ripley 2002), pscl (Zeileis et al. 2008), and moments (Komsta 2022) R-packages. Only the bird species is not considered as a predictor in the models because its dimension is too high to compute the parameter estimations. Its effect is investigated by the Brunner-Dette-Munk (BDM) test, which is the alternative of the Kruskal–Wallis test in the case of the variance homogeneity assumption being violated (Brunner et al. 1997). The AIC and over-dispersion parameter are used to define the best model fit.

Modeling the lice prevalence and abundance

In this section, the ZINB model is used for modeling the effects of the considered factors on lice prevalance and abundance because the number of chewing lice consists of an extreme number of zero observations (74%). The model consists of two parts: the first part is the binomial part which models response indicating the prevalance as ($Y = 0$) shows there is no lice and with lice ($Y = 1$), and the second part is the count part which models the number of chewing lice, that is, the abundance for those birds ($Y > 0$).

We consider the variables habitat, food guild, migratory behavior, weight, wingspan, and length in this phase. To construct the model, we use forward variable selection method. Firstly, it begins with no candidate predictors and selects the predictor that has the highest R-squared value. At each step, we select the predictor that most increases the R-squared value. Finally, we stop adding predictors when none of the remaining predictors is significant. The Akaike Information Criterion (AIC) is applied to identify the relative importance of the candidate models. A dispersion parameter is also used to identify the dispersion of the model. In practice, the model is the best when the dispersion parameter is about to 1. It can be seen that in S2 (Supplementary Material) the ZINB model is the best to identify the relationship between the predictors and the lice prevalence and abundance according to the closeness of the value of the dispersion parameter to 1 and the lowest AIC. Thus, we use the ZINB model as a final model.

To investigate the effect of bird species on the lice abundance, we concluded to use the BDM test after checking the assumption of its parametric equivalent. The dataset is not normally distributed according to the results of the Shapiro–Wilk normality test, and the skewness of 12.42 and kurtosis of 199.50. The result of the Bartlett test shows the data is non-homogenous in variances according to the bird species at a nominal level of $\alpha = 0.05$. When the 59-bird species are compared according to the number of chewing lice, a BDM test is used instead of the classical F-test, because the violation of the assumptions is normality and variance homogeneity. The P-value of the BDM test is close to 0, so indicating that the lice abundance is different in bird species for a nominal level $\alpha = 0.05$.

Modeling lice richness

In this section, the NBH model is used for modeling the effects of the considered factors on lice richness because the number of chewing lice species consists of an extreme number of zero observations (74%). The NBH model has two parts: one zero part which models response indicating birds without ($Y = 0$) or with chewing lice ($Y = 1$, where all values larger than 0, that is, are fixed at 1), and the count part that models the lice richness for those birds (for those with $Y > 0$). In this model, the count part is only considered because the zero part indicates whether birds are with any lice.

The forward variable selection method is used to define the model as in the model for lice prevalence and abundance with same variables. It can be seen that in S3 (Supplementary Material), the NBH model is the best to identify the relationship between the predictors and the lice richness in terms of the values of the AIC and dispersion parameter. Thus, we use the NBH model as a final model.

To investigate the effect of bird species on the lice richness, we again used the BDM test, because the data is non-normally distributed, with skewness of 2.36 and kurtosis of 8.75. The result of a Bartlett test shows the data is non-homogenous in variances according to the bird species at a nominal level of $\alpha = 0.05$. When the 59-bird species are compared according to the lice richness, the BDM test is used and the P-value is close to 0, so indicating that the lice richness is different in bird species for a nominal level $\alpha = 0.05$. The forward selection method is used to define the model.

Results

The summary statistics for the lice abundance is given in Table 1. It represents the number of the observed birds (n), the observed minimum (min) chewing lice in a bird, the observed maximum (max) chewing lice in a bird, the mean (mean), the variance (var), and the sum (sum) of the lice number. The maximum abundance and the highest mean chewing lice number were 454 and 53.81, respectively, in *Pelecanus onocrotalus*. The minimum abundance was determined in *Tringa totanus*. Only 1 individual has been identified in this species (Table 1).

The coefficients' estimates, standard error, and the P-value of the significance testing of the coefficients of the ZINB model for the lice prevalence (binomial part) and abundance (count part) are given in Table 2. The interpretation of the coefficients from the ZINB model is straightforward. A count model is constructed with the statistically significant predictors being habitat, migratory behavior, and length. The zero part is a binary logistic regression contracted with predictors being migratory behavior, wingspan, and habitat. The habitat (**O**pen areas) and migratory behavior (**MI**grant) are the reference levels of the variables in the model; thus, they are not seen in Table 2.

In the binomial part which models the lice prevalence, the odds ratio of the habitat (**M**ore than one habitat) is 0.6006, which implies that the birds from habitat (**M**ore than one habitat) are about 0.6 times less likely to have a chewing louse than those from other habitats. The birds from habitat (**U**rban areas) are 5.78 times more likely to have a chewing louse. The birds from habitat (**M**ore than one habitat) having the maximum wingspan are the least likely to have lice.

In the count part which models the lice abundance, the relative ratio of the habitat (**M**ore than one habitat) is 0.2076, which implies that birds from habitat (**M**ore than one habitat) are about 0.2 times less likely to lice abundance. Therefore, the birds from habitat (**M**ore than one habitat), migratory

Table 1 Summary statistics of the data of the lice abundance from birds in Turkey

Bird order	Bird species	n	Characteristics of birds			Lice abundance				
			Habitat	Food guild	Migratory behavior	min	max	mean	var	sum
Anseriformes	*Anas acuta*	11	W	OM	MI	0	55	6	268.40	66
	Anas crecca	22	W	OM	D	0	14	2.59	15.30	57
Galliformes	*Meleagris gallopavo*	11	M	OM	R	0	16	4.10	33.10	45
	Alectoris chukar	14	O	OM	MI	0	32	7.93	94.84	111
Columbiformes	*Columba livia*	45	U	OM	R	0	58	6.27	115.29	282
Gruiformes	*Fulica atra*	17	W	OM	D	0	99	41.35	616.86	703
Podicipediformes	*Podiceps cristatus*	62	W	C	D	0	146	16	444.78	992
Charadriiformes	*Calidris minuta*	10	W	OM	MI	6	51	21	221.55	210
	Gallinago gallinago	11	W	OM	MI	0	6	1.27	4.42	14
	Tringa glareola	11	W	OM	MI	1	101	23.54	721.87	259
	Larus michahellis	22	W	C	D	0	9	0.91	5.32	20
Ciconiiformes	*Ciconia ciconia*	43	O	C	MI	0	365	27.72	5564.77	1192
Pelecaniformes	*Pelecanus onocrotalus*	21	W	C	D	0	454	53.81	11,321.4	1130
	Ixobrychus minutus	17	W	C	MI	0	4	0.29	0.97	5
Accipitriformes	*Buteo buteo*	46	O	C	R	0	17	2.87	18.96	132
	Buteo rufinus	73	O	C	R	0	416	32.14	4187.87	2346
Strigiformes	*Asio otus*	13	F	C	D	0	28	5.84	82.64	76
Coraciiformes	*Merops apiaster*	29	O	I	MI	0	41	6.41	78.89	186
Psittaciformes	*Melopsittacus undulatus*	16	M	H	R	0	5	0.38	1.58	6

Table 1 (continued)

Bird order	Bird species	*n*	Characteristics of birds			Lice abundance				
			Habitat	Food guild	Migratory behavior	min	max	mean	var	sum
Passeriformes	*Lanius collurio*	28	O	C	MI	0	21	1.75	28.34	49
	Pica pica	76	M	OM	D	0	44	1.28	27.99	97
	Corvus cornix	14	M	OM	R	0	0	0	0	0
	Periparus ater	15	F	OM	D	0	0	0	0	0
	Cyanistes caeruleus	10	F	OM	R	0	0	0	0	0
	Parus major	22	F	H	R	0	0	0	0	0
	Remiz pendulinus	15	W	OM	D	0	0	0	0	0
	Panurus biarmicus	50	W	OM	R	0	3	0.2	0.28	10
	Hirundo rustica	114	M	I	MI	0	13	0.91	4.24	104
	Cettia cetti	37	W	C	D	0	1	0.03	0.03	1
	Aegithalos caudatus	13	M	OM	MI	0	0	0	0	0
	Phylloscopus trochilus	111	F	OM	MI	0	13	0.61	5.18	68
	Phylloscopus collybita	62	F	OM	D	0	12	0.39	2.57	24
	Acrocephalus arundinaceus	33	W	OM	MI	0	0	0	0	0
	Acrocephalus melanopogon	71	W	OM	D	0	2	0.07	0.09	5
	Acrocephalus schoenobaenus	39	W	C	MI	0	3	0.08	0.23	3
	Acrocephalus scirpaceus	23	M	OM	MI	0	1	0.13	0.12	3
	Sylvia atricapilla	103	F	OM	D	0	3	0.09	0.14	9
	Sylvia borin	56	F	OM	MI	0	10	0.84	3.37	47
	Curruca nisoria	11	F	OM	MI	0	2	0.54	0.47	6
	Curruca curruca	10	M	OM	MI	0	0	0	0	0
	Curruca melanocephala	15	F	OM	D	0	9	0.93	6.07	14
	Curruca communis	31	F	OM	MI	0	1	0.10	0.09	3
	Sitta krueperi	75	F	OM	R	0	5	0.12	0.54	9
	Sturnus vulgaris	60	O	OM	D	0	28	1.07	14.54	64
	Turdus merula	47	F	OM	D	0	100	5.60	257.25	263
	Turdus philomelos	17	F	OM	D	0	8	0.71	4.47	12
	Muscicapa striata	28	F	OM	MI	0	6	0.25	1.30	7
	Erithacus rubecula	48	F	OM	D	0	4	0.17	0.40	8
	Luscinia svecica	14	M	OM	D	0	0	0	0	0
	Luscinia luscinia	30	F	OM	MI	0	3	0.1	0.3	3
	Ficedula parva	16	F	C	MI	0	0	0	0	0
	Ficedula albicollis	16	F	OM	MI	0	1	0.063	0.063	1
	Phoenicurus phoenicurus	65	F	OM	MI	0	1	0.01	0.02	1
	Passer domesticus	75	U	OM	R	0	12	0.23	1.96	17
	Passer hispaniolensis	68	F	OM	D	0	2	0.18	0.21	12
	Motacilla flava	15	O	OM	MI	0	33	2.73	71.06	41
	Anthus spinoletta	15	O	OM	D	0	2	0.20	0.31	3
	Fringilla coelebs	29	F	OM	D	0	1	0.03	0.03	1
	Emberiza schoeniclus	30	W	OM	D	0	20	1.43	17.63	43

Habitat (W: wetlands, O: open areas, U: urban areas, F: forest areas, M: more than one habitat)
Food guild (OM: omnivore, C: carnivore, I: insectivore, H: herbivore)
Migratory behavior (R: resident, MI: migrant, D: mixed group)

Table 2 Output of the ZINB model for the lice prevalence and abundance from birds in Turkey

Count model coefficients					
	Estimate	Relative ratio	Std. error	*Z* value	*P*-value
intercept	0.7817	2.1851	0.3006	2.600	0.0093*
habitat (M)	−1.5718	0.2076	0.2919	−5.384	0.0000*
habitat (U)	0.0721	1.0748	0.3616	0.200	0.8418
habitat (F)	−0.3372	0.7137	0.3368	−1.001	0.3168
habitat (W)	0.6459	1.9078	0.2823	2.288	0.0221*
migration (D)	−0.1747	0.8396	0.1832	−0.954	0.3420
migration (R)	0.5326	1.7034	0.2510	2.122	0.0338*
length	0.0255	1.0258	0.0038	6.682	0.0000*
log(theta)	−1.4297	-	0.0681	−21.000	0.0000*
Binomial model coefficients (binomial with logit link)					
	Estimate	Odds ratio	Std. error	*Z* value	*P*-value
intercept	3.4981	33.0526	0.7222	4.823	0.0000*
habitat (M)	−0.5097	0.6006	0.7197	−0.708	0.4789
habitat (U)	1.7551	5.7840	0.7058	2.487	0.0129*
habitat (F)	0.9863	2.6813	0.5535	1.782	0.0748
habitat (W)	0.8709	2.3890	0.5711	1.525	0.1273
wingspan	−0.1480	0.8624	0.0211	−6.994	0.0000*

* *P*-value < 0.05

behaviour (D: mixed group) and which are of minimum length, are those which are least likely to lice abundance (Table 2). The relative ratio combinations of the habitat and migratory behavior for the count part of the ZINB model are given in Table 3. These relative ratio combinations are calculated by multiplying the individual relative ratio of the habitat and migration variables. It is easier to interpret the relative ratio of categorical variables in the model. It shows the relative ratio from low to high with a color scale of green to red. According to Table 3, the birds from habitat (**M**ore than one habitat) have the lowest lice abundance, while they have the highest from habitat (**W**etland) among the other habitats. The birds that have migratory behavior (**D**: mixed group) have the lowest lice abundance, while they have the highest one for their migratory behavior is **R**esident. Moreover, the birds that have migratory behavior (**D**: mixed group) from habitat (**M**ore than one habitat) have the lowest lice abundance, while the birds that have migratory behavior (**R**esident) from habitat (**W**etland) have the highest in all combinations (Table 3).

The summary statistics for the lice richness is given in Table 4. It represents the number of the observed birds (n), the observed minimum (min) chewing lice species in a bird, the observed maximum (max) chewing lice species in a bird, the mean (mean), the variance (var), and the sum (sum) of the lice richness. The highest lice richness was observed in *Turdus merula* with six chewing lice species (Table 4). The highest chewing lice richness in an individual bird was recorded on *Fulica atra*. In the *Phoenicurus phoenicurus*, although 65 individuals were examined, only one chewing lice species was detected (Table 4).

The coefficient estimates, standard error, and the *P*-value of the significance testing of the coefficients of the NBH model for the lice richness are given in Table 5. The count part of the model is constructed with statistically significant predictors of habitat, wingspan, and migratory behavior. The relative ratio of the habitat (**M**ore than one habitat) is 0.0905, which implies that birds from habitat (**M**ore than one habitat) are about 0.09 times less likely to the lice richness than those from other habitats. The birds from habitat (**W**etland) are 1.04 times more likely to the lice richness. The birds from habitat (**F**orest areas) with migration (**R**esident) and the minimum wingspan have the least lice richness. The relative ratio combinations of the habitat and migratory behavior for the count part of the NBH model are given in Table 6. According to Table 6, the birds from habitat (**M**ore than one habitat) have the lowest lice richness, while they have the highest from habitat (**W**etland) among the other habitats. This finding is same as the finding for the lice abundance. The birds that have migratory behavior (**R**esident) have the lowest lice richness, while they have the highest one for their

Table 3 Relative ratio combinations of habitat and migratory behavior in the ZINB model for lice abundance (only count part) from birds in Turkey

		Habitat				
		M	F	O	U	W
Migratory behaviour	D	0.1582	0.5791	0.8229	0.8746	1.5868
	MI	0.1923	0.7037	1.0000	1.0628	1.9283
	R	0.3376	1.2353	1.7555	1.8657	3.3851

Habitat (W: wetlands, O: open areas, U: urban areas, F: forest areas, M: more than one habitat)

Migratory behavior (R: resident, MI: migrant, D: mixed group)

migratory behavior is **MI**grant. Moreover, the birds that have migratory behavior (**R**esident) from habitat (**M**ore than one habitat) have the lowest lice richness, while the birds that have migratory behavior (**MI**grant) from Habitat (**W**etland) have the highest in all the combinations (Table 6).

Discussion

Prevalence of chewing lice

According to lice species presence or absence data, the highest prevalence was determined on bird species living in urban areas compared to other habitats in this study. Although it has been reported that urbanization can negatively affect lice prevalence on birds (Delgado-V and French 2012; Gutiérrez-Galán and Martínez-Fernández 2023), Ahmed et al. (2017) found higher prevalence in urban-dwelling bird which is in agreement with our results.

Possible explanation for higher prevalence in urban area can be low defense against pathogens. It is known that urban areas support urban-tolerant bird species by providing feeding opportunities (Galbraith et al. 2015; Ortega-Álvarez and MacGregor-Fors 2009). On the other hand, the nutritional quality of anthropogenic resources is lower than that in natural environments, which have high diversity and quality of food (Isaksson and Andersson 2007; Meyrier et al. 2017; Murray et al. 2018). Poor nutrition can affect immunity negatively (Sheldon and Verhulst 1996). Several urban bird species are reported to possess a reduced immune responsiveness (Bailly et al. 2016). The negative effects of urbanization on immune systems can result in low defense against pathogens (Roulin et al. 2003). As a result, urban-dwelling bird species can have a higher parasites prevalence. Indeed, the lowest prevalence was detected in bird species which are distributed throughout different habitats in this study. This finding may indicate that different habitats can provide adequate resources, which positively affect the immune response against parasites for bird species.

Another possible explanation for the higher lice prevalence in urban-dwelling bird species can be the Dilution Effect Hypothesis. According to this hypothesis, the parasites' prevalence is reduced in habitats where species richness is high (Keesing et al. 2010; Halliday et al. 2020). It is reported that the richness of bird species is lower in urban areas (Sol et al. 2017; Batáry et al. 2018; Leveau 2018; Anılır 2021). As reported by Bradley and Altizer (2007), the low species richness may have caused the high prevalence in this study.

Many studies have indicated decreased species richness, but increased bird abundance, in urban areas (Palomino and Carrascal 2007; Silva et al. 2015). Marzluff (2001) reports that urban-dwelling species have higher densities than those dwelling in less-disturbed areas. It is thought that as another explanation, horizontal transmission of lice between birds may occur during feeding or roosting

Table 4 Summary statistics of the data of the lice richness from birds in Turkey

Bird order	Bird species	*n*	Characteristics of birds			Lice richness				
			Habitat	Food guild	Migratory behavior	min	max	mean	var	sum
Anseriformes	*Anas acuta*	11	W	OM	MI	0	3	0.73	1.02	4
	Anas crecca	22	W	OM	D	0	3	1.14	1.27	4
Galliformes	*Meleagris gallopavo*	11	M	OM	R	0	1	0.45	0.27	2
	Alectoris chukar	14	O	OM	MI	0	3	1.57	2.11	4
Columbiformes	*Columba livia*	45	U	OM	R	0	4	1.09	0.99	4
Gruiformes	*Fulica atra*	17	W	OM	D	0	5	3.64	1.49	5
Podicipediformes	*Podiceps cristatus*	62	W	C	D	0	2	1.47	0.40	2
Charadriiformes	*Calidris minuta*	10	W	OM	MI	2	4	2.60	0.49	4
	Gallinago gallinago	11	W	OM	MI	0	3	0.63	1.05	4
	Tringa glareola	11	W	OM	MI	1	3	2.36	0.45	3
	Larus michahellis	22	W	C	D	0	2	0.27	0.40	3
Ciconiiformes	*Ciconia ciconia*	43	O	C	MI	0	4	0.91	2.32	4
Pelecaniformes	*Pelecanus onocrotalus*	21	W	C	D	0	3	1.29	1.11	3
	Ixobrychus minutus	17	W	C	MI	0	1	0.11	0.11	1
Accipitriformes	*Buteo buteo*	46	O	C	R	0	4	0.89	1.03	5
	Buteo rufinus	73	O	C	R	0	4	1.68	1.27	5
Strigiformes	*Asio otus*	13	F	C	D	0	1	0.61	0.25	1
Coraciiformes	*Merops apiaster*	29	O	I	MI	0	3	1.31	1.15	3
Psittaciformes	*Melopsittacus undulatus*	16	M	H	R	0	1	0.13	0.12	2

Table 4 (continued)

Bird order	Bird species	*n*	Characteristics of birds			Lice richness				
			Habitat	Food guild	Migratory behavior	min	max	mean	var	sum
Passeriformes	*Lanius collurio*	28	O	C	MI	0	2	0.36	0.31	3
	Pica pica	76	M	OM	D	0	2	0.31	0.25	3
	Corvus cornix	14	M	OM	R	0	0	0	0	0
	Periparus ater	15	F	OM	D	0	0	0	0	0
	Cyanistes caeruleus	10	F	OM	R	0	0	0	0	0
	Parus major	22	F	H	R	0	0	0	0	0
	Remiz pendulinus	15	W	OM	D	0	0	0	0	0
	Panurus biarmicus	50	W	OM	R	0	2	0.18	0.19	3
	Hirundo rustica	114	M	I	MI	0	2	0.46	0.33	2
	Cettia cetti	37	W	C	D	0	1	0.03	0.03	1
	Aegithalos caudatus	13	M	OM	MI	0	0	0	0	0
	Phylloscopus trochilus	111	F	OM	MI	0	2	0.13	0.13	3
	Phylloscopus collybita	62	F	OM	D	0	1	0.13	0.11	4
	Acrocephalus arundinaceus	33	W	OM	MI	0	0	0	0	0
	Acrocephalus melanopogon	71	W	OM	D	0	1	0.06	0.09	1
	Acrocephalus schoenobaenus	39	W	C	MI	0	1	0.03	0.03	1
	Acrocephalus scirpaceus	23	M	OM	MI	0	1	0.13	0.12	1
	Sylvia atricapilla	103	F	OM	D	0	1	0.07	0.06	1
	Sylvia borin	56	F	OM	MI	0	1	0.29	0.21	3
	Curruca nisoria	11	F	OM	MI	0	2	0.45	0.67	4
	Curruca curruca	10	M	OM	MI	0	0	0	0	0
	Curruca melanocephala	15	F	OM	D	0	1	0.20	1.17	2
	Curruca communis	31	F	OM	MI	0	1	0.10	0.09	2
	Sitta krueperi	75	F	OM	R	0	1	0.03	0.03	1
	Sturnus vulgaris	60	O	OM	D	0	3	0.38	0.61	4
	Turdus merula	47	F	OM	D	0	2	0.49	0.60	6
	Turdus philomelos	17	F	OM	D	0	2	0.18	0.28	3
	Muscicapa striata	28	F	OM	MI	0	1	0.07	0.07	2
	Erithacus rubecula	48	F	OM	D	0	1	0.10	0.10	1
	Luscinia svecica	14	M	OM	D	0	0	0	0	0
	Luscinia luscinia	30	F	OM	MI	0	1	0.03	0.03	1
	Ficedula parva	16	F	C	MI	0	0	0	0	0
	Ficedula albicollis	16	F	OM	MI	0	1	0.06	0.07	1
	Phoenicurus phoenicurus	65	F	OM	MI	0	1	0.01	0.02	1
	Passer domesticus	75	U	OM	R	0	1	0.08	0.07	2
	Passer hispaniolensis	68	F	OM	D	0	2	0.18	0.21	2
	Motacilla flava	15	O	OM	MI	0	2	0.40	0.40	2
	Anthus spinoletta	15	O	OM	D	0	1	0.13	0.12	1
	Fringilla coelebs	29	F	OM	D	0	1	0.03	0.03	1
	Emberiza schoeniclus	30	W	OM	D	0	1	0.16	0.14	1

Habitat (W: wetlands, O: open areas, U: urban areas, F: forest areas, M: more than one habitat)
Food guild (OM: omnivore, C: carnivore, I: insectivore, H: herbivore)
Migratory behavior (R: resident, MI: migrant, D: mixed group)

Table 5 Output of the NBH model for the lice richness from birds in Turkey

Count model coefficients					
	Estimate	Relative ratio	Std. error	*Z* value	*P*-value
Intercept	0.3241	1.3828	0.1251	2.590	0.0096*
habitat (M)	−2.4017	0.0905	0.4563	−5.263	<0.0001*
habitat (U)	−0.5740	0.5632	0.2438	−2.354	0.0185*
habitat (F)	−1.6614	0.1898	0.3003	−5.532	<0.0001*
habitat (W)	0.0441	1.0451	0.1499	0.294	0.7684
wingspan	0.0022	1.0022	0.0007	2.991	0.0028*
migration (D)	−0.2352	0.7903	0.1479	−1.591	0.1171
migration (R)	−0.3090	0.7341	0.1472	−2.098	0.0358*
log(theta)	13.8148	-	75.4090	0.158	0.8748

Migratory behavior (R: resident, MI: migrant, D: mixed group)

Habitat (W: wetlands, O: open areas, U: urban areas, F: forest areas, M: more than one habitat)

* *P*-value < 0.05

in large groups. All chewing lice are obligate permanent ectoparasites. They complete their entire life cycle and are usually host specific (Johnson and Clayton 2003). They can be transmitted to other hosts by contact (Darolova et al. 2001). Therefore, a higher infestation rate of colonial birds than of terrestrial birds was reported (Rózsa et al. 1996; Tomás et al. 2016; Diakou et al. 2017). Furthermore, it is found that birds at bird feeder which individuals become highly clustered have a higher abundance of parasites (Galbraith et al. 2017).

The potential explanations that are indicated above cannot be mutually exclusive. On the other hand, more detailed studies are needed to investigate these possibilities concerning the high prevalence in urban areas.

Abundance of chewing lice

The most abundant lice were detected on wetland bird species. Moyer et al. (2002b) found higher prevalence and density in wetland birds. It is thought that this result is further supported by findings in this study.

A correlation is found between the number of chewing lice and the length of birds that are living in aquatic environments in this study. To the best of our knowledge, interaction between abundance of lice and bird length has not been reported. On the other hand, it has been indicated that body mass has a positive effect on the lice abundance (Galloway and Lamb 2017; Lamb and Galloway 2019). As an explanation, it is stated that more lice individuals can obtain a greater area for refuge and food on larger birds (Rózsa 1997; Clayton and Walther 2001; Poulin 2007). Also, Rózsa (1997) indicated that larger birds have long life span which is advantage for lice species by low transmission probability. Although no effect of body weight on lice density was detected in this study, a bird's length can provide more area for refuge, food sources, or longevity which are not necessarily mutually exclusive alternatives.

In the present study, the results show that a higher number of lice individuals were recorded on resident bird species than those of migrants. Higher prevalence on resident birds has been reported in many studies (Sychra et al. 2011; Diakou et al. 2017; Gustafsson et al. 2019). It is claimed that heavily infested birds are more vulnerable in migration (Diakou et al. 2017). In fact, it is known that in species with abundant chewing lice, their body mass decreases, and they become more susceptible to infestation (Hoi et al. 2012). Since heavily infected birds may die on migration, the survival of birds on migration may depend on them being low infected or non-infected by parasites. As a result, resident birds may have more lice than migrants.

In this study, the highest lice abundance and the lowest lice species richness were found on resident birds. On the other hand, Clayton and Walther (2001) find a positive correlation between the richness of lice species and individuals. Also, Møller and Rozsa (2005) report that the number of Ischnoceran species is positively correlated with the abundance of the Amblyceran species. The low number of species in the host may have led to the high number of individuals, due to the absence of interspecies competition. But detailed studies are conducted to gain further assessment on the relationship between the number of louse species and individuals.

Table 6 Relative ratio combinations of habitat and migration behavior in the NBH model for lice richness (only count part) from birds in Turkey

		Habitat				
		M	F	U	O	W
Migratory behaviour	R	0.0671	0.1391	0.4237	0.7333	0.7658
	D	0.0723	0.1500	0.4569	0.7907	0.8257
	MI	0.0915	0.1897	0.5778	1.0000	1.0443

Habitat (W: wetlands, O: open areas, U: urban areas, F: forest areas, M: more than one habitat)

Migratory behavior (R: resident, MI: migrant, D: mixed group)

The feeding type effect was not detected on the prevalence of chewing lice, species richness, or individual numbers in this study. On the other hand, Chu et al. (2019) report a higher prevalence on insectivore birds than on omnivores and frugivores. The effect of the shape of a bird's bill, as indicated in a study by Moyer et al. (2002a), may be evaluated in future studies.

Richness of chewing lice species

The recorded number of chewing lice species on bird species is between 1 and 6 in this study. The most louse species were recorded from *Turdus merula* with six species. According to Vas et al. (2012), eight louse species were found on *Turdus merula.* Although ten different lice species were reported on the same bird (Ward 1957; Price et al. 2003), the highest number of chewing lice species hosted by one individual bird was five (mean of 3.64) (*Fulica atra*). The five lice species (*Pseudomenopon pilosum*, *Fulicoffula lurida*, *Incidifrons fulicae*, *Rallicola fulicae*, and *Laemobothrion atrum*) identified on the *Fulica atra* are consistent with the species reported previously for this species (Hellenthal et al. 2004; Palma and Jensen 2005; Rékási et al. 2017; Ziani et al. 2020). Although sixty-five individuals were examined belonging to the *Phoenicurus phoenicurus* species, only one individual louse (*Penenirmus silvicultrix*) was found with the lowest mean number of chewing lice. Similarly, Açici et al. (2011) and Dik et al. (2011ab) report that chewing lice species are not recorded on *Phoenicurus phoenicurus* in Turkey.

In this study, the highest number of lice species is recorded on bird species living in wetlands. Although there are findings that the infestation rate is high on bird species living in warm and dry environmental conditions (Tomás et al. 2016), studies showing that the infestation rate and abundance of lice increase in humid environments have also been reported (Moyer et al. 2002b). Explanation for the lice richness on wetland bird species may be humidity, in this study. Dry weather has detrimental effects on lice species. As a result, louse infestations and the number of lice species are higher on bird species living in the aquatic environments. Larger uropygial glands may be the other explanation for lice richness. Galván et al. (2008) indicate that birds that are living in aquatic environments have larger uropygial glands. In addition, it is reported that the lice richness is higher on bird species with larger uropygial glands (Møller et al. 2010).

A positive correlation between lice richness and wingspan was found in wetland bird species. Although Silva et al. (2014) report a positive correlation between wingspan and abundance of lice, no correlation was found between wingspan and lice diversity in a previous study (Hughes and Page 2007). A long wingspan may provide more habitat for different lice species. To support the relationship between wingspan and species richness, detailed studies should be conducted.

In the current study, migrant species living in aquatic environments have higher species richness than resident birds. It is reported that migrant bird species host more parasites (Møller and Erritzøe 1998; Koprivnikar and Leung 2015). Moreover, Figuerola and Green (2000) indicate that there is a positive correlation between the number of parasite species and migration distance in waterfowl. A possible explanation for the high abundance and richness of parasites could be the transmission of parasites between the same or mixed bird species at stopover sites (Altizer et al. 2011; Tomás et al. 2016).

Conclusion

We conclude that urban birds tend to have a higher prevalence of chewing lice infestation. Habitat (wetland), wingspan, length, and migratory behavior influence lice richness and abundance. It is recommended to carry out further studies to get more detailed results regarding the data obtained by evaluating a large number of host individuals. For example, to evaluate the effect of urban areas on prevalence, it would be appropriate to conduct detailed studies that will reveal the relationship of urban bird species with their immune systems. In addition, comparing the prevalence of the colonial bird species in urban areas with the territorial species will also provide data. Research should also be conducted to determine which of the possible explanations put forward by Rózsa (1997) are potential causes determining the effects of body length and wingspan on the abundance and richness of lice species.

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Declarations

Competing interests The authors declare no competing interests.

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