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Chewing lice richness and occurrence in non-breeding shorebirds in Paracas, Perú

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Chewing lice often appear benign; however, they can also negatively impact their hosts. We know little about seasonal and spatial variation in the exposure, acquisition, or loss of these putative ectoparasites by shorebirds. Here we provide the first description of chewing lice richness and occurrence from seven shorebird species captured in the Paracas National Reserve, Perú. We summarize seasonal patterns of abundance, and test for relationships between parasite numbers and shorebird body condition. We collected 160 ectoparasite specimens of the families Menoponidae and Philopteriidae from 108 shorebirds and classified them into four genera and at least nine species. The Philopteriidae family showed higher prevalence (62%), richness, and number of host species (seven parasitic species being hosted by seven shorebird species) than the Menoponidae (prevalence = 49%; two parasitic species in five host species). Among species, *Actornithophilus umbrinus*, found on all four *Calidris* species, had the highest number of hosts, while *A. pediculoides* and all the Philopteriidae species were only found on a single host. *Lunaceps actophilus* had the highest prevalence, mean intensity, and mean abundance of infection, being found on 64% of the Sanderlings *Calidris alba*. Sanderlings hosted the highest abundance of lice, whilst Semipalmated Sandpipers *C. pusilla* had the highest richness. In Sanderlings, we found an apparent, but not statistically significant, decrease in parasite loads through the non-breeding season. Sanderling body condition varied with capture period, but we found no significant relationship between body condition and total parasites within each time period or in pooled analysis by date. Paracas appears to be a site at which shorebirds maintain or possibly slightly shed the loads of chewing lice rather than acquire them; these low parasite loads do not appear to negatively affect body condition.

Keywords

waders
ectoparasites
body condition
Calidridae
South America

INTRODUCTION

Avian parasite loads can shape the physiology, behavior, ecology, life history and migration strategies of their hosts (Ashford 1971, Piersma 1997, Hicks *et al.* 2018). The negative impacts of parasites, including infection-

induced mortality, host manipulation, and cost of dispersal, demonstrate how strong their consequences for host fitness can be (Bonte *et al.* 2012, McElroy & de Buron 2014, Binning *et al.* 2017). Regarding the ecological factors affecting the rate of mortality among infected

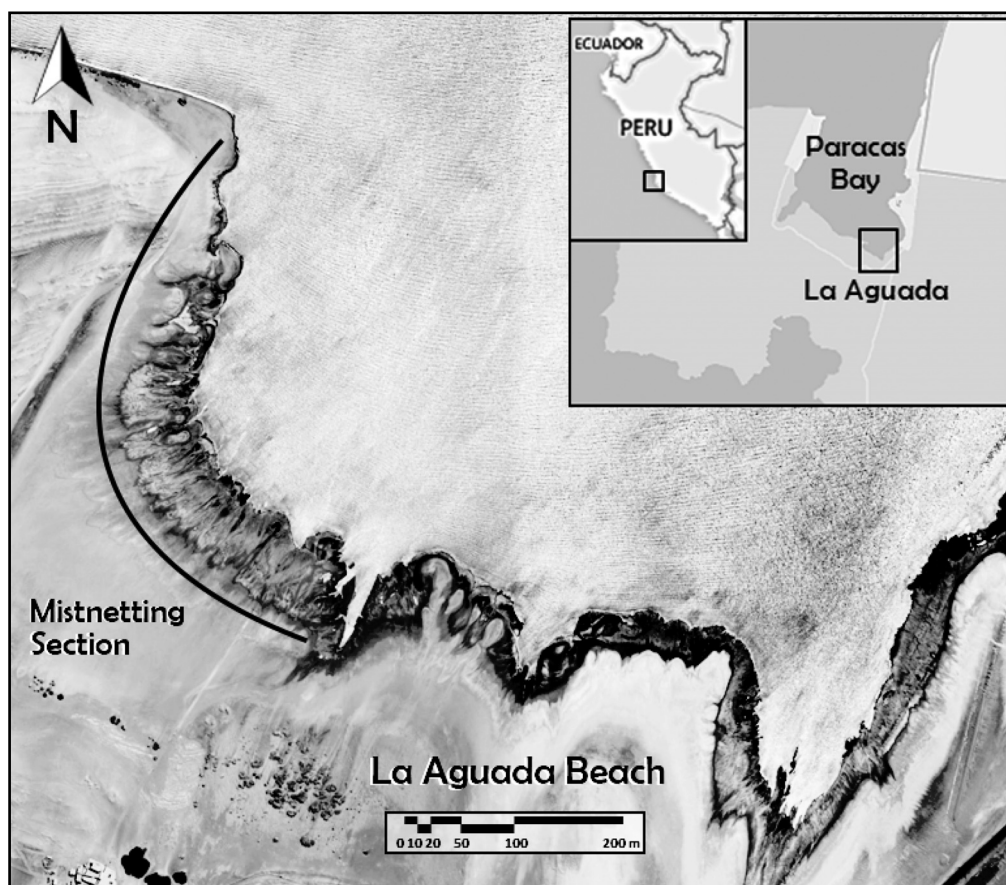


Fig. 1. Location of the fieldwork on 'La Aguada' beach in Paracas National Reserve, Ica, Perú.

birds, Møller *et al.* (2009) suggested that parasite-induced nestling mortality is mainly determined by geographical location, as virulence increases towards the tropics. To a lesser extent, it is also determined by nest characteristics, given that open nesters suffer from greater parasite-induced mortality than hole nesters, and by prevalence, as greater prevalence is associated with reduced virulence. However, the ecological relationship between ectosymbionts and birds may not only be parasitic. Galván *et al.* (2012) proposed a commensalistic (*i.e.* symbiosis in which one member benefits from the relationship, but the other neither gains nor loses; Proctor & Owens 2000) relationship between feather mites and birds after they had observed that feather mite abundance explained little about the variance in birds' body condition.

Bird chewing lice Phthiraptera are obligate ectoparasites that live permanently on the body of a host, feeding mainly on feathers, blood, dead skin or secretions (Clayton & Walther 2001, Price *et al.* 2003, Clayton *et al.* 2008). Birds are parasitized by two of the four suborders of chewing lice that make up the Phthiraptera group: Amblycera and Ischnocera (Gomes *et al.* 2014). The physiological, ecological, and evolutionary relationships between chewing lice and their hosts are diverse and may vary among species and environments. Some studies have found adverse effects on hosts, including increasing the occurrence of infections by acting as vectors for microorganisms

(Philips 1990), increasing rates of dispersal from natal colonies (McCoy *et al.* 2005) and directly decreasing survival of the hosts (Booth *et al.* 1993, Clayton *et al.* 1999). Intense parasitic infections can produce direct pathological effects such as hyperkeratosis and feather damage, or have indirect effects, via *e.g.* sexual selection against parasitized birds (Liébana *et al.* 2011, Moreno-Rueda & Hoi 2012). Whiteman & Parker (2004) found louse load to be negatively correlated with body condition and to predict variation in the host's territorial behavior.

Our study addressed the richness and occurrence of chewing lice sampled from shorebirds spending the non-breeding season in Paracas, Perú. The Peruvian coastline hosts over half a million shorebirds, including *ca.* 136,000 Sanderlings *Calidris alba*, 38% of the hemispheric population (Senner & Angulo Pratolongo 2014). Research on shorebird ectoparasites in the Western Hemisphere has been conducted at temperate (Hunter & Colwell 1994, Palma 1999, Palma & Jensen 2005) and a few tropical areas (D'Amico *et al.* 2008, Haase & Alava 2014). Studies of chewing lice from birds in Perú are few and primarily descriptive (Gomez-Puerta & Cribillero 2015, Gomez-Puerta & Luján-Vega 2018). Here, we provide the first description of chewing lice species richness and occurrence on seven species of host shorebirds, look for seasonal patterns of abundance, and test for relationships between parasite numbers and individual shorebird body condition.

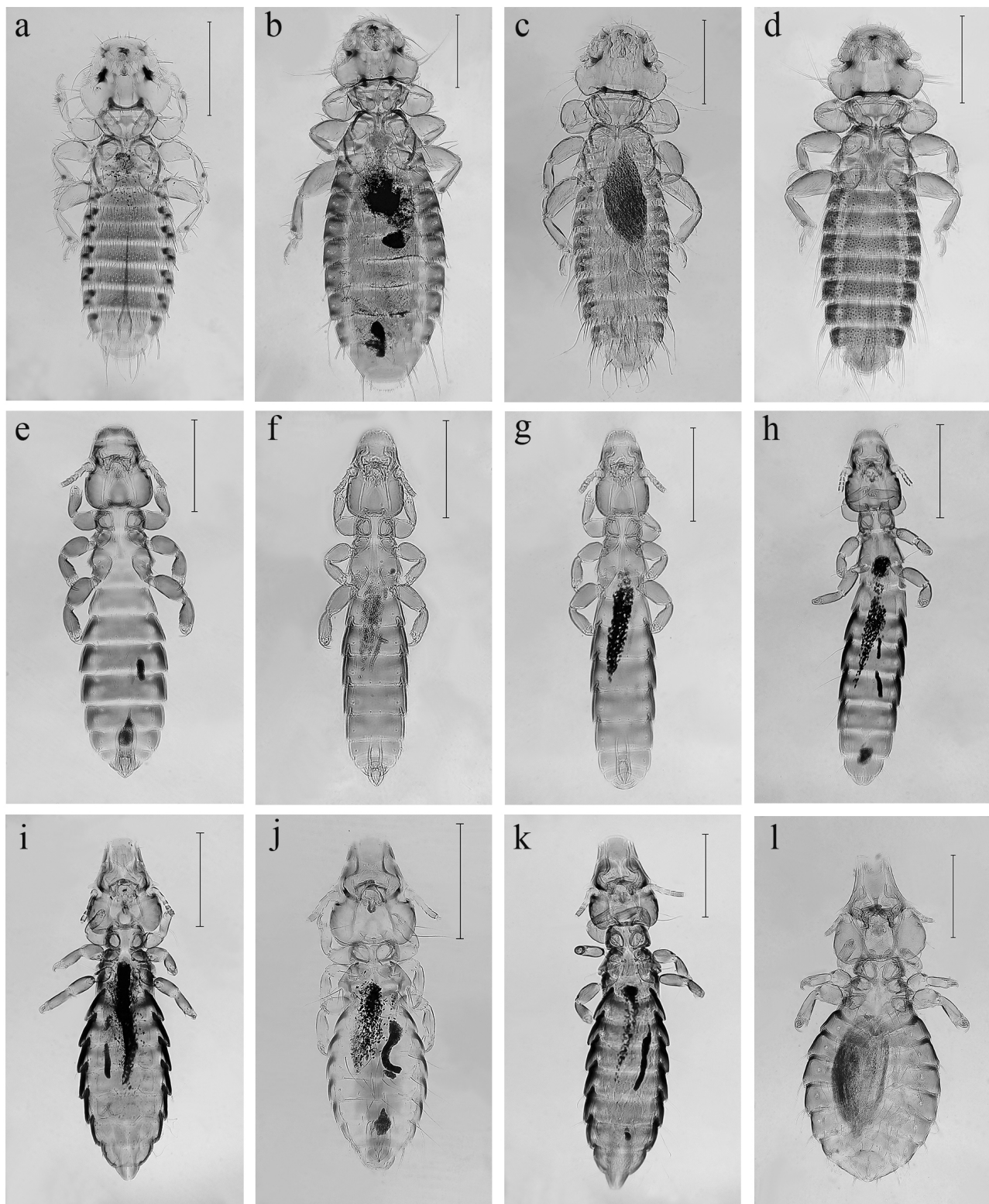


Fig. 2. Chewing lice collected from shorebirds captured at the Paracas National Reserve, Perú, in September 2017, January 2018 and March 2018 of the non-breeding season. **(a)** *Actornithophilus pediculoides*, male from *Arenaria interpres*. **(b)** *A. umbrinus*, female from *Calidris alba*. **(c)** *A. umbrinus*, male from *Calidris mauri*. **(d)** *A. umbrinus*, male from *Calidris pusilla*. **(e)** *Lunaceps actophilus*, male from *Calidris alba*. **(f)** *L. incoenis*, male from *Calidris mauri*. **(g)** *L. rothkoi*, female from *Calidris pusilla*. **(h)** *L. superciliosus*, male from *Calidris pusilla*. **(i)** *Quadriceps fissus*, male from *Charadrius semipalmatus*. **(j)** *Q.* (aff) *strepsilaris*, male from *Arenaria interpres*. **(k)** *Quadriceps* sp., female from *Charadrius nivosus*. **(l)** *Saemundssonina* (*Saemundssonina*) *tringae*, female from *Calidris pusilla*. Scale bar = 0.4 mm. Specimens were deposited in the Natural History Museum of the Universidad Nacional Federico Villareal in Lima, Perú.

Conceptually, body condition is used to describe the degree to which an organism's physiological state influences its performance (Brown 1996). In practice, body mass relative to structural size can provide an index of avian energetic 'body condition' and is widely used to do so (e.g. Dinsmore & Collazo 2003, Whiteman & Parker 2004). This measure of body condition has been related to migratory performance and behavioral decisions throughout the annual cycle of long-distance migratory shorebirds (Lehnen & Krementz 2007, Choi et al. 2009, Tulp et al. 2009, Duijns et al. 2017, Alfaro et al. 2018). In this study, we test for a relationship between parasite load and body condition during the non-breeding season. We predict that if ectoparasites impose a cost, or if birds in better condition can more readily suppress parasites, the number of parasites on each bird should be negatively correlated with body condition. Alternatively, if parasites prefer to live on hosts in better body condition, without imposing detectable costs, we should find a positive relationship.

At an evolutionary level, it has been suggested that the broad spatial distributions of parasites influence habitat selection and spatial behavior, including the evolution of long-distance migration patterns in shorebirds (Piersma 1997). Some long-distance migrant shorebirds appear to have lower resistance to parasites and pathogens, and thus are potentially more vulnerable when in higher parasite load zones found particularly in the freshwater tropics. Piersma (1997) suggested that some species might tradeoff longer-distance migration to sites with lower prey availability in exchange for the benefit of lower parasite pressure in more sterile environments. For example, D'Amico et al. (2008) found substantially higher ectoparasite infestation in Nearctic-breeding Red Knots *Calidris canutus* at a tropical stopover and non-breeding site in northern Brazil than at a non-breeding site in

Tierra del Fuego, Argentina, where 96% of birds were completely free of ectoparasites. If Perú is a less parasite-prone environment than that experienced on the breeding grounds and/or migration, we predict that the prevalence or intensity of ectoparasitism should decrease over the course of the non-breeding season.

METHODS

Study area

The Paracas National Reserve is a Natural Protected Area located in the Department of Ica, Perú. It is numerically the second most important site for shorebirds in the country, hosting more than 56,000 amongst its different habitats (Senner & Angulo Pralongo 2014). Fieldwork was conducted at La Aguada beach (13°51'35.47"S, 76°16'16.16"W), an intertidal mudflat <2 km long surrounded by coastal desert (Fig. 1). The near-shore section of the mudflat lacks vegetation. Most of the lower intertidal zone consists of soft mud inhabited by polychaetes, fly larvae, microscopic sea shrimp, and beetles (Pellissier 2013), and covered by decaying algae and biofilm.

Field methods

Shorebirds were captured in the non-breeding season, using 12 mist-nets set in the intertidal zone at night, during three nine-day campaigns conducted in September 2017, January 2018 and March 2018. Most of the Semipalmated Sandpipers *Calidris pusilla*, however, were captured during banding campaigns in the non-breeding seasons of 2012 and 2013. Birds were identified based on external characteristics (Schulenberg et al. 2010) and banded with an incoloy metal band (CORBIDI Bird-Banding Program, the Peruvian bird-banding scheme). They were weighed on a digital scale (0.5 g), a straightened

Table 1. Analysis of the parasitic ecological indices for host shorebird species. *n* = number of birds evaluated, *nP* = number of birds with at least one ectoparasite, *A* = total number of parasites collected, *P%* = prevalence (percentage of parasitized hosts), *MI* = mean intensity of parasitized hosts (total number of parasites divided by the number of infected hosts), *MA* = mean abundance of parasitized hosts (total number of parasites divided by the number of birds sampled). *P%* was not calculated for Red Knot and the Snowy Plover, because only one individual of each species was sampled. *P* and *MA* were not calculated for Semipalmated Sandpipers because the number without parasites in 2012 and 2013 was unknown.

Host species	<i>n</i>	<i>nP</i>	<i>A</i>	<i>P%</i>	<i>MI</i>	<i>MA</i>
Ruddy Turnstone <i>Arenaria interpres</i>	5	4	5	80	1.25	1
Sanderling <i>Calidris alba</i>	45	36	120	80	3.33	2.66
Red Knot <i>Calidris canutus</i>	1	1	3	–	3	3
Western Sandpiper <i>Calidris mauri</i>	14	5	5	36	1	0.36
Semipalmated Sandpiper <i>Calidris pusilla</i>	–	18	20	–	1.11	–
Snowy Plover <i>Charadrius nivosus</i>	1	1	3	–	3	3
Semipalmated Plover <i>Charadrius semipalmatus</i>	4	1	4	25	4	1

and flattened wing measurement was taken using a wing ruler (0.5 mm), and culmen and total head length were measured with dial calipers (0.5 mm). Finally, to minimize variation in sampling effort and technique, D. Minaya examined body and flight feathers from all birds for ectoparasitic lice for 2–3 min. All lice found were collected using entomological forceps and stored in 70% pure ethanol (Lamothe 1997).

Laboratory methods

In the lab, each louse specimen was clarified with 20% KOH for 12 hr and left for 24 hr in distilled water to remove excess clarifier. Specimens were dehydrated by placing them in ascending solutions of ethanol (50%, 70%, 90% and 100%) for 5–10 min in each solution, then diaphanized in Eugenol for 1 hr. Finally, each specimen was mounted on Canada Balm, dried in an incubator at 50–60°C for two weeks, and identified under a light microscope based on morphology (Palma 1978, Lamothe 1997, Price *et al.* 2003, González-Acuña *et al.* 2009). The nomenclature and identification of lice species followed the taxonomic keys of Clay (1962), Keirans (1967), Price

et al. (2003) and Gustafsson & Olsson (2012). The material examined was deposited in the Collection of Parasitic and Related Invertebrate Helminths at the Natural History Museum of the Universidad Nacional Federico Villareal in Lima, Perú.

Analyses

Occurrences of lice and host species were tabulated and ecological indices for totals or individual louse species were calculated. These indices included percentage of prevalence (P%: percentage of parasitized hosts), mean intensity on parasitized hosts (MI: total number of parasites divided by the number of infected hosts), and mean abundance (MA: total number of parasites divided by the total number of shorebirds sampled; Bush *et al.* 1997, Bautista-Hernández *et al.* 2015). Percentage of prevalence and mean abundance were not calculated for Semipalmated Sandpipers because the number lacking parasites in 2012 and 2013 was unknown. Also, percentage of prevalence was not calculated for the Red Knot *Calidris canutus* and the Snowy Plover *Charadrius nivosus* because only one individual of each species was evaluated (Table 1).

Table 2. Chewing lice (Phthiraptera) occurrence and ecological prevalence indices for ectoparasite species collected from seven shorebird species in Paracas National Reserve, Ica, Perú. P% = percentage of prevalence (percentage of parasitized hosts), *nHP* = number of parasitized hosts, MI = mean intensity of parasitized hosts (total number of parasites divided by the number of infected hosts), MA = mean abundance of parasitized hosts (total number of parasites divided by the number of birds sampled), MCD = material code deposited in Collection of Parasitic and Related Invertebrate Helminths at the Natural History Museum of the Universidad Nacional Federico Villareal in Lima, Perú.

Chewing lice species	Host	P%	<i>nHP</i>	MI	MA	MCD
MENOPONIDAE						
<i>Actornithophilus pediculoides</i>	<i>Arenaria interpres</i>	25	1	1	0.25	108
<i>A. umbrinus</i>	<i>Calidris alba</i>	36	16	1.4	0.5	101
	<i>Calidris canutus</i>	–	1	1	1	103
	<i>Calidris mauri</i>	14	2	1	0.1	111
	<i>Calidris pusilla</i>	32	12	1.2	0.4	105
PHILOPTERIDAE						
<i>Lunaceps actophilus</i>	<i>Calidris alba</i>	64	28	3.3	2.1	102
<i>L. incoenis</i>	<i>Calidris mauri</i>	21	3	1	0.2	112
<i>L. superciliosus</i>	<i>Calidris pusilla</i>	11	4	1	0.11	104
<i>L. rothkoi</i>	<i>Calidris pusilla</i>	5	2	1	0.05	106
<i>Lunaceps</i> sp.	<i>Calidris canutus</i>	–	1	2	2	114
<i>Quadriceps fissus</i>	<i>Charadrius semipalmatus</i>	25	1	1	0.25	110
<i>Q.</i> (aff) <i>strepsilaris</i>	<i>Arenaria interpres</i>	40	2	1.5	0.6	109
<i>Quadriceps</i> sp.	<i>Charadrius nivosus</i>	–	1	3	3	113
<i>Saemundssonina tringae</i>	<i>Calidris pusilla</i>	3	1	1	0.03	107

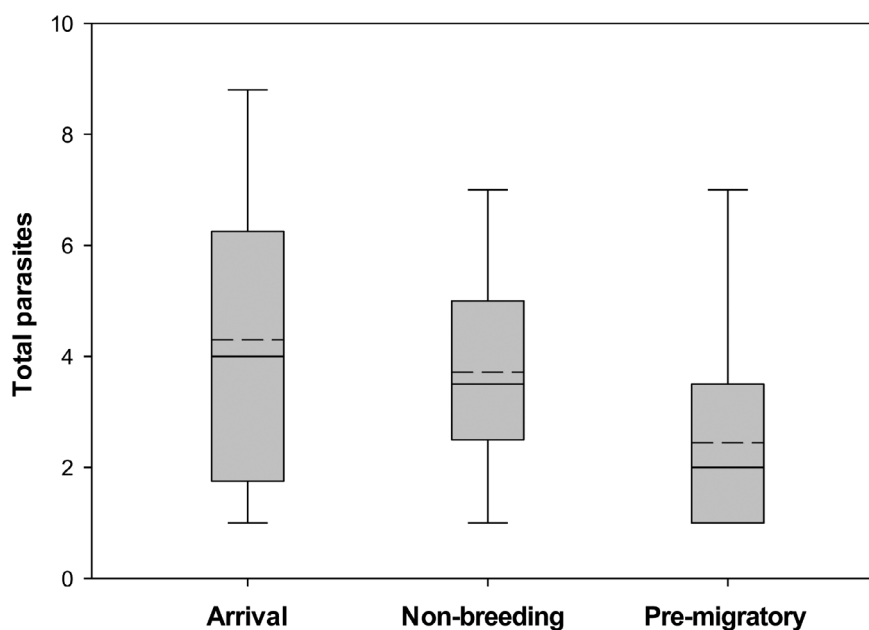


Fig. 3. Total number of parasites collected in 45 Sanderlings *Calidris alba* in relation to three time periods across the non-breeding season ($n = 13, 19,$ and $13,$ respectively). Continuous line represents the median and the dotted line the mean. Boxes indicate the first and third quartiles and upper and lower whiskers indicate maximum and minimum values respectively.

In Sanderlings, for which we had moderate statistical power ($n = 45$), we tested for seasonal changes in prevalence and the number of parasites per individual, and for potential relationships with body condition. We analyzed prevalence with respect to date with a binary logistic regression, and report Wald χ^2 values for a date effect. A linear regression was performed to evaluate the relationship between the number of parasites per individual and date.

For body condition analyses, we first calculated an index of body size for all Sanderlings as PC1 from a principal component analysis of three structural morphometric measurements: flattened wing, culmen and total head length (Wunderle & Latta 2000, Schamber *et al.* 2009, Labocha & Hayes 2012). PC1 had concordant signs for all three variables, and thus can be interpreted as relative body size, and accounted for 71% of total variance. We then calculated a body condition index, accounting for structural size, as the residuals from the regression of body mass against PC1. Individuals with positive residuals from the regression, being heavier for their size, were considered to be in better body condition than those with negative residuals (Jakob *et al.* 1996, Schulte-Hostedde *et al.* 2001). There were large seasonal differences in mass between migratory arrival in September, the heart of non-breeding season in January, and the pre-migratory period in March (see *Results*). Since the effect of parasite number as a predictor of body condition might change with overall mass or time, we modeled these relationships separately by time period. For greater statistical power, we also ran an overall analysis of body condition index as a function of both number of parasites and time period as factors. Analyses were performed in InfoStat v. 2016 (Di Rienzo *et al.* 2016).

RESULTS

Chewing lice richness and occurrence

We sampled 108 individuals of seven shorebird species and collected 160 specimens of ectoparasites of the Menoponidae and Philopteridae families that were classified into four genera and nine species (Tables 1 & 2, Fig. 2). Twenty specimens of chewing lice collected from 38 Semipalmated Sandpipers were excluded from Table 1 because the number of birds lacking parasites was unknown. All shorebirds were adults, except for four juvenile Semipalmated Sandpipers. Thirty-six of 45 Sanderlings had at least one louse. The highest prevalences occurred in Ruddy Turnstone *Arenaria interpres* and Sanderling, with 80% of birds parasitized. The least parasitized species was Western Sandpiper *Calidris mauri*, with a prevalence of 36%. Sanderlings hosted the highest abundance of lice with both Menoponidae and Philopteridae representatives, while Semipalmated Sandpipers had the highest richness hosting *Actornithophilus umbrinus*, *Lunaceps rothkoi*, *L. superciliosus* and *Saemundsonia tringae*.

Chewing lice species and their respective hosts are shown in Table 2. The Philopteridae family showed higher prevalence (62%), richness, and number of host species (seven parasitic species being hosted by seven shorebird species) than the Menoponidae (prevalence of 49% and two parasitic species in five host species). The Menoponidae louse *A. umbrinus*, found in all four *Calidris* species, had the highest number of hosts, while *A. pediculoides* and all the Philopteridae species were only found on a single host. *L. actophilus*, found on 64% of the Sanderlings, was the chewing louse with the highest prevalence, mean

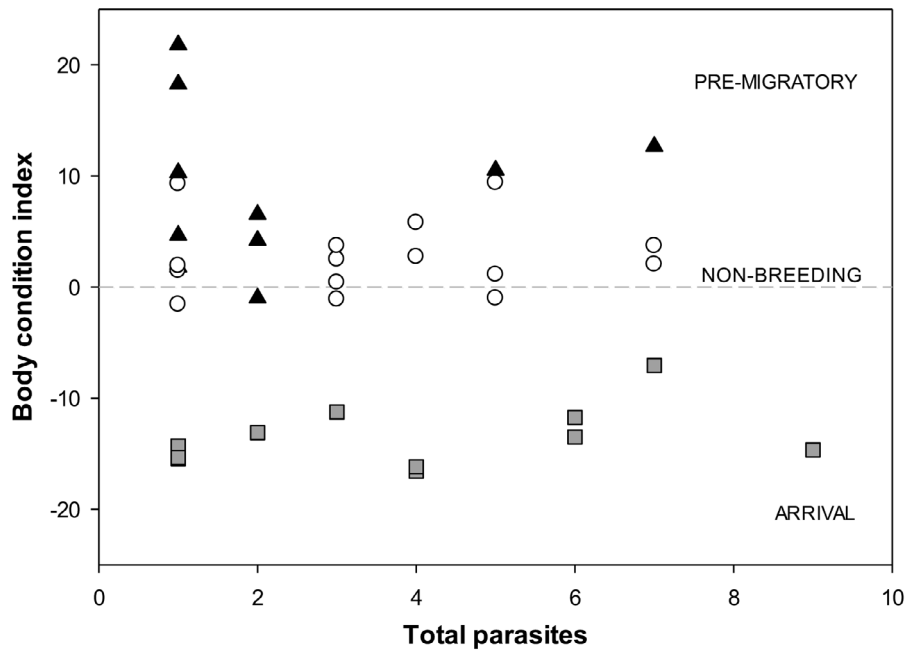


Fig. 4. Body condition index in relation to total parasites in Sanderlings *Calidris alba* ($n = 45$) during three time periods across the non-breeding season: arrival in September (grey squares), non-breeding in January (open circles) and pre-migratory period in March (black triangles).

intensity, and mean abundance of infection (Table 2).

Seasonal parasite loads and body condition in Sanderlings

Forty-five Sanderlings were sampled across September, January and March, of which 36 were parasitized with at least one ectoparasite. We found no evidence of a significant difference in prevalence with respect to date (Wald $\chi^2 = 0.24$, $P = 0.62$), nor in the number of parasites per bird ($F_{1,43} = 2.45$, $P = 0.12$). However, total parasite number per individual does suggest a decrease through the non-breeding season (Fig. 3) from mean values of 3.4 ± 2.9 SD ($n = 13$) in September to 2.8 ± 2.3 SD ($n = 19$) in January and 1.8 ± 2.0 SD in March ($n = 13$).

Body condition increased over the non-breeding season (Fig. 4). Birds arrived thin for their size, but by January they had increased in mass relative to body size, and those preparing to migrate in March had the highest masses relative to their body size (body condition index -12.4 ± 5.0 g (mean \pm SD) in September, 2.5 ± 3.1 in January and 8.9 ± 7.1 in March, $F_{1,43} = 124.69$, $P < 0.0001$). We found no significant relationship between body condition and total parasites within each time period (September: $F_{1,11} = 0.17$, $P = 0.69$; January: $F_{1,17} = 0.42$, $P = 0.52$; March: $F_{1,11} = 0.07$, $P = 0.79$). The pooled analysis including time period as a factor also failed to detect an effect of parasite number as a predictor of body condition (full model with interaction term: time period*total parasites term: $F_{1,41} = 0.06$, $P = 0.81$; for model excluding the nonsignificant interaction term: parasite number: $F_{1,42} = 0.73$, $P = 0.40$).

DISCUSSION

Chewing lice richness and occurrence

All chewing lice species reported in this study are new geographical records for shorebirds in Perú. Our results suggest that the least specific ectoparasite was *Actornithophilus umbrinus*, which was found on all the *Calidris* species we checked. This resembles a similar survey from Ecuador (Haase & Alava 2014), where *A. umbrinus* was found in Western Sandpipers, Least Sandpipers *Calidris minutilla*, Stilt Sandpipers *Calidris himantopus*, Semipalmated Plovers, and Wilson's Phalaropes *Phalaropus tricolor*.

In contrast, we found that *Lunaceps* species were specific to a single *Calidris* species. Dik *et al.* (2011) stated that the level of specificity of *Lunaceps* ectoparasites was higher than in other groups. *Lunaceps actophilus*, which in our work occurred only in Sanderlings, was the species with the highest prevalence, mean abundance and mean intensity of infection. Due to these characteristics, we could consider *L. actophilus* as a 'core' species for Sanderling ectoparasitic structure, as defined by Bush & Holmes (1986a, b), who consider parasitic species with prevalence above 40% as core species that interact frequently enough with the host to reach a balance. *L. actophilus* was described previously as *Nirmus actophilus* with Sanderlings as a host, with most reports in this shorebird species, but has also been recently reported in Dunlins *Calidris alpina* (Gustafsson & Olsson 2012). We also registered a louse from the genus *Saemundssonina* which is known to be common in shorebirds in general (Price *et al.* 2003), but in this study we recorded only three individuals of *S. tringae* on a single Semipalmated Sandpiper. On the latter

host, we also recorded *L. superciliosus*; this louse was described from Sharp-tailed Sandpipers *Calidris acuminata* and Long-toed Stints *Calidris subminuta*, being morphologically separated from other species by the presence of a small suture near the post-nodular setae (Gustafsson & Olsson 2012).

The mean intensities of ectoparasites on shorebirds at Paracas are roughly comparable to those reported for White-rumped Sandpipers *Calidris fuscicollis* wintering in southern Brazil (Gomes et al. 2015). However, they are lower than those reported for many shorebird species in Turkey (Dik et al. 2011), and far lower than ectoparasite loads reported for Red Knots in northern Brazil (D'Amico et al. 2008), where many birds harbored hundreds of lice, although Red Knots are much larger than most of the species in the other studies. For the only Red Knot sample that we had, it was not possible to identify the species of *Lunaceps* due to the poor state of the parasite collected and the consequent difficulty of its morphological identification. Different species of the *Lunaceps* genus differ primarily only in size, intensity of color, and with minimal distinctions in the male genitalia and in the prenatal area (Gustafsson & Olsson 2012, Gomes et al. 2014).

Seasonal parasite loads and body condition in Sanderlings

Total ectoparasite numbers seemed to show a slight decrease across the non-breeding season (Fig. 3), although, we found no evidence of a significant trend given the variance and our limited sample size. If real, this pattern could indicate that individuals are losing ectoparasites during their stay at Paracas. This would be consistent with Piersma's (1997) hypothesis that high arctic and alpine-nesting species, with lower immunocompetence levels, will utilize lower-parasite marine habitats rather than more productive, but more parasite-infested boreal, temperate and tropical freshwater habitats. Sanderlings are high arctic nesters, which use all migratory flyways in the Western Hemisphere (Myers et al. 1990). They may arrive at Paracas relatively parasite-infested from breeding and migration stopover sites, get somewhat de-parasitized during the non-breeding season, and then prepare to migrate north in a less-infested state.

A reduction of ectoparasite number could also indicate that more parasitized birds are leaving the population by emigration or death. However, our failure to document a relationship between parasitism load and body condition within time periods does not provide support for differential fitness or emigration as likely mechanisms. A third explanation could reflect seasonality in the presence of adult versus egg and larval life stages, as was found for a passerine in Spain (Carrillo et al. 2007). Since the life cycles of ectoparasites in the region of our study are not well-documented, we cannot assess the likelihood of the quite plausible seasonal life-stage mechanism. Finally, body molt could also be a potential reason for reducing load of ectoparasites, especially in cases where the molt begins at arrival to the non-breeding areas. However,

Sanderlings arrive at Paracas almost entirely molted into their non-breeding plumage (E. Tavera unpubl. data), and thus it could not substantially affect ectoparasite load.

Despite the examples of negative effects of ectoparasites cited in the introduction, we did not find that Sanderlings incur substantial direct physical or physiological effects from the number of chewing lice at Paracas during our study period. However, detailed immunological studies and/or long-term studies would help assess the effects of chewing lice on fitness.

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