



Article

Host Migration and Size Do Not Influence the Prevalence of Most Chewing Lice (Phthiraptera: Amblycera and Ischnocera) on Shorebirds (Aves: Charadriiformes) across the World

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Abstract: Patterns of prevalence in chewing lice (Phthiraptera) on wild birds are poorly known, as are the underlying factors that influence these patterns. Here, we analyze a data set consisting of published prevalence data of lice on shorebirds, as well as new prevalence data from shorebirds examined in Australia, Canada, China, Japan, and Sweden between 2007 and 2020. In total, prevalence data from 10 genera of lice from over 110 host species were included, including all major families of shorebirds. Using a generalized linear mixed model, we examine how the prevalence of lice of different genera varies between different sets of birds, focusing on two factors associated with migration (migration length and migration route). We found that host body size does not influence prevalence of lice in the Charadriiformes for any of the four most common and widely distributed louse genera (*Actornithophilus*, *Austromenopon*, *Quadriceps*, and *Saemundssonina*). Moreover, neither of the two migration variables showed any statistically significant correlations with prevalence, except for the genus *Saemundssonina* in which the prevalence of lice on short-distance migrants was significantly higher than on intermediate- and long-distance migrants. We also present 15 new records of chewing lice for China and 12 for Australia.

Keywords: Phthiraptera; Charadriiformes; prevalence; migration; new records; index of specificity



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1. Introduction

Bird migration involves many of the longest [1,2] and highest [3] seasonal movements of any animal. These movements may be very costly for birds [4], in extreme cases involving the shrinkage of internal organs [5]. Molting behavior may be timed to the migration cycle (e.g., [6–8]) and have in some cases changed due to changes in migration patterns [9]. Long-distance migration, in particular, has been shown to correlate with many different aspects of bird morphology, such as wing aspect ratio, wing shape, development of the distal wing [10], and even skull and bill shape [11].

Given the importance of migration to many groups of birds, an overabundance of parasites, or an overly negative impact of parasites on their hosts, would likely affect migratory birds more than non-migratory birds. Even usually benign parasites may have an outsized negative impact on migrating birds, especially for birds that must traverse, e.g., large bodies of water or deserts where refueling may be impossible. These effects of parasitism could also include non-fatal effects, such as delayed arrival times to breeding grounds for parasitized birds [12] or lower fat deposits and smaller body sizes of parasitized birds (e.g., [13]) which may disadvantage birds during mating. Moreover, long-distance migration may expose birds to novel parasites (e.g., [14,15]). Alternatively, migration may

lower parasite prevalence by, e.g., killing off more heavily infested members of the host population [16] or moving hosts into environments less suitable for parasite transmission or survival [17]. However, Sychra et al. [18] suggested that if conditions are more favorable for parasites at wintering grounds than on breeding grounds, migration may increase populations of lice on migratory birds.

Studies on the impact of host migration on the prevalence, abundance, and species richness of parasites have yielded contradictory results (e.g., [19,20]) and seem to differ between major host groups. Most available data concern blood or internal parasites, and data for arthropod ectoparasites on birds are limited. Figuerola [21] found no correlation between the prevalence of feather mites and migratory behavior in songbirds in Europe, and Chu et al. [22] found no significant differences in the prevalence of chewing lice between resident and migratory birds in South China. However, Gustafsson et al. [23] contrasted the results of Chu et al. [22] with data from songbirds from Yunnan, where the overall prevalence of chewing lice was two orders of magnitude higher for resident birds than for migratory birds.

Here, we test the impact of host migration on the prevalence of amblyceran and ischnoceran lice on shorebirds (Charadriiformes). Lice of both orders are relatively common on their hosts (Table S1), and most well-studied shorebirds are parasitized by three to five species of lice (Table 1), typically one species from each of the genera: *Actornithophilus* Ferris, 1916 [24]; *Austromenopon* Bedford, 1939 [25]; *Quadriceps* Clay & Meinertzhagen, 1939 [26]; and *Saemundssonina* Timmermann, 1936 [27]. Each of these lice has a distinct ecology and often co-occur on the same host individual. Lice in the genus *Saemundssonina* are typical “head lice” [28] and are largely restricted to the head of the host, where they cannot easily be preened away except by allopreening [29] and scratching [30]. Lice in the genus *Quadriceps* are often considered “generalist” lice (e.g., [28]), but the group is likely paraphyletic and contains both head lice and wing lice. Of the two amblyceran lice, *Austromenopon* is a generalist, whereas some species of *Actornithophilus* are known to live inside feather quills (e.g., [31]) and have been implicated in adventitious molt of feathers [32]. Consequently, it may be expected that different groups of lice could be affected differently by host migration. For instance, lice that have a more adverse impact on their host may be less likely to survive on long-distance migrants, if presence of lice means that migration fails. Similarly, lice that have a low tolerance for fluctuations in, e.g., ambient humidity, temperature or salinity may be less able to adapt to changing circumstances during the migration period.

Specifically, we test whether migration distance has an impact on chewing louse prevalence in shorebirds. If chewing lice have a detrimental effect on survival in migrating shorebirds, this effect may increase with increasing migration distance. Moreover, as each of the major flyways offer different opportunities for staging grounds and stop-over areas, as well as for obstacles encountered (e.g., open oceans), we contrast data from different flyways. Finally, we test whether host size influences louse prevalence in shorebirds, under the assumption that larger birds may be more able to tolerate a small louse population compared to smaller birds without being adversely affected during migration. Abundance data is rarely published for shorebird lice, but in general, abundances of at least ischnoceran lice of shorebirds is higher than that for Passeriformes, but lower than that of, e.g., waterfowl (DRG, *in prep.*).

Table 1. Distribution of ischnoceran and amblyceran lice on charadriiform families. Host families follow Clements et al. [33] and louse classification follows Price et al. [34], Gustafsson and Olsson [35], and Eduardo [36]. Louse species considered stragglers in either of these publications are not included in the summary below. For each of the four most widely distributed genera, an “X” signifies that at least one host species in this family is known to be parasitized by lice in this genus, whereas dashes (“–”) signify that no lice of this genus are known from any host in this family. Note that the genus *Quadriceps* is morphologically variable and may consist of multiple genera with, e.g., *Cummingsiella*, *Luniceps*, and *Saemundssonina* nested within *Quadriceps*; a revision of this genus is sorely needed.

Host Family	<i>Actornithophilus</i>	<i>Austromenopon</i>	Other Amblycera	<i>Quadriceps</i>	<i>Saemundssonina</i>	Other Ischnocera
Alcidae	–	X	–	X	X	<i>Craspedonirmus</i>
Burhinidae	X	–	–	X	–	–
Charadriidae	X	X	–	X	X	–
Chionidae	X	–	–	X	X	–
Dromadidae	X	–	–	X	–	–
Glareolidae	X	X	<i>Rediella</i>	X	–	–
Haematopodidae	X	X	–	X	X	–
Ibidorhynchidae	X	–	–	X	–	–
Jacanidae	–	–	<i>Pseudomenopon</i>	–	X	<i>Rallicola</i>
Laridae	X	X	–	X	X	–
Pedionomidae	–	–	–	–	–	–
Pluvianellidae	–	–	–	–	–	–
Pluvianidae	–	–	–	X	–	–
Recurvirostridae	X	X	–	X	X	<i>Cirrothirus</i>
Rostratulidae	X	–	<i>Pseudomenopon</i>	X	X	–
Scolopacidae	X	X	–	X	X	<i>Carduiceps</i> , <i>Cummingsiella</i> , <i>Luniceps</i> , <i>Rhynonirmus</i> , <i>Rotundiceps</i>
Stercorariidae	–	X	–	X	X	<i>Haffneria</i>
Thinocoridae	–	–	–	X	–	–
Turnicidae	–	–	–	–	–	<i>Turnicola</i>

2. Materials and Methods

2.1. Collection and Identification of Lice

Birds were caught during normal banding activities in several localities in Australia, Canada, China, Japan, and Sweden between 2007 and 2020 (Table S1) and examined for lice, following the methodology outlined by Gustafsson and Olsson [35]. In short, birds were placed in fumigation chambers filled with ethyl acetate but allowed to have their heads outside the chambers to avoid negatively affecting the birds. Glass jars were normally used as fumigation chambers. In the case of some larger-bodied birds (e.g., gulls), plastic zip-lock bags were used as fumigation chambers instead of glass jars [23]. Birds were kept in the chambers for 10–20 min, depending on body size, whereupon the plumage was ruffled gently over a sheet of white paper, and all lice found in the chamber or on other paper were collected. The heads of birds were searched manually. Birds were released after louse collection.

As far as possible, lice collected during this study were identified to species level through published keys or descriptions. As a starting point, the following identification sources were used (arranged by genus): *Actornithophilus* [Clay (1962) [37]]; *Austromenopon* [Clay (1959) [38]]; *Carduiceps* [Timmermann (1954) [39]]; *Luniceps* [Gustafsson & Olsson (2012) [40]]; *Quadriceps* [Timmermann (1949, 1950, 1971) [41–43]; Hopkins & Timmermann (1954) [44]]; *Saemundssonina* [Clay (1949) [45]; Timmermann (1949b, 1950) [42,46]; Ward (1955) [47]]. For other genera, and for many species that have not been adequately illustrated and described, comparisons with identified specimens (including type specimens) deposited at the Natural History Museum (London, UK), the Price Institute for Parasite

Research (Salt Lake City, UT, USA), the Naturhistoriska Museet (Gothenburg, Sweden), the Museum für Naturkunde (Berlin, Germany), and the Naturhistoriska Riksmuseet (Stockholm, Sweden) were necessary. It should be noted that it is only with difficulty that some species can be identified from published descriptions and illustrations, and that a general revision of especially *Quadriceps* and *Saemundssonina* are sorely needed.

2.2. Literature Survey

In addition to specimens collected during this survey, we conducted a literature survey of published reports of the prevalence of any species of louse from any species of shorebird (as circumscribed by Clements et al. [33]). Searches were made during May–July 2022 in Google Scholar (scholar.google.com, accessed on 02 May 2022) and in the literature database on phthiraptera.myspecies.info. Search terms included all genera of chewing lice listed in Table 1, either in isolation or in combination with the terms: “prevalence”, “occurrence”, “[new] records of”, “survey”, and “population”. In addition, all families of shorebirds listed by Clements et al. [33] were also used as search terms in combination with the terms: “parasites”, “lice”, “chewing lice”, “ectoparasites”, “Mallophaga”, “Ischnocera”, “Amblycera” and “Phthiraptera”.

Prevalence data were extracted from these publications and combined with our own data from birds we have examined (Table S1). Collection methods of published data vary, but generally include either fumigation similar to that used by us or, in rare cases, the examination of dead birds. Identification of hosts and lice in published records were accepted as given, as specimen deposition data and resources used for identification of hosts and lice are often not given.

2.3. Data Analysis

Prevalence data from published and unpublished sources were analyzed together. To account for uncertainty in louse species identification, all analyses were made at the louse genus level. Moreover, all data points for which the number of examined hosts was <10 were excluded. Unfortunately, this means that ~55% of the data points collected were not included in the analysis. The records from *Calidris pusilla* of Tavera et al. [48] are excluded, as no exact number of examined species was given. Similarly, publications in which prevalence data were not included, or could not be calculated based on given data, were excluded. Moreover, the report by Literák [49] is listed in Table S1, but not included in the analysis, as no data were given for how many hosts were examined, only the number of hosts that were parasitized by lice.

We used the flyway (Americas, African-Eurasian, and East Asian-Australian) and migration length (short, intermediate, and long) as the main explanatory variables. Migration lengths were primarily derived from Billerman et al. [50]. In cases where more than one migration length was listed (e.g., “short to intermediate”), the longer distance was used; “medium” and “intermediate” distances were counted as the same. Sedentary species and altitudinal migrants were counted as short distance migrants. Species listed as only “migratory” were categorized based on species with similar ranges and migration patterns. However, movements across large bodies of water (e.g., Mediterranean Sea or Pacific Ocean) or across the Equator were always counted as long-distance migrants. For species in which migration patterns differ depending on population, categorization was based on collection locality (e.g., all *Chlidonias hybridus* examined in Australia are long-distance migrants). Short-distance migrants in our dataset comprise a mixture of sedentary species, altitudinal migrants, and birds that move from breeding grounds to oceanic wintering grounds in a longitudinal rather than latitudinal direction, or that move around regionally but not across regions. These birds do not here count as following flyways, even if some individual birds may migrate along flyways, and the same stop-over grounds may be used by short-distance and long-distance migrants simultaneously. Unsurprisingly, the birds that use flyways almost always have intermediate or long migration lengths. For this reason, flyway and migration length were analyzed separately.

We also considered median host length, which was log-transformed prior to analysis as an additional variable. Host length was used as a proxy for overall host size. Length measurements of hosts were obtained from Hayman [51] and Message and Taylor [52] for most waders; Madge and McGowan [53] for buttonquail; Olsen [54] for gulls; Menkhorst et al. [55] for skuas; and Svensson et al. [56] and Billerman et al. [50] for terns, auks, and other bird families. As a comparison, we also performed the same analyses using host mass, derived from Billerman et al. [50], instead of host length. While host mass is commonly used for analyses of louse abundance and prevalence [e.g., 22], migration may significantly affect mass [5,6], which may make it a poor proxy for host size for migration studies of this kind; by contrast, length is constant for a single host individual over the migration period.

In our study, prevalence (the proportion of hosts infested) was calculated as # host infested/# hosts examined. It ranged from 0% (none of the hosts examined is infested) to 100% (all of the hosts are infested); this is treated as the range 0–1 in our analysis. Our data set also includes many cases in which the same host species is infested with multiple species of lice, showing nested data structure. We considered host species as a random effect in the analysis and built generalized linear mixed models (GLMMs) with beta distribution and logit-link function. However, beta distribution can only deal with values greater than 0 and less than 1. We rescaled the proportion of hosts infested using the transformation $y' = \left[y(N - 1) + \frac{1}{2} \right] / N$, where y is the proportion of infested hosts and N is the number of hosts examined [57]. GLMMs were fitted using the “glmmTMB” function in the glmmTMB package [58] implemented in RStudio v.2021.9.0.351, RStudio Team, Boston, USA [59]. For the flyway, a GLMM was fitted for each of the three most prevalent louse genera (*Actornithophilus*, *Austromenopon*, and *Quadraceps*) and for the most abundant host family (Scolopacidae). For migration length, a GLMM was fitted for the same groups as the flyway, with the addition of the louse genus *Saemundssonina*. Before the final analysis, we included an interaction term between flyway and host length or migration length and host length depending on the model. Interaction terms did not significantly improve the model fit (tested with a likelihood ratio test) and thus were excluded from the model. For each model, the statistical significance of the full model was determined by comparing its fit with that of the null model (containing only the random effect, i.e., no explanatory variables) and applying a likelihood ratio test using the “anova” function. Only if there was a significant difference from the null model were the influence of individual predictor variables investigated further. Overdispersion was checked for by using the “simulateResiduals” function in the DHARMA package [60]. The predicted values and standard errors were extracted using the “ggpredict” function in the ggeffects package [61] and graphed using ggplot2 [62] in RStudio. Pairwise comparisons were made using the emmeans package [63].

3. Results

3.1. Louse Identification

Several of the louse species collected during this survey constituted new records for Sweden, which were previously reported by Gustafsson et al. [64]. In addition, 15 species of lice collected in the Leizhou area constituted new records for China, which are listed in Table 2. A complete list of lice on shorebirds recorded from China is given in Table 3. Similarly, a list of new records for Australia is provided in Table 4, with previous records listed by Timmermann [27,43], Murray et al. [65,66] and Gustafsson and Olsson [35]. No complete updated checklists of chewing lice have been published for Canada or Japan, and it is unknown whether any of the species collected in these countries during this survey constitute new national records.

Table 2. Lice collected from shorebirds (Charadriiformes) in the Leizhou area, Guangdong Province, China, in 2020. Specimens marked with an asterisk (*) are presumed to be stragglers. All collected species of chewing lice constitute new records for China. Abbreviations used: F = females; ID = resources used for identification of lice; M = males; N = nymphs; NE = number of hosts examined; NI (P) = number of hosts infested (prevalence). No lice were obtained from *Calidris temminckii* and *Pluvialis squatarola*, which we signify with dashes (“—”).

Host	NE	Louse	NI (P)	M	F	N	ID
<i>Calidris alpina</i>	24	<i>Austromenopon</i> sp.	1 (4.1%)	0	0	2	Nymphs, unidentifiable
		<i>Carduiceps meinertzhageni</i>	8 (33.3%)	11	11	4	Timmermann (1954) [39]
		<i>Lunaceps schismatus</i>	18 (75.0%)	53	89	44	Gustafsson and Olsson (2012) [40]
<i>Calidris canutus</i>	1	<i>Actornithophilus canuti</i>	1 (100%)	0	1	0	Price and Leibovitz (1969) [31]
		<i>Lunaceps drosti</i>	1 (100%)	0	2	0	Gustafsson and Olsson (2012) [40]
<i>Calidris pygmeus</i>	2	<i>Lunaceps falcinellus</i>	2 (100%)	0	7	0	Gustafsson and Olsson (2012) [40]
<i>Calidris ruficollis</i>	2	<i>Lunaceps falcinellus</i>	1 (50%)	0	1	0	Gustafsson and Olsson (2012) [40]
<i>Calidris temminckii</i>	3	—	0	0	0	0	
<i>Charadrius alexandrinus</i>	12	<i>Lunaceps falcinellus</i> *	2 (16.7%)	1	1	0	Gustafsson and Olsson (2012) [40]
		<i>Quadriceps macrocephalus</i>	9 (75%)	22	15	1	Specimen comparisons
<i>Charadrius leschenaultii</i>	2	<i>Quadriceps ptyadis</i>	1 (50%)	3	7	3	Specimen comparisons
<i>Charadrius mongolus</i>	3	<i>Quadriceps ptyadis</i>	3 (100%)	15	20	4	Specimen comparisons
<i>Chlidonias hybrida</i>	1	<i>Quadriceps anagrapsus</i>	1 (100%)	1	0	0	Specimen comparisons
<i>Gallinago gallinago</i>	13	<i>Quadriceps obscurus</i> *	1 (7.7%)	1	0	0	Specimen comparisons
		<i>Rhynonirmus scolopacis</i>	1 (7.7%)	2	1	2	Specimen comparisons
<i>Himantopus himantopus</i>	1	<i>Actornithophilus himantopi</i>	1 (100%)	5	7	1	Clay (1962) [37]
<i>Limosa lapponica</i>	1	<i>Lunaceps limosae</i>	1 (100%)	2	5	0	Gustafsson and Olsson (2012) [40]
<i>Pluvialis squatarola</i>	1	—	0	0	0	0	
<i>Saundersilarus saundersi</i>	1	<i>Saemundssonsonia lari</i>	1 (100%)	1	1	0	Specimen comparisons
<i>Tringa stagnatilis</i>	10	<i>Actornithophilus totani</i>	5 (50%)	1	0	10	Clay (1962) [37]
		<i>Austromenopon</i> sp.	1 (10%)	0	1	0	Clay (1959) [38]
		<i>Carduiceps meinertzhageni</i> *	1 (10%)	0	1	0	Timmermann (1954) [39]; Specimen comparisons
		<i>Lunaceps</i> sp. *	1 (10%)	0	1	0	Unidentifiable specimen
		<i>Quadriceps obscurus</i>	9 (90%)	17	25	9	Hopkins and Timmermann (1954) [44]; Specimen comparisons
<i>Tringa totanus</i>	5	<i>Actornithophilus totani</i>	1 (20%)	1	2	8	Clay (1962) [37] Hopkins and
		<i>Quadriceps obtusus</i>	4 (80%)	3	7	0	Timmermann (1954) [44]; Specimen comparisons

3.2. Literature Survey

In total, 51 publications were found that included prevalence data of at least one species of shorebird (Table S1).

3.3. Host Migration and Prevalence of Lice

A total of 257 prevalence data points were obtained where the number of examined hosts exceeded 10 birds. As shorebirds are often co-infested with more than one louse species, this included many cases where data for more than one louse species from the same host species could be included.

Table 3. Checklist of known shorebird lice from China. Gustafsson and Olsson [40] reported *Lunaceps limosae* Bechet, 1968 [67], from “[China?], Tonghoo”, but this locality is likely referring to Taungu, which is in Myanmar. No further reports of *L. limosae* from China have been published, and the species is not included here.

Louse Species	Host Species in China	Known Range in China	Source
Amblycera			
<i>Actornithophilus canuti</i> Price & Leibovitz, 1969 [31]	<i>Calidris canutus</i>	Guangdong	New record in this study
<i>Actornithophilus himantopi</i> Blagoveshtchensky, 1951 [68]	<i>Himantopus himantopus</i>	Guangdong	New record in this study
<i>Actornithophilus hoplopteri</i> (Mjöberg, 1910) [69]	<i>Vanellus cinereus</i>	Yunnan	Gustafsson et al. [23,70]
<i>Actornithophilus totani</i> (Schrank, 1803) [71]	<i>Tringa totanus</i>	Guangdong	New record in this study
Ischnocera			
<i>Carduiceps meinertzhageni</i> Timmermann, 1954 [39]	<i>Calidris alpina</i>	Guangdong	New record in this study
<i>Lunaceps drosti</i> Timmermann, 1954 [72]	<i>Calidris canutus</i>	Guangdong	New record in this study
<i>Lunaceps falcinellus</i> Timmermann, 1954 [72]	<i>Calidris pygmaea</i>	Guangdong	New record in this study
<i>Lunaceps numenii phaeopi</i> (Denny, 1842) [73]	<i>Ibidorhynchus struthersii</i> ¹	Tibet	Gustafsson and Olsson [40]
<i>Lunaceps schismatus</i> Gustafsson & Olsson, 2012 [40]	<i>Calidris alpina</i>	Guangdong	New record in this study
<i>Quadriceps altoasiaticus</i> Timmermann, 1954 [74]	<i>Ibidorhynchus struthersii</i>	Tibet	Timmermann [74]
<i>Quadriceps anagrapsus</i> (Nitzsch [in Giebel], 1866) [75]	<i>Chlidonias hybridus</i>	Guangdong	New record in this study
<i>Quadriceps macrocephalus</i> (Waterston, 1914) [76]	<i>Charadrius alexandrinus</i>	Guangdong	New record in this study
<i>Quadriceps obscurus</i> (Burmeister, 1838) [77]	<i>Tringa stagnatilis</i>	Guangdong	New record in this study
<i>Quadriceps obtusus</i> (Kellogg & Kuwana, 1902) [78]	<i>Tringa totanus</i>	Guangdong	New record in this study
<i>Quadriceps pyadis</i> (Séguy, 1949) [79]	<i>Charadrius leschenaltii</i> , <i>Charadrius mongolus</i>	Guangdong	New record in this study
<i>Quadriceps sinensis</i> Timmermann, 1954 [80]	<i>Vanellus cinereus</i>	Yunnan	Gustafsson et al. [23,39]
<i>Rhynonirmus scolopacis</i> (Denny, 1842) [73]	<i>Gallinago gallinago</i>	Guangdong	New record in this study
<i>Saemundssonina tringae</i> (Fabricius, 1780) [81]	<i>Calidris pygmaea</i>	“China”	Martens [82]
<i>Saemundssonina weidneri</i> Martens, 1974 [82]	<i>Gallinago megala</i>	“Atchang, China”	Martens [82]
<i>Saemundssonina lari</i> (Fabricius, 1780) [81]	<i>Saundersilarus saundersi</i>	Guangdong	New record in this study

¹ The natural host of *L. n. phaeopi* is *Numenius phaeopus* ssp., and this record is most likely a straggler.

We compared the proportion of hosts infested and flyway use in three genera of lice and one family of birds; none of the models tested was significantly different from the null model (Tables 5 and 6 for host length, and Tables 7 and 8 for host weight). We also compared the proportion of hosts infested and migration length in four genera of lice and one family of birds, but only the model that contained lice in the genus *Saemundssonina* was significantly different from the null model ($\chi^2 = 13.334$, $df = 3$, p -value = 0.004; Tables 9 and 10 for host length, Tables 11 and 12 for host weight). For migration length, a *post hoc* Tukey test (pairwise comparisons) illustrated that short migrants were infested with *Saemundssonina* lice significantly more often than intermediate- (p -value = 0.04) or long- (p -value = 0.045)

length migrants, and the prevalence of intermediate- and long-length migrants are not significantly different (p -value = 0.503) (Figure 1).

Table 4. New records of chewing lice for Australia. As these specimens are not accessible to us during the current period of restricted travel from China, only overall prevalence and the total number of louse specimens collected from that host are given. Abbreviations used: ID = resources used for identification of lice; NE = number of hosts examined; NI (P) = number of hosts infested (prevalence); #SP = total number of specimens collected.

Host Species	NE	Louse Species	NI	#SP	ID
<i>Calidris alba</i>	5	<i>Lunaceps actophilus</i> (Kellogg & Chapman, 1899) [83]	4 (80%)	11	Gustafsson and Olsson [40]
<i>Charadrius leschenaultii</i>	14	<i>Quadraceps ptyadis</i> Séguy, 1949 [79]	11 (78.6%)	108	Séguy [79]
<i>Charadrius veredus</i>	8	<i>Quadraceps assimilis</i> (Piaget, 1890) [84]	6 (75%)	24	Specimen comparisons
<i>Gelochelidon nilotica</i>	5	<i>Quadraceps baliola</i> (Blagoveshtchensky, 1951) [68]	2 (40%)	3	Specimen comparisons
		<i>Saemundssonina gelochelidoni</i> Touleshkov, 1959 [85]	2 (40%)	8	Touleshkov [85] ¹
<i>Tringa brevipes</i>	9	<i>Actornithophilus kilauensis</i> (Kellogg & Chapman, 1902) [86]	5 (55.6%)	19	Clay [37]
		<i>Quadraceps impar</i> Hopkins & Timmermann, 1954 [44] ²	4 (44.4%)	382	Hopkins and Timmermann [44]
<i>Tringa nebularia</i>	4	<i>Actornithophilus paludosus</i> Clay, 1962 [37]	2 (50%)	2	Clay [37]
		<i>Quadraceps similis</i> (Giebel, 1866) [75]	3 (75%)	9	Hopkins and Timmermann [44]
<i>Tringa stagnatilis</i>	7	<i>Actornithophilus totani</i> (Schrank, 1803) [71]	2 (28.6%)	3	Clay [37]
		<i>Quadraceps obscurus</i> (Burmeister, 1838) [77]	6 (85.7%)	50	Hopkins and Timmermann [44]
<i>Xenus cinereus</i>	12	<i>Carduiceps fulvofasciatus</i> (Grube, 1851) [87]	4 (33.3%)	9	Specimen comparisons

¹ The original description of *S. gelochelidoni* is poor, but specimens correspond to what can be seen in Touleshkov's illustrations. A redescription of this species is needed. ² This species was also recorded as stragglers on *Calidris acuminata*, *Calidris canutus*, *Calidris tenuirostris*, and *Xenus cinereus*, all of which occurred in mixed-species flocks during collection.

Table 5. Likelihood ratio test results for fitted model with flyway and host length compared to null model (containing only the random effect).

Response	χ^2	df	p -Value
<i>Actornithophilus</i>	3.253	3	0.354
<i>Austromenopon</i>	1.769	3	0.622
<i>Quadraceps</i>	1.196	3	0.754
Scolopacidae	2.875	3	0.411

Table 6. Summary of GLMM (beta distribution and logit-link function) of the effects of flyway and host length on the prevalence of lice. An asterisk (*) designates the only statistically significant value.

Response	n	Predictor	Coefficient	Standard Error	z-Value	p-Value
<i>Actornithophilus</i>	35	Intercept [Flyway (African-Eurasian)]	−4.416	2.331	−1.894	0.058 *
		Flyway (Americas)	0.291	0.304	0.960	0.337
		Flyway (East Asian-Australian)	0.485	0.410	1.183	0.237
		Median Host Length	0.604	0.425	1.419	0.156
<i>Austromenopon</i>	25	Intercept [Flyway (African-Eurasian)]	−4.361	3.957	−1.102	0.270
		Flyway (Americas)	−0.231	0.501	−0.460	0.645
		Flyway (East Asian-Australian)	−0.552	0.634	−0.870	0.384
		Median Host Length	0.582	0.721	0.807	0.419
<i>Quadriceps</i>	29	Intercept [Flyway (African-Eurasian)]	−3.174	5.758	−0.551	0.581
		Flyway (Americas)	−0.700	0.713	−0.982	0.326
		Flyway (East Asian-Australian)	0.282	0.657	0.429	0.668
		Median Host Length	0.630	1.046	0.602	0.547
Scolopacidae	125	Intercept [Flyway (African-Eurasian)]	−3.385	2.135	−1.585	0.113
		Flyway (Americas)	0.057	0.233	0.246	0.805
		Flyway (East Asian-Australian)	0.276	0.253	1.088	0.276
		Median Host Length	0.509	0.394	1.292	0.196

Table 7. Likelihood ratio test results for fitted model with flyway and host weight compared to null model (containing only the random effect).

Response	χ^2	df	p-Value
<i>Actornithophilus</i>	3.317	3	0.345
<i>Austromenopon</i>	1.525	3	0.677
<i>Quadriceps</i>	0.884	3	0.829
Scolopacidae	2.878	3	0.411

Table 8. Summary of GLMM (beta distribution and logit-link function) of the effects of flyway and host weight on the prevalence of lice. An asterisk (*) designates the only statistically significant value.

Response	n	Predictor	Coefficient	Standard Error	z-Value	p-Value
<i>Actornithophilus</i>	35	Intercept [Flyway (African-Eurasian)]	−2.463	0.955	−2.580	0.009 *
		Flyway (Americas)	0.344	0.308	1.116	0.264
		Flyway (East Asian-Australian)	0.478	0.410	10167	0.243
		Median Host Weight	0.294	0.204	1.441	0.150
<i>Austromenopon</i>	25	Intercept [Flyway (African-Eurasian)]	−2.109	1.512	−1.395	0.163
		Flyway (Americas)	−0.124	0.457	−0.270	0.787
		Flyway (East Asian-Australian)	−0.542	0.644	−0.842	0.400
		Median Host Weight	0.203	0.325	0.625	0.532
<i>Quadriceps</i>	29	Intercept [Flyway (African-Eurasian)]	0.760	20237	0.340	0.734
		Flyway (Americas)	−0.448	0.671	−0.668	0.504
		Flyway (East Asian-Australian)	0.183	0.669	0.274	0.784
		Median Host Weight	−0.101	0.475	−0.213	0.831
Scolopacidae	125	Intercept [Flyway (African-Eurasian)]	−1.597	0.755	−2.115	0.034 *
		Flyway (Americas)	0.077	0.239	0.324	0.746
		Flyway (East Asian-Australian)	0.280	0.253	1.105	0.269
		Median Host Weight	0.215	0.166	1.296	0.195

Table 9. Likelihood ratio test results for fitted model with migration length and host length compared to null model (containing only the random effect). An asterisk (*) designates the only statistically significant value.

Response	χ^2	df	p-Value
<i>Actornithophilus</i>	4.136	3	0.182
<i>Austromenopon</i>	3.932	3	0.269
<i>Saemundssonina</i>	13.334	3	0.004 *
<i>Quadriceps</i>	1.842	3	0.606
Scolopacidae	4.221	3	0.239

Table 10. Summary of GLMM of the effects migration length and host length on the prevalence of lice. An asterisk (*) designates the only statistically significant value.

Response	n	Predictor	Coefficient	Standard Error	z-Value	p-Value
<i>Actornithophilus</i>	46	Intercept [Migration Length (Intermediate)]	−6.228	3.534	−1.762	0.078
		Migration Length (Long)	0.509	0.595	0.856	0.392
		Migration Length (Short)	0.899	0.675	1.287	0.198
		Median Host Length	0.858	0.603	1.421	0.155
<i>Austromenopon</i>	49	Intercept [Migration Length (Intermediate)]	−0.424	2.782	−0.152	0.879
		Migration Length (Long)	0.381	0.398	0.956	0.339
		Migration Length (Short)	0.815	0.464	1.757	0.079
		Median Host Length	−0.178	0.508	−0.350	0.726
<i>Saemundssonina</i>	52	Intercept [Migration Length (Intermediate)]	−2.594	2.257	−1.149	0.251
		Migration Length (Long)	0.618	0.548	1.127	0.260
		Migration Length (Short)	1.450	0.578	2.510	0.012 *
		Median Host Length	0.162	0.394	0.411	0.681
<i>Quadriceps</i>	55	Intercept [Migration Length (Intermediate)]	−1.968	3.293	−0.598	0.550
		Migration Length (Long)	0.345	0.565	0.610	0.542
		Migration Length (Short)	0.567	0.569	0.997	0.319
		Median Host Length	0.311	0.555	0.559	0.576
Scolopacidae	133	Intercept [Migration Length (Intermediate)]	−2.810	1.828	−1.537	0.124
		Migration Length (Long)	0.291	0.226	1.289	0.197
		Migration Length (Short)	−0.212	0.422	−0.502	0.615
		Median Host Length	0.366	0.344	1.064	0.287

Table 11. Likelihood ratio test results for fitted model with migration length and host weight compared to null model (containing only the random effect). An asterisk (*) designates the only statistically significant value.

Response	χ^2	df	p-Value
<i>Actornithophilus</i>	2.865	3	0.413
<i>Austromenopon</i>	5.065	3	0.167
<i>Saemundssonina</i>	15.032	3	0.002 *
<i>Quadriceps</i>	2.442	3	0.486
Scolopacidae	4.085	3	0.252

Table 12. Summary of GLMM (beta distribution and logit-link function) of the effects migration length and host weight on the prevalence of lice. An asterisk (*) designates the only statistically significant value.

Response	<i>n</i>	Predictor	Coefficient	Standard Error	<i>z</i> Value	<i>p</i> -Value
<i>Actornithophilus</i>	46	Intercept [Migration Length (Intermediate)]	−1.789	1.491	−1.99	0.230
		Migration Length (Long)	0.317	0.591	0.536	0.592
		Migration Length (Short)	0.985	0.678	1.453	0.146
		Median Host Weight	0.092	0.245	0.348	0.728
<i>Austromenopon</i>	49	Intercept [Migration Length (Intermediate)]	−2.471	1.020	−2.423	0.015 *
		Migration Length (Long)	0.243	0.393	0.617	0.537
		Migration Length (Short)	0.388	0.500	0.776	0.438
		Median Host Weight	0.241	0.214	1.128	0.260
<i>Saemundssonina</i>	52	Intercept [Migration Length (Intermediate)]	−2.655	0.875	−3.036	0.002 *
		Migration Length (Long)	0.651	0.549	1.166	0.244
		Migration Length (Short)	1.304	0.571	2.286	0.022 *
		Median Host Weight	0.193	0.139	1.391	0.164
<i>Quadriceps</i>	55	Intercept [Migration Length (Intermediate)]	−1.330	1.327	−1.002	0.316
		Migration Length (Long)	0.364	0.552	0.659	0.510
		Migration Length (Short)	0.409	0.594	0.688	0.510
		Median Host Weight	0.228	0.236	0.964	0.335
Scolopacidae	133	Intercept [Migration Length (Intermediate)]	−1.464	0.623	−2.352	0.019 *
		Migration Length (Long)	0.282	0.228	10239	0.215
		Migration Length (Short)	−0.241	0.433	−0.556	0.578
		Median Host Weight	0.144	0.144	0.999	0.318

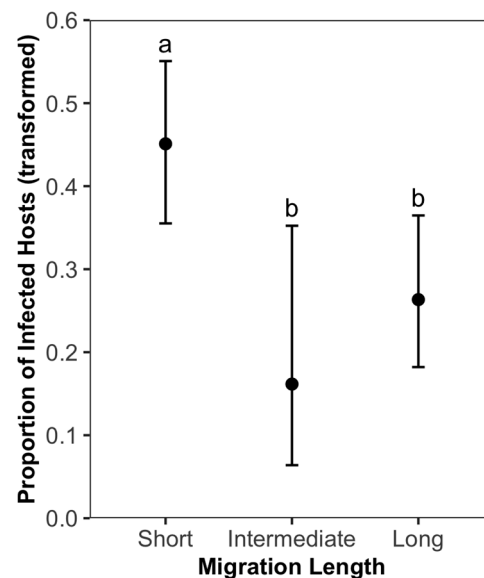


Figure 1. Comparison of prevalence of *Saemundssonina* lice between hosts that migrate different lengths. Letters indicate results from pairwise comparisons and denote significant differences between groups.

4. Discussion

Migration length and flyway do not seem to affect the prevalence of shorebird lice of any genus in our analyses, with the exception of the head louse genus *Saemundssonina*, which

is more prevalent on short-distance migrants than on intermediate- and long-distance migrants. Host body size also did not influence louse prevalence in our data.

4.1. Flyways

Limited data are available of the effect of flyway differences in louse community composition. Gustafsson and Olsson [35] showed that flyways did not affect host-lice associations in several species of *Lunaceps* sampled on different flyways. However, whereas lice on conspecific hosts in that study were genetically similar along two Eurasian flyways, lice from North America represented a different species. In contrast, lice in the genus *Carduiceps* showed no significant division between New and Old World hosts [88]. Notably, most of the *Lunaceps* and *Carduiceps* samples in these studies were derived from the same host species, indicating that the evolutionary history of different louse genera on the same host may be very different (e.g., [89,90]).

Nevertheless, whether the same host species is parasitized by the same or different species of lice along different flyways, environmental conditions may affect the prevalence of these lice. Conceivably, chewing louse community composition may differ between two conspecific host populations that migrate along different flyways. For instance, lice that are negatively affected by low ambient humidity (e.g., [91]) may be unequally distributed across the host's range if some migration paths include significant stop-over time in low-humidity regions. Meinertzhagen [92] suggested that availability of alkaline lakes in wintering grounds may adversely affect louse prevalence, as all shorebirds examined at the highly alkaline Lake Magadi in Kenya were louse free. Notably, habitat choice during wintering has been shown to be important for the prevalence and species richness of parasitic mites and helminths [93,94].

Our analysis suggests that louse prevalence does not differ significantly for shorebirds migrating along different flyways (Table 6). This may indicate that environmental conditions are either not so significantly different between different flyways as to affect the louse communities on these hosts, or that shorebird lice are less affected by differences in environmental conditions compared to lice on other hosts. The majority of the hosts for which data are available are primarily coastal migrants, suggesting that environmental conditions may be similar along different flyways. More data are needed, specifically from birds that preferentially or exclusively stop over and winter in freshwater habitats, to examine this question further. Notably, primarily freshwater and primarily saltwater wintering birds along the East Asian–Australasian flyway are parasitized by different generalist species of *Lunaceps* [35].

4.2. Host Body Size

Both louse prevalence [22] and louse abundance (e.g., [95–97]) have been shown to correlate with host body size in terrestrial birds. In at least some cases, this is true even for within-host species varying in body size [98]. However, this correlation does not always hold [99]. Rózsa [95] suggested three explanations for this correlation: increasing available resources on larger hosts, more refugia during preening on larger hosts, and larger hosts having longer lifespans. In contrast, our analysis of lice on shorebirds did not show any significant influence of host body size on the prevalence of lice (Tables 5–12), regardless of whether host weight or host length was used as a proxy for host size. Notably, our dataset included both some of the smallest shorebirds (e.g., *Calidris minuta*; 120–140 mm) and some of the largest (e.g., *Larus argentatus*; 610–780 mm).

Likely, a large part of the explanation for the discrepancy between expected lower prevalence and observed higher prevalence in smaller shorebirds is the propensity for these birds to form large, dense flock at stop-over and wintering grounds (e.g., [100]). For lice that rely on direct contact between hosts for transmission between hosts, any increase in the opportunities of transmission may increase the prevalence of that louse. However, transmission as such is not enough; lice would also need to successfully establish on new hosts without being removed by, e.g., preening.

Possibly, prevalence may be more closely related to host preening capabilities than to host size in shorebirds. For instance, shorebirds as a group show great variability in bill length, which is known to correlate with the proportion of grooming time that is spent scratching with the feet rather than preening with the bill [101]. In pigeons, foot scratching seems to mainly be used to flush lice from the head to the body, where they can be preened off [30]. However, all experimental data refer to lice of the “wing louse” ecomorph that only partially live on the host’s head. It is unclear whether scratching works the same for typical head lice such as *Saemundssonina* that are virtually never found outside the host’s head and that are poorly suited morphologically to survive under intense preening. The often large heads and mandibles of head lice may provide better attachment during scratching than is the case for lice of other ecomorphs, and scratching may have no flushing effect on head lice. More research on a wider variety of louse groups is needed to test this.

Moreover, many shorebirds, including most small-bodied species such as sandpipers and plovers, have soft-tipped bills, which may be less well suited for preening. This is also suggested by the relatively high prevalence of lice in most shorebirds (Table S1), compared to in more hard-billed, e.g., passeriforms that usually have much lower louse prevalence rates (e.g., [18,23,102,103]). Bill morphology in pigeons has been suggested to be strongly influenced by the need for efficient preening, as experimental trimming on the bill overhang had no effect on feeding, but a large effect on louse abundance [104]. This may not be the case in smaller shorebirds, where mechanoreceptors located in sensory pits near the tip of the bill are vital for feeding (e.g., [105–107]). Variation in bill morphology on several scales is more tightly correlated to feeding mode in sandpipers than in pigeons [108], and conclusions drawn based on data from lice on one host group may not translate to other host groups. Larger, hard-billed shorebirds such as gulls and auks may be better analogues of the data from pigeons.

Data on the percentage of time spent on maintenance behavior (including preening) in shorebirds are scarce, but do not seem to differ much from corresponding times in other bird groups, and show great variation among shorebird species (e.g., [109–111]). Moreover, at least some soft-billed shorebirds spend more time in maintenance behavior than hard-billed passeriforms [110]. Maintenance behavior covers more activities than preening, but overall, it seems that an increase in maintenance behavior does not correspond to an overall reduction in louse prevalence. Notably, some of the birds with the highest maintenance times listed by Cotgreave and Clayton [110] are soft-billed shorebirds.

If shorebirds have high louse prevalence rates, it is not for lack of trying to remove them. It seems likely that the limitations on bill morphology forced by feeding methods are interfering with preening success in many shorebirds. In general, it is thus possible that two contrasting mechanisms influence the prevalence of lice on shorebirds. In larger-bodied hosts, prevalence is high for the reasons outlined by Rózsa [95], whereas in small-bodied hosts prevalence is high because of deficiencies in preening capabilities.

4.3. Migration Length

Due to the high energy cost of migration, any negative effects of chewing lice on, e.g., host metabolic rate or plumage condition may have an increasingly adverse effect as migration length and time increase. Long-distance migrants would therefore be expected to have lower louse prevalence, as birds without lice would spend less energy on migration than birds with lice. Resident or short-distance birds would be less influenced by the presence of lice and would therefore be able to support a larger overall metapopulation of lice.

Similarly, the process of long-distance migration may have an adverse impact on lice even if increased energy costs were not a problem for the hosts. Gustafsson et al. [23] speculated that lice infesting hosts that migrate to areas that are climatically similar to their breeding grounds (e.g., intra-tropical migrants) may not experience any significant differences in any relevant environmental variables across their lifetime. In contrast, lice on hosts that migrate between, e.g., boreal and tropical regions and stay in each for extended

periods of time may experience significant environmental differences at different parts of the year. As louse generations are typically on the scale of ~30–35 days (e.g., [112–114]), this indicates that successive generations of lice on long-distance migrants may experience dramatically different ambient temperatures, humidity levels, and other environmental conditions. If lice are not biologically flexible enough to adapt to both boreal and tropical conditions, long-distance migration may limit the prevalence and abundance of lice.

Published data supporting this are sparse. However, both Ash [102] and Sychra et al. [18] found significantly lower prevalence of lice on migratory birds than on resident birds in Europe. Gustafsson et al. [23] reported prevalence rates an order of magnitude higher on non-migratory tropical birds than on migratory boreal birds caught in South China. Little is known about the prevalence of lice on intra-tropical migrants, and almost all migratory birds included in the present study migrate between boreal and tropical habitats.

However, for shorebirds as a whole, there are no significant differences in prevalence between lice on short-, intermediate-, and long-distance migrants (Tables 9 and 10). The sole exception to this pattern is the head louse genus *Saemundssonina*, which is more prevalent on short-distance migrants than on other hosts (Table 10; Figure 1).

It is unclear why head lice would be the exception to this pattern. For instance, species of *Actornithophilus* live on or in the wing feathers, and deterioration of wing feather quality may be expected to have an adverse impact on birds that fly long distances, especially those that cross oceans. Similarly, lice that drink blood or eat body feathers may be expected to influence the general condition of the birds by, e.g., lowering the thermoinsulation or water resistance of the plumage. In contrast, lice that exclusively eat head feathers may be expected to have a less significant impact on the overall condition of the host.

Possibly, the higher prevalence of *Saemundssonina* on short-distance migrants may be unrelated to migration patterns and be caused by other aspects of host biology. For instance, many birds counted as short-distance migrants here are auks and gulls, which nest in dense colonies and may even nest underground. Perhaps significantly for the prevalence of *Saemundssonina* on some short-distance migrant hosts, non-breeding adults may congregate below or at breeding ledges before the breeding period [115,116], and even breeding adults may arrive and stay at breeding sites months before egg-laying (e.g., [117–119]). In contrast, most of the long-distance migrants included here make open nests (or no nests) at low densities. Moreover, many long-distance migrants included here spend very short periods at the breeding grounds, with females often leaving shortly after egg-laying and letting the male raise the chicks [120]. The differences in southwards migration dates may be several weeks in some species [121].

If head lice are less capable than other lice of spreading between hosts other than during mating and nesting, differences in host colony density and time spent at breeding grounds may affect the prevalence of head lice differently from that of other lice. Potentially, the often dense feeding flocks and roosts of long-distance migrants at wintering grounds may offer many opportunities for between-host transfer of, e.g., *Quadraceps* or *Austromenopon*, which live on the host's body, without offering the same increased opportunities for lice that live on the head. Notably, Rózsa et al. [122] found prevalence of head lice to be higher on colonial rooks (59%; *Corvus frugilegus*) than on non-colonial hooded crows (38%; *Corvus cornix*). There appear to be no consistent differences in percentage of time spent on maintenance behavior in shorebirds between colonial and non-colonial hosts [110].

5. Conclusions

With the exception of head lice on short-distance migrants, the prevalence of lice on shorebirds appears to be unaffected by migration patterns and host body size. However, more data are needed, especially from inter-tropical migrants or tropical non-migrants (e.g., lapwings, plovers, jacanas, pratincoles), as well as from boreal birds with complicated dispersal and migration patterns that do not follow the North-South axis most common in birds (e.g., [123]). Moreover, the influence of breeding coloniality on louse prevalence in shorebirds could not be adequately evaluated here, as most of the available data concerns

hard-billed birds (gulls, auks), and the data from soft-billed colonial birds are limited (e.g., [124,125]).

Nevertheless, the lack of clear impact by flyways and migration length on the prevalence of shorebird lice strengthens the results of Chu et al. [22], who found the same results in an analysis of mainly terrestrial birds in South China. However, the contrasting results of Ash [102], Sychra et al. [18], and Gustafsson et al. [23] indicate that migration may have different impacts in different louse-host systems. A similar analysis on, e.g., migratory and non-migratory passerines or ducks would be enlightening.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15020200/s1>, Table S1: Prevalence data of chewing lice infesting shorebirds from new collections records and literature survey.

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Institutional Review Board Statement: The studies involving animals in China were reviewed and approved by the Animal Care and Welfare Committee, Institute of Zoology, Guangdong Academy of Sciences [then: Guangdong Institute of Applied Biological Resources], and the lice studied for this paper were collected in strict accordance with the Regulation for the Administration of Laboratory Animals (Decree No. 2, State Science and Technology Commission of the People's Republic of China). A collection permit was previously obtained from the Panel on Laboratory Animal Care of the Institute of Zoology, Guangdong Academy of Sciences [then: Guangdong Institute of Applied Biological Resources]. Collections in Sweden were carried out under ethical approvals 171-2006 and 157-2010 (Jordbruksverket). Collections in Australia were carried out under license SF006502 (Department of Environment and Conservation, Western Australia) and exported under license OS002459 (Department of Environment and Conservation, Western Australia). None of these agencies had any hand in study design, collection, analysis, or interpretation.

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