ORIGINAL PAPER

The helminth community structure as an indicator of habitat use: the case of the Baird's Sandpiper (*Calidris bairdii*) and the White-Rumped Sandpiper (*Calidris fuscicollis*) on their non-breeding grounds in Patagonia

Sofia Capasso[1] · Verónica L. D'Amico[2] · Graciela Minardi[1] · Julia I. Diaz[1]

Abstract

During migrations, birds are exposed to a wide variety of parasites. It has been suggested that shorebird migration and other movements play a critical role in structuring their parasite communities. The objective of this study was to characterize the helminth communities of two sympatric Nearctic migratory shorebird species in their non-breeding grounds in Argentine Patagonia and to assess what factors influence their structuring. The migration of these two bird species span from pole to pole as they breed in the Canadian Arctic and winter at southernmost South America. In contrast to the Arctic, the helminth communities of these birds have never been studied at their austral non-breeding sites. A total of 44 *Calidris bairdii* and 50 *Calidris fuscicollis* collected at various coastal marine and inland sites were analyzed for helminths. Ecological parameters were calculated at component community (host population) and infracommunity (single individual hosts) levels. A total of 26 helminth taxa were found, included in 14 families and 20 genera. Results showed that parasite richness and total prevalence were higher in *C. bairdii* than in *C. fuscicollis*. Richness, diversity, dominance and abundance values in the infracommunities were generally low, being lower in *C. fuscicollis*. The infracommunities were characterized by being heterogeneous, unstructured and unpredictable. Possible causes of this pattern are discussed. It is clear that multiple factors influence parasitic diversity; however, considering our observations, we think that habitat use is possibly the main structuring factor of the helminth communities of these two shorebird species.

Keywords Argentina · Gastrointestinal parasites · Ecology · Migratory birds · Parasitology · Southern South America

Introduction

Parasite communities are defined by a set of species that live in a host population, the intra- and interspecific relationships between them, the parasite-host association and the environmental factors structuring that community (Bautista-Hernández et al. 2015). A descriptive study of parasite communities can be performed mainly at two different levels.

One level is the component community, which includes all parasite populations in the analyzed host population. This level is related to evolutionary time scale processes, and its analysis provides a global view of the system (Poulin 2011). The other level is the infracommunity level, which includes all parasite populations in a single individual host. Comparisons can be made between individual hosts or "replicate communities." This analysis provides a limited view in time since infracommunities are short-lived, and their maximum lifetime is the host's life. Therefore, they provide more precise information in relation to the individual host (Bush et al. 1997; Magurran and McGill 2011).

In bird hosts, parasite diversity has been associated with long life span, grade of immune response and dietary breadth, among others (Gutiérrez et al. 2019). Parasite richness has been associated with life history traits of the hosts, especially the migratory strategy (e.g., distance migrations,

✉ Sofia Capasso
capasso.sofia@gmail.com

1 Centro de Estudios Parasitológicos y de Vectores (CEPAVE), FCNyM, UNLP, CONICET, Boulevard 120 s/n e/61 y 62, 1900 La Plata, Argentina

2 Centro Para el Estudio de Sistemas Marinos (CESIMAR), CONICET, Brown 2915, 9120 Puerto Madryn, Chubut, Argentina

variety of habitats, geographic range size), immunocompetence, aggregations of host species in stopover sites and dietary preferences (e.g., generalist vs. specialist) (Thieltges et al. 2013; Hannon et al. 2016; Gutiérrez et al. 2019). Therefore, parasite communities provide reliable information for inferring patterns, interactions and ecological processes occurring in natural host-parasite systems.

Argentine Patagonia provides significant habitats to wintering migrant shorebirds, most of which breed in the Artic. This area is an important habitat for the two shorebird species chosen as avian model for this study, the Baird's sandpiper *Calidris bairdii* (Coues, 1861) and the White-rumped sandpiper *Calidris fuscicollis* Vieillot, 1819. Both species breed in the Arctic tundra (O'Brien et al. 2006). *Calidris bairdii* migrate using mainly the Mid-continental flyway and are observed using several diverse inland wetlands, such as river and lake shores, flooded grasslands and paddy fields. *Calidris fuscicollis* use mainly the Atlantic flyway route, being typically observed at the same latitude as *C. bairdii* but in large numbers over marine coastal areas in temperate regions of South America (O'Brien et al.2006). Despite these general patterns, individuals of both species often overlap their use of Patagonian sites feeding in mixed flocks.

Although helminth assemblages of migratory shorebirds are well studied in North America (Canaris and Kinsella 2001, 2007; Canaris et al. 2003; Didyk et al. 2007; Bondarenko and Kontrimavichus 2018), this topic has not been thoroughly considered in South America, and especially

Argentina is a scarcely studied area, with few taxonomic records prior to the start of this research project (Table 1). To understand whether the parasitic fauna changes from non-breeding with respect to breeding grounds or whether birds carry parasites when they move along the route, it is first necessary to know the species involved in this dynamic.

The aim of this study is to describe and compare the helminth communities (i.e., their composition and structure) of *C. bairdii* and *C. fuscicollis* in their non-breeding sites in Patagonia, Argentina. We aim to determine whether they exhibit similarities and/or differences, considering that their hosts make similar distance migrations but differ in habitat preferences consistent with their migration routes. We expect that the specific richness and structure of their helminth communities give us some information about the habitat use and trophic behavior.

Materials and methods

Study area and sample processing

Birds either died accidentally or were found dead during different research projects performed in the austral summer (January) carried out from 1999 to 2009 in different inland and coastal marine sites in Patagonia, Argentina. Collection sites were located along two important migratory routes of these birds: the Mid-continental flyway and the Atlantic

Table 1 Helminth taxa reported worldwide for *C. bairdii* (BASA) and *C. fuscicollis* (WRSA) before the present research project

Helminth taxa	Host	Locality	References
Cestoda			
Aploparaksis (A.) brachyphallos	BASA	Greenland, Russia, Alaska, Canada, Antarctica, Ukraine, Iceland	Bondarenko and Kontrimavichus (2018)
A. (T.) regelae	BASA	Russia, Alaska	Bondarenko and Kontrimavichus (2018)
Nadejdolepis burgessi	WRSA	Brazil	Nunes Gomes et al. (2016)
N. litoralis	WRSA	Belize	Canaris and Kinsella (2001)
N. paranitidulans	WRSA	Belize	Canaris and Kinsella (2001)
N. sp.	WRSA	Brazil	Nunes Gomes et al. (2016)
Digenea			
Haematotrephus brasilianum	WRSA	Brazil	Nunes Gomes et al. (2016)
Maritrema sp.	WRSA	Brazil	Nunes Gomes et al. (2016)
Pachytrema proximum	WRSA	Brazil	Travassos (1921, 1928)
Paramonostomum fuscicollis	WRSA	Venezuela	Nasir et al. (1970
Nematoda			
Eulimdana sp.	BASA	Island	Bartlett (1992)
Stellocaronema skrjabini	BASA	Canada	Wong and Anderson (1991)
Tetrameres megaphasmidiata	WRSA	Argentina	Cremonte et al. (2001)
Acanthocephala			
Arhythmorhynchus longicolle	WRSA	Belize	Canaris and Kinsella (2001)
Polymorphus cucullatus	WRSA	Brazil	Nunes Gomes et al. (2016)

flyways. The former presents two different areas: the mountain range and the plateau, where areas with permanent or temporary bodies of fresh or brackish water can be observed with varied vegetation, predominantly halophytes and grass species (Blanco et al. 2012) (Fig. 1). In the Atlantic flyway, the marine coasts are characterized by the presence of cliffs and estuary ecosystems with long intertidal plains. There are also sandbanks areas, caves and rocky shelters. The intertidal plains allow the development of diverse benthic invertebrate communities. These ecosystems provide food for many bird species, including important populations of Nearctic migratory shorebirds (Blanco et al. 2012).

All samples taken from birds were in compliance with all appropriate research permissions (permit numbers 19/04, 02/05, 10/6, 02/08, 48/08, 92/05 DF and FS Chubut and 06/05 DFS Santa Cruz province). Birds were dissected in the field, and viscera were fixed in 10% formalin or 96% ethanol.

Identification of gastrointestinal parasites

The viscera and body cavity were examined at the laboratory under a stereomicroscope. Collected helminths were recovered, counted and preserved in 70% or 96% ethanol.

Nematodes and acanthocephalans were studied in temporary mounts using glycerin alcohol, lactophenol or eugenol. Digeneans and cestodes were stained using acetocarmine, cleared and mounted on permanent slides using natural Canada balsam. Also, scanning electron microscope and histological sections were made to assist in their identification. Specimens were identified to the lowest possible taxonomic level considering the material condition and the number of collected specimens. Helminths were identified according to Yamaguti (1963), McDonald (1981), Khalil et al. (1994), Gibson et al. (2002, 2005), Bray et al. (2008), Anderson et al. (2009), Gibbons (2010) and Amin (2013).

Data analysis

For component community analysis, prevalence (P = number of parasitized hosts/number of examined hosts), mean intensity (MI = number of parasites/number of parasitized hosts) and mean abundance (MA = number of parasites/number of examined hosts) were calculated for all parasites and for each parasite population following Bush et al. (1997). In addition, the following community descriptors were calculated: specific richness S = number of species in
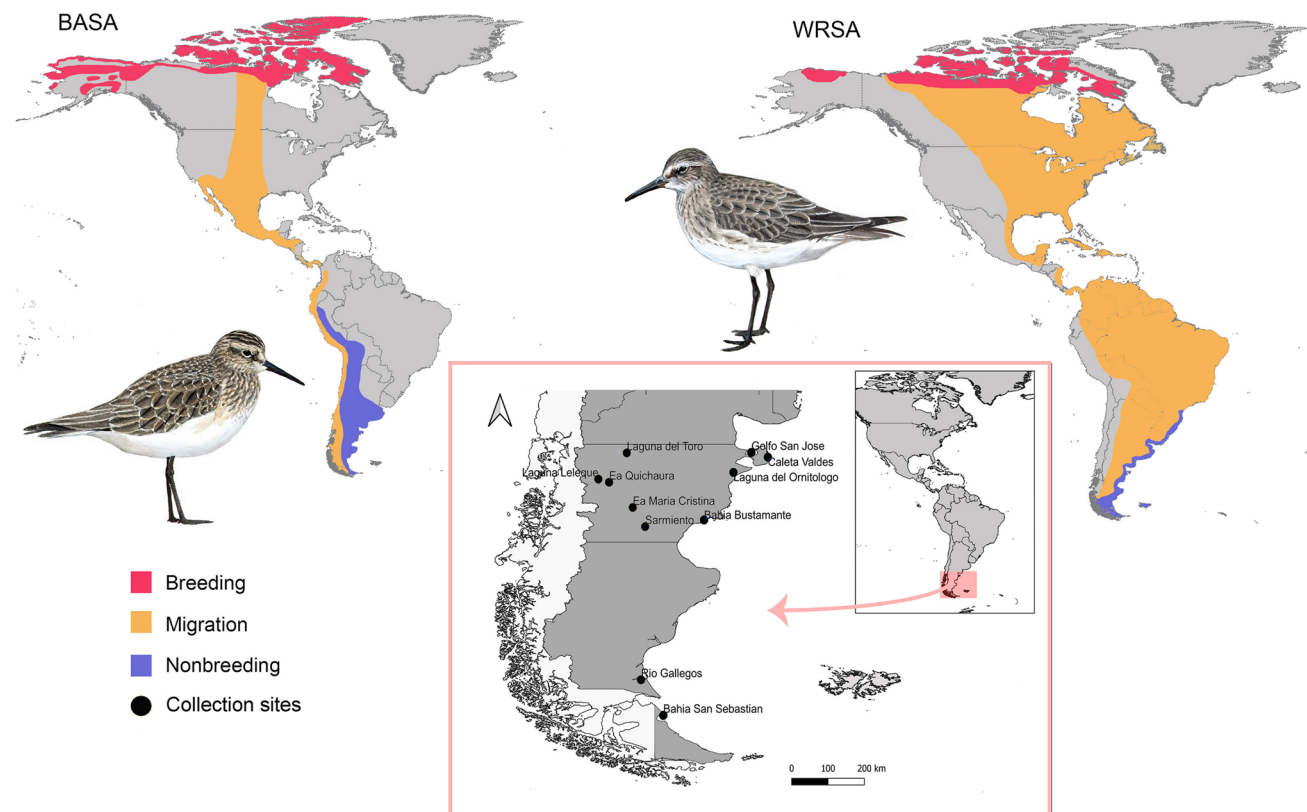

Fig. 1 Geographical distribution and migration strategies of *Calidris bairdii* (BASA) and *Calidris fuscicollis* (WRSA) and study area in the nonbreeding range in Argentinean Patagonia. Dots show collec-
tion sites. Distribution data were consulted in BirdLife International (2021). Bird illustrations by Carl Christian Tofte

each component community; abundance N = number of helminth specimens; Shannon diversity index HB = $-\Sigma pi \ln pi$, where $pi = ni/N$ proportion of individuals in the ith species; Berger-Parker's measure of relative dominance $D = N_t/N_{max}$, where N_{max} = number of individuals of the most abundant species and N_t = total abundance; and evenness $E = H/D_{max}$, observed diversity (H) is the value calculated previously (Shannon's diversity index), and the maximum diversity (D_{max}) is the natural logarithm of the observed richness.

Statistical differences for total prevalence between host species were tested using confidence intervals with the correction given in Agresti and Caffo (2000) for cases of extreme prevalence (e.g., > 95%). Similarity between component communities was analyzed through the Sørensen coefficient of similarity index (Magurran and McGill 2011) following the formula $C\text{ss} = 2c/S_a + S_b$, where S_a = number of species present at component community a (specific richness of a), Sb = specific richness of component community b and c = species common to both component communities.

The infracommunity analyses were based on the following descriptors: specific richness S = number of species that exists in each infracommunity, Billouin diversity index HB = $(\ln N! - \sum \ln n_i!)/N$, which is applied for communities that have been fully surveyed; N is the total number of individuals in the sample, and ni is the number of individuals belonging to the ith species; Berger-Parker's measure of relative dominance $D = N t/N max$, where $N max$ = number of individuals of the most abundant species and $N t$ = total abundance; D shows the proportion of the most abundant species to the total number of parasites in each host; evenness $E = HB/HBmax$, where $HBmax$ is $HB_{max} = \frac{1}{N}\ln\frac{N!}{[[N/S]]!^{S-r}+([[N/S]]+1)!^r}$ where $r = N - S[[N/S]]$ the maximum value of the diversity for the number of present species in each infracommunity. Statistical differences were tested between host species using confidence intervals under a 99% of significance level.

Similarity between infracommunities was assessed with Sørensen's coefficient of similarity index (Magurran and McGill 2011) following the formula $C_N = 2jN/(aN + bN)$ where jN = sum of lowest recorded abundances of common species between infracommunities a and b, aN = abundance in the infracommunity a and bN = abundance in the infracommunity b. This index compares the number of shared species with the average number of species in a single infracommunity and indicates the proportion of shared species in each infracommunity (Magurran and McGill 2011).

Principal components analysis (PCA) was used to detect patterns in infracommunities between host species and migratory flyways. The values of richness, abundance, diversity, dominance and evenness from each infracommunity were used as attributes. Birds with helminth abundance = 0 were removed from the data set. For the purpose of this analysis, sites were combined according to the migratory flyway, Mid-continental flyway: Laguna Leleque (45° 21′ S; 71° 6′ W), Estancia Quichaura (43° 25′ S; 70° 12′ W), Laguna del Toro (48° 14′ S; 67° 22′ W), Estancia María Cristina (44° 34′ S; 69° 35′ W), Sarmiento (45° 21′ S; 69° 2′ W) and Atlantic flyway: Bahía Bustamante (45° 5′ S; 66° 25′ W), Laguna del Ornitólogo (43° 8′ S; 65° 7′ W), Río Gallegos (51° 37′ S; 69° 13′ W), Bahía San Sebastián (53° 4′ S; 68° 14′ W), Golfo San José (42° 19′ S; 64° 19′ W) and Caleta Valdés (42° 31′ S; 63° 36′ W).

All statistical analyses were performed in R version 3.6.0 and Rstudio version 1.3.959 (R Core Team 2020) using the BiodiversityR (Kindt and Coe 2005), Vegan (Oksanen et al. 2020), dabestr (Ho et al. 2019) and factoextra (Kassambara and Mundt 2020) packages.

Results

A total of 44 *C. bairdii* and 50 *C. fuscicollis* were analyzed. In the Mid-continental flyway most collected specimens were *C. bairdii* ($N_{bairdii} = 37$, $N_{fuscicollis} = 4$), whereas in Atlantic flyway most were *C. fuscicollis* ($N_{bairdii} = 7$, $N_{fuscicollis} = 46$). Table 2 shows the helminth taxa found parasitizing each bird species and the values of their population parameters (i.e., P, MA, MI). Some of the species found during the course of this project have been taxonomically described in previous publications (Diaz et al. 2011; Capasso and Diaz 2016; Capasso et al. 2017, 2019, 2020). We found two species of the genus *Nadejdolepis* but for statistical analysis they were grouped as a single taxon due to difficulties in their differentiation under the magnifying glass.

Component community

Of the 94 birds examined, 77 were parasitized (P for total parasitism = 82%). The total prevalence was higher in *C. bairdii* ($P = 100\%$, 95% CI 100–100, $N = 44$) than in *C. fuscicollis* ($P = 66\%$, 95% CI 52.9–79.1, $N = 50$). The most prevalent group in both host species was cestodes, followed by nematodes. Cestodes were also the most abundant in both communities (Table 2; Fig. 2).

In *C. bairdii* hosts, 22 helminth species were represented by 2804 specimens, whereas in *C. fuscicollis* hosts, 17 helminth species were represented by 315 specimens. The similarity between both helminth component communities was $C_{SS} = 0.75$. The S, N, HB, D and E for each component community are shown in Table 3.

Table 2 Summary of helminth component communities for sampled shorebirds in Patagonia, Argentina

Component communities	BASA ($n = 44$)			WRSA ($n = 50$)		
Helminth taxa	P ± SE	MI ± SE	MA ± SE	P	MI ± SE	MA ± SE
Cestoda	$P_T = 84\%$			$P_T = 44\%$		
Echinocotyle sp.*	63.6 ± 7.25	33.8 ± 7.23	21.5 ± 5.2	–	–	–
Nadejdolepis spp.	40.9 ± 7.41	11.2 ± 5.88	4.6 ± 2.51	22 ± 5.86	6.1 ± 2.17	1.3 ± 0.58
Microsomacanthus sp. *	4.5 ± 3.14	15.5 ± 6.5	0.7 ± 0.54	2 ± 1.98	1	0 ± 0.02
Aploparaksis brachyphallos §	27.3 ± 6.71	10.3 ± 2.89	2.8 ± 1.04	2 ± 1.98	1	0 ± 0.02
Kowalewskiella cingulifera *§	27.3 ± 6.71	5.2 ± 1.5	1.4 ± 0.53	4 ± 2.77	2 ± 0	0.1 ± 0.06
Trichocephaloidis sp. 1 *§	20.5 ± 6.08	10.8 ± 4.5	2.2 ± 1.1	–	–	–
Trichocephaloidis sp. 2 *§	–	–	–	4 ± 2.77	1.5 ± 0.5	0.1 ± 0.04
Dilepididae sp. 1 *	9.1 ± 4.33	4 ± 0.91	0.4 ± 0.19	24 ± 6.04	6 ± 1.67	1.4 ± 0.53
Digenea	$P_T = 52\%$			$P_T = 24\%$		
Echinoparyphium sp.*	6.8 ± 3.8	4 ± 2.52	0.3 ± 0.21	2 ± 1.98	1	0 ± 0.02
Brachylecithum lari§	4.5 ± 3.14	1 ± 0	0 ± 0.03	2 ± 1.98	3	0.1 ± 0.06
Notocotylus chionis *	–	–	–	10 ± 4.24	11.4 ± 3.14	1.1 ± 0.56
N. sp.*	4.5 ± 3.14	2.5 ± 0.5	0.1 ± 0.08	–	–	–
*Maritrema formicae**	15.9 ± 5.51	22.7 ± 8.83	3.6 ± 1.83	–	–	–
M. pichi§	4.5 ± 3.14	205.5 ± 172.5	9.3 ± 8.61	–	–	–
Levinseniella cruzi *	2.3 ± 2.25	17	0.4 ± 0.39	–	–	–
Odhneria odhneri *	4.5 ± 3.14	37 ± 19	1.7 ± 1.33	–	–	–
Parorchis sp. nov*§	11.4 ± 4.78	1.2 ± 0.2	0.1 ± 0.06	4 ± 2.77	2 ± 1	0.1 ± 0.06
Plagiorchis sp.*	20.5 ± 6.08	12 ± 5.94	2.5 ± 1.37	8 ± 3.84	3.5 ± 1.85	0.3 ± 0.19
Nematoda	$P_T = 66\%$			$P_T = 26\%$		
Strongyloides sp.*	56.8 ± 7.47	18.6 ± 7.65	10.6 ± 4.53	6 ± 3.36	1.7 ± 0.33	0.1 ± 0.06
Echinuria skrjabiniensis§	9.1 ± 4.33	3.2 ± 0.48	0.3 ± 0.15	6 ± 3.36	18 ± 16.01	1.1 ± 1
Tetrameres sp.	6.8 ± 3.8	1.7 ± 0.33	0.1 ± 0.07	12 ± 4.6	3 ± 0.73	0.4 ± 0.16
Eucoleus sp.*	9.1 ± 4.33	5.2 ± 2.5	0.5 ± 0.3	2 ± 1.98	1	0 ± 0.02
Acanthocephala	$P_T = 27\%$			$P_T = 10\%$		
*Arhythmorhynchus comptus**	25 ± 6.53	2.5 ± 0.76	0.6 ± 0.24	10 ± 4.24	2.4 ± 1.4	0.2 ± 0.16
Profilicollis sp.*	2.3 ± 2.25	3	0.1 ± 0.07	2 ± 1.98	1	0 ± 0.02

P % prevalence, P_T total prevalence, *MI* mean intensity, *MA* mean abundance, *SE* standard error. Birds are indicated as follows: *BASA C. bairdii*, *WRSA C. fuscicollis*,

*New host record

§New geographic record

Fig. 2 Prevalence of main helminth taxa of *Calidris bairdii* (BASA) and *Calidris fuscicollis* (WRSA) from Argentinean Patagonia
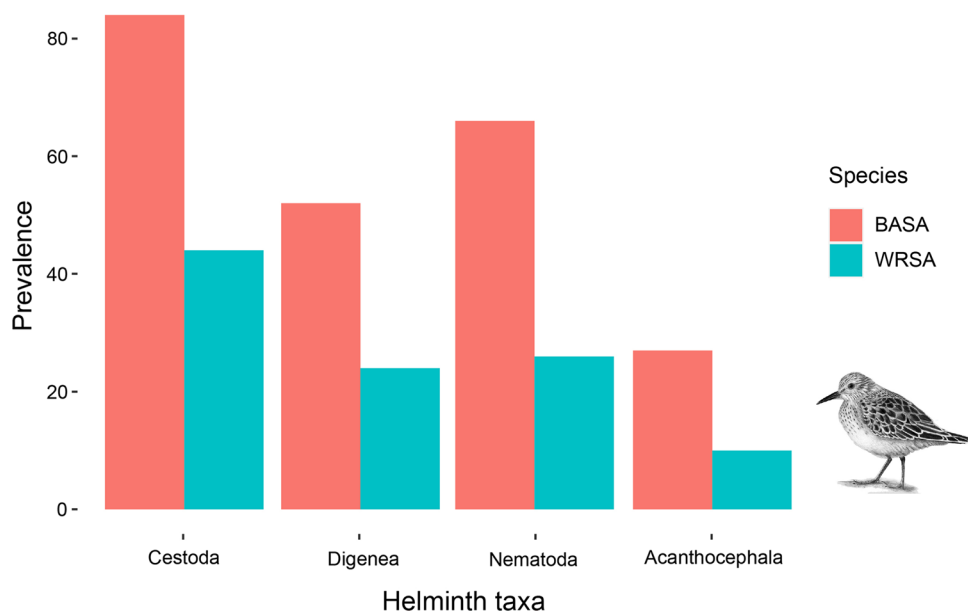

Table 3 Ecological descriptors for helminth communities of shorebirds from Patagonia, Argentina

	BASA (*n*=44)		CI values for statistical mean difference between IC	WRSA (*n*=50)	
	CC	IC		IC	CC
S	22	4±0.31, 1, 10, 3*	**− 2.87; − 1.12**	2±0.19, 0, 6, 0*	17
N	2804	64±12.09, 1, 415, 5*	**− 98.4; − 31.3**	10±2.11, 0, 58,0*	318
HB	2.15	0.65±0.06	**− 0.612; − 0.196**	0.25±0.05	2.05
D	0.34	0.68±0.03	**0.0202; 0.263**	0.82±0.04	0.23
E	0.69	0.6±0.05	− 0.383; 0.0562	0.43±0.07	0.72

BASA C. bairdii, *WRSA C. fuscicollis*, *CC* component community, *CI* confidence interval 99%, *D* dominance, *E* evenness, *HB* diversity, *IC* infracommunity, *N* abundance, *S* species richness

Significant values are shown in bold

*Mean ± SE, minimum, maximum, mode

Infracommunities

The analysis of infracommunities showed low values of diversity. The S, N, HB and D of *C. bairdii* infracommunities were significantly higher (mean = 4 species, 64 individuals, 0.65, 0.68 and 0.6, respectively) than *C. fuscicollis* (mean = 2 species, 10 individuals, 0.25, 0.82 and 0.43, respectively) (Fig. 3; Table 3). Most infracommunities in *C. bairdii* were composed of more than three species, reaching a maximum richness of ten parasite species, while in most *C. fuscicolllis* richness did not exceed two parasite species. No differences were found in evenness between infracommunities (Table 3). The values of C_N for *C. bairdii* hosts were low, and only 5% of the comparisons showed a value > 0.5. Similarly, the values of C_N for *C. fuscicollis* hosts were very low, ranging from 0 to 0.8, although in most cases no similarity was observed. Only 3% of the values were > 0.5.

The first two axes of the principal component analysis, which sorted the infracommunities according to host species, explained 93% of the association between the variables (Table 4). The first component (66%) was positively associated with richness, diversity, evenness and abundance and negatively with dominance. In Fig. 4a, a gradient is observed from higher richness and diversity values (and to a lesser extent abundance) in the positive quadrant of axis 1 represented mostly by *C. bairdii* infracommunities to high dominance values in the negative quadrant of axis 1, represented mostly by *C. fuscicollis*. Only *C. bairdii* infracommunities are located at the upper right quadrant of axis 1, showing the highest values of abundance, richness and diversity. The second component (27%) was positively associated with abundance and negatively with evenness. This axis showed high abundance variability for *C. bairdii* and low for *C. fuscicollis* and high values of dominance in *C. fuscicollis* and low in *C. bairdii*. In Fig. 4b, the principal component analysis could not identify clear aggregation or progressive change in the
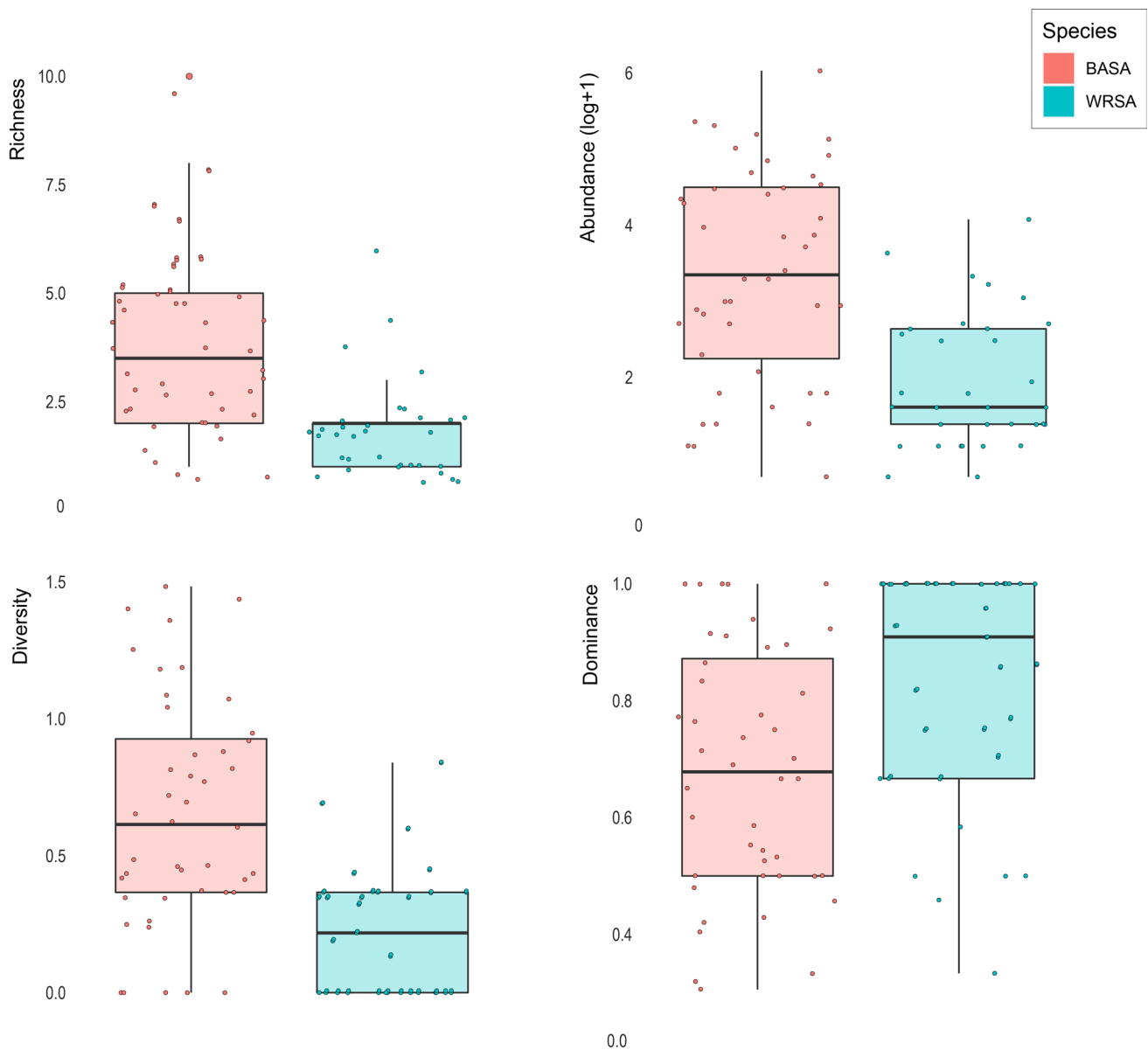
Fig. 3 Ecological parameter distribution in *Calidris bairdii* (BASA) and *Calidris fuscicollis* (WRSA) infracommunities. Dots show the underlying distribution of observations in each group

Table 4 Eigenvalues and factor loadings of the first two axes of principal component analysis

	Dim.1	Dim.2
Variance	3.278	1.371
% of variance	65.560	27.429
Cumulative % of variance	65.560	92.989
Factor loadings		
Abundance	0.505	0.817
Richness	0.865	0.458
Diversity	0.956	− 0.013
Evenness	0.754	− 0.568
Dominance	− 0.890	0.414

structure of infracommunities between flyways (environmental inland-marine gradient).

Discussion

In the present study, 26 helminth taxa were found, included in 14 families and 20 genera. Of these taxa ten were cestodes, ten digeneans, four nematodes and two acanthocephalans. Cestodes and nematodes were the predominant groups. Nine taxa were determined to species level, 16 to genus level and 1 to family level. Two species were found to be new to science: *Parorchis* sp. nov. and *Maritrema pichi*
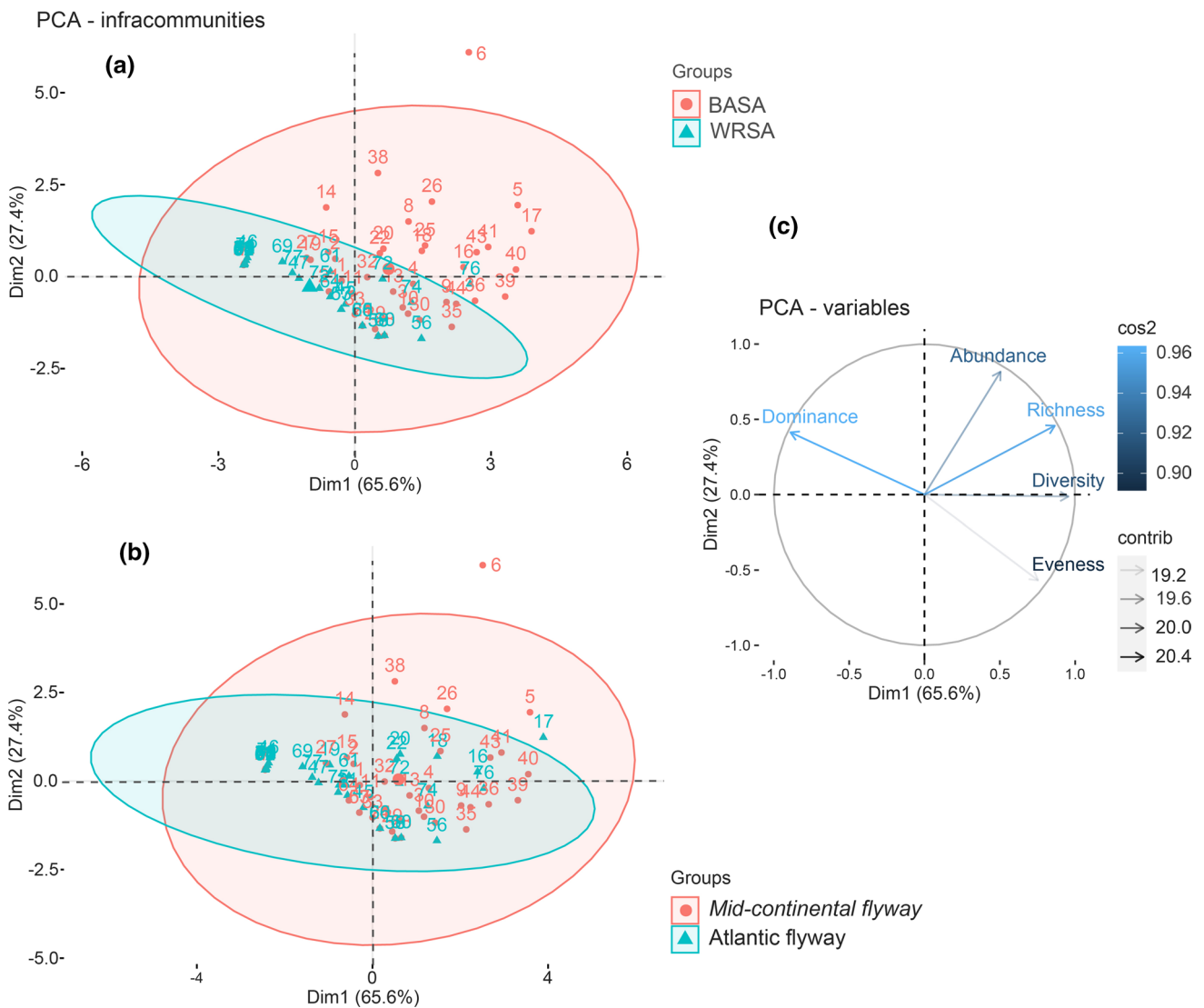
PCA - infracommunities

Fig. 4 **a** Ordination of infracommunities produced by principal component analysis (PCA) based on community variables. Numbers correspond to hosts. Hosts 1 to 44 belong to *Calidris bairdii* (BASA) species (circles and ellipse in red) and from 45 to 77 to *Calidris fusci-* *collis* (WRSA) species (triangles and ellipse in blue). **b** Ordination of infracommunities located within the Mid-continental flyway (circles in red) and Atlantic flyway (triangles in blue). **c** Correlation circle showing the variables (vectors) in relation to component 1 and 2

(see Capasso et al. 2019). Two species were found as immature stage: *Profilicollis* sp. and *Microsomacanthus* sp. The remaining taxa were found as adults.

During stopovers, hosts having low degree of specific overlap will be characterized by a low parasite richness and parasite species with high host specificity. In contrast, in areas with a high overlap of host species, hosts will have a greater number of parasite species, most of which are generalists (Edwards and Bush 1989). Most helminth genera and some species found in *C. bairdii* and *C. fuscicollis* were also found in other shorebird species in the northern hemisphere, e.g., *Nadejdolepis*, *Aploparaksis brachyphallos*, *Trichocephaloidis*, *Kowalewskiella cingulifera*, *Microsomacanthus*, *Plagiorchis*, *Levinseniella*, *Strongyloides*, *Echinuria*,

Tetrameres, Eucoleus, Arhythmorhynchus comptus (Canaris and Kinsella 2000, 2007; Kinsella et al. 2007; Canaris et al. 2012), suggesting that they have low host specificity. This could be related to the opportunities for parasite transmission at stopover sites. During migrations, these birds do not spread out randomly over wide areas but congregate at a few sites where the availability of prey species and roosting places are predictable. The overlap of host species would be reflected in a high number of generalist parasite species.

At component community level, it was observed that parasite richness and diversity were higher in *C. bairdii* than in *C. fuscicollis*. The evenness and dominance indices indicated that helminth species were uniformly represented in each component community. As migratory behavior is

a main characteristic of these birds, and throughout their migration they frequent different types of environments, they are exposed to a variety of parasites. Commonly, birds with more diverse feeding habits (generalists) will be positively associated with high helminth species richness because they consume more potential intermediate hosts (Thieltges et al. 2013; Gutiérrez et al. 2017). Considering that most helminth parasites have indirect life cycles, the variety of food resources during stopovers may increase the risk of parasite transmission. This was most evident in *C. bairdii*. The overall similarity between the two component communities was high, and they shared most of the helminth species. However, the overall similarity between infracommunities in both host species was very low. These results reflect a high number of helminth species that parasitize few host specimens and are found in low abundances. This phenomenon destabilizes the community structure and gives a low predictability to infracommunities, suggesting that parasite infracommunities in both host species are heterogeneous and unpredictable. Furthermore, infracommunities are unsaturated, which means that their richness does not coincide with that observed at the component community level, generally reaching half the value of the component community.

Previous studies in helminth communities of several Scolopacidae species carried out in North America showed similar results to the present study (Canaris and Kinsella 2000, 2007; Kinsella et al. 2007; Canaris et al. 2012). Helminth component communities from North America tend to have a single dominant helminth species, associated with many unpredictable species, high species richness and high diversity. As in the present study, authors indicated that those communities are the result of a continuous recruitment of a few helminth species in low abundances (Canaris and Kinsella 2007). These features seem to be generally true for several shorebirds whose annual life cycle includes occupation of both inland and marine habitats. Considering that some avian hosts can switch seasonally between freshwater and saline habitats, increasing the diversity of habitats frequented, it is assumed that the parasite richness also increases (Gutiérrez et al. 2017). The results of the PCA indicated that the structures of the infracommunities are not strictly in relation with the preponderance of continental or marine environments in their migratory flyways. As evidence of this, in the present work we found some parasite species with terrestrial or freshwater life cycles in birds captured in marine environments (e.g., *A. brachyphallos*, *Echinocotyle* sp., *Trichocephaloidis* spp., *Eucoleus* sp.) and parasite species with marine life cycles in birds caught inland (e.g., *Parorchis* sp. nov., *A. comptus*). This demonstrates a mixed habitat use.

Regarding the higher prevalence, richness and diversity of helminths in *C. bairdii*, it is to be expected that they would make more stopovers in more diverse foraging sites than *C. fuscicollis* during southbound migration and in their non-breeding grounds in Patagonia. We outlined before that bird species with a broad diet will ingest prey that act as intermediate hosts for a wide range of parasites and parasite richness will increase (Thieltges et al. 2013; Gutiérrez et al. 2017). Accordingly, this might be the case for *C. bairdii*.

Based on the present results, some new questions have arisen: Are the lower parasite prevalence, richness and abundance of *C. fuscicollis* related to a narrower diet during their stay in Patagonia or are those features related to the use of less diverse habitats than *C. bairdii*? Are these parasitological parameters related to physiological characteristics of the hosts, for example, reducing the impact of parasites activating immune responses? The hypothesis that high helminth richness communities reflect a generalist trophic pattern is supported by the high diversity of prey items observed in *C. bairdii* stomach contents (Capasso 2019). Therefore, it can be suggested that the broad food spectrum facilitates an increase in parasite incorporation pathways (Anderson and Sukhdeo 2011). Given the higher values in the ecological parameters (richness, prevalence and abundance), as well as the high intensities of infection by parasites with complex life cycles such as cestodes and digeneans, it is expected that *C. bairdii* incorporates a greater variety of prey than *C. fuscicollis*.

According to Morand (2015), environmental diversity would increase encounters with a greater variety of parasitic species. One plausible explanation for the patterns observed in these two bird species may be related to the migratory strategies: birds that fly over the continent may have more opportunities to stop over to refuel, while birds that migrate following the seashore may find fewer suitable stopovers (Piersma 2003). Also, present parasitological results are consistent with the recent confirmation that *C. fuscicollis* conducts extensive non-stop flights from the northern to southern hemisphere (Anderson et al. 2019), explaining the lower helminth prevalence found (i.e., less chance of encountering parasites along the route).

However, it should be considered that the structure of the helminth communities also reflects the ability of host species to tolerate different parasite loads. So far, no studies have been carried out to determine the immunological condition of these two bird species that can help to understand whether the parasite load is related to factors intrinsic to each host bird species and/or to each bird specimen. Future studies combining parasitological and immunity indices will be necessary to determine whether immune inversion differs between host species and between populations that frequent different types of environments.

Conclusions

The present study represents a valuable contribution to the knowledge of the helminth diversity of migratory shorebirds migrating between Arctic and sub-Antarctic regions. Ecological results suggest that the characteristics of the helminth communities of these two migratory shorebird species in Argentine Patagonia depend on the differential use of environments, considering that the migration distance performed by birds is similar and they are frequenting both marine and freshwater environments. In this way, helminth communities' structure is directly related to the opportunities for the transmission of parasites, in both the non-breeding areas and stopovers during migration. It can be inferred that helminth communities of studied shorebirds are structured based on similarities and differences. The similarities would be determined by the fact that (1) both host species share, partially, breeding and non-breeding grounds in the Nearctic, (2) cover the same migration distances and (3) have a generalist trophic habit. Differences could be attributed to: (1) diversity of frequented environments, (2) number of stopovers and (3) prey item variability and availability during stopovers in the sub-Antarctic.

Declarations

Conflict of interest The authors declare that no conflicts of interest exist.

References

Agresti A, Caffo B (2000) Simple and effective confidence intervals for proportions and differences of proportions result from adding two successes and two failures. Am Stat 54:280–288

Amin OM (2013) Classification of the Acanthocephala. Folia Parasit 60:273–305. https://doi.org/10.14411/fp.2013.031

Anderson TK, Sukhdeo MV (2011) Host centrality in food web networks determines parasite diversity. PLoS ONE 6:e26798. https://doi.org/10.1371/journal.pone.0026798

Anderson RC, Chabaud AG, Willmott S (2009) Keys to the nematode parasites of vertebrates: archival volume. Wallingford

Anderson AM, Duijns S, Smith PA, Friis C, Nol E (2019) Migration distance and body condition influence shorebird migration strategies and stopover decisions during southbound migration. Front Ecol Evol 7:251. https://doi.org/10.3389/fevo.2019.00251

Bartlett CM (1992) New, known and unidentified species of *Eulimdana* (Nematoda): additional information on biologically unusual filarioids of charadriiform birds. Syst Parasitol 23:209. https://doi.org/10.1007/BF00010874

Bautista-Hernández CE, Monks S, Pulido-Flores G, Rodríguez-Ibarra AE (2015) Revisión bibliográfica de algunos términos ecológicos usados en parasitología, y su aplicación en estudios de caso. Estudios En Biodiversidad 1:11–19

Blanco DE, Espinosa DG, Quevedo DL (2012) Plan de recuperación de aves playeras en la Patagonia. Manomet Center

Bondarenko S, Kontrimavichus V (2018) Revision of *Aploparaksis* Clerc, 1903 (Cestoda: Cyclophyllidea, Aploparaksidae), with keys to the species of the genus. Biologija 64:1–64. https://doi.org/10.6001/biologija.v64i1.3659

Bray RA, Gibson DI, Jones A (2008) Keys to the Trematoda, vol 3. Wallingford

Bush AO, Lafferty KD, Lotz JM (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol 83:575–583. https://doi.org/10.2307/3284227

Canaris AG, Kinsella JM (2000) Helminth Parasites of Six Species of Shorebirds (Charadrii) from Bristol Bay, Alaska, USA. Comp Parasitol 67:250–252

Canaris AG, Kinsella JM (2001) Helminth parasites in six species of shorebirds (Charadrii) from the coast of Belize. Mem I Oswaldo Cruz 96:827–830. https://doi.org/10.1590/S0074-02762001000600015

Canaris AG, Kinsella JM (2007) Helminth communities of three sympatric species of shorebirds (Charadrii) from four summer seasons at Bristol Bay, Alaska. J Parasitol 93:485–490. https://doi.org/10.1645/GE-3550.1

Canaris AG, Kinsella JM, Braby R (2003) Helminth parasite communities in two species of shorebirds (Charadrii) from Namibia. Comp Parasitol 70:155–161. https://doi.org/10.1654/4069

Canaris AG, Kinsella JM, Didyk AS (2012) Helminth parasites of the western willet, *Tringa semipalmata inornata*, from Montana and Texas with a checklist of helminth parasites. J Parasitol 98:216–221. https://doi.org/10.1645/GE-2871.1

Capasso S (2019) Las comunidades de helmintos de aves playeras migratorias neárticas en humedales costeros e interiores de la Patagonia argentina (Doctoral dissertation, Universidad Nacional de La Plata).

Capasso S, Diaz JI (2016) *Arhythmorhynchus comptus* (Acanthocephala: Polymorphidae) from shorebirds in Patagonia, Argentina, with some comments on a species of *Profilicollis*. Check List 12:1910. https://doi.org/10.15560/12.3.1910

Capasso S, D'Amico VL, Diaz JI (2017) *Odhneria odhneri* Travassos, 1921 (Trematoda: Microphallidae) in Migrant Shorebirds from Patagonia, Argentina. Rev Arg Parasitol 6:15–20

Capasso S, D'Amico VL, Diaz JI (2019) A new species of *Maritrema* (Trematoda: Microphallidae) parasitizing the Baird's sandpiper *Calidris bairdii*, and comments about diversity of Microphallidae in two Nearctic shorebirds at Patagonian sites in Argentina. Acta Trop 189:10–14. https://doi.org/10.1016/j.actatropica.2018.09.018

Capasso S, Servián A, Tkach VV, Diaz JI (2020) *Notocotylus chionis* (Trematoda: Notocotylidae) and *Notocotylus* sp. from shorebirds

in southern Patagonian wetlands of Argentina: morphological and molecular studies. Polar Biol 43:1957–1966. https://doi.org/10.1007/s00300-020-02753-9

Cremonte F, Digiani MC, Bala LO, Navone GT (2001) *Tetrameres (Tetrameres) megaphasmidiata* n. sp. (Nematoda: Tetrameridae), a parasite of the two-banded plover, *Charadrius falklandicus*, and white-rumped sandpiper, *Calidris fuscicollis*, from Patagonia, Argentina. J Parasitol 87:148–151. https://doi.org/10.1645/0022-3395(2001)087[0148:TTMNSN]2.0.CO;2

Diaz JI, Panisse G, Escudero G, Kinsella JM (2011) New host and geographical records and morphological details for *Echinuria skrjabiniensis* (Nematoda, Acuariidae) from shorebirds in Argentina. Acta Parasitol 56:315–319. https://doi.org/10.2478/s11686-011-0063-5

Didyk AS, Canaris AG, Kinsella JM (2007) Intestinal Helminths of the Spotted Sandpiper, *Actitis macularius* (L.), During Fall Migration in New Brunswick, Canada, with a Checklist of Helminths Reported from this Host. Comp Parasitol 74:359–363. https://doi.org/10.1654/4280.1

Edwards DD, Bush AO (1989) Helminth communities in avocets: importance of the compound community. J Parasitol 75:225–238. https://doi.org/10.2307/3282771

Gibbons LM (2010) Keys to the nematode parasites of vertebrates: supplementary volume. London

Gibson DI, Jones A, Bray RA (2002) Keys to the Trematoda (Vol 1). The Natural History Museum, London

Gibson DI, Jones A, Bray RA (2005) Keys to the Trematoda. The Natural History Museum, London

Gutiérrez JS, Rakhimberdiev E, Piersma T, Thieltges DW (2017) Migration and parasitism: habitat use, not migration distance, influences helminth species richness in Charadriiform birds. J Biogeogr 44:1137–1147. https://doi.org/10.1111/jbi.12956

Gutiérrez JS, Piersma T, Thieltges DW (2019) Micro-and macroparasite species richness in birds: the role of host life history and ecology. J Anim Ecol 88:1226–1239. https://doi.org/10.1111/1365-2656.12998

Hannon ER, Kinsella JM, Calhoun DM, Joseph MB, Johnson PT (2016) Endohelminths in bird hosts from Northern California and an analysis of the role of life history traits on parasite richness. J Parasitol 102:199. https://doi.org/10.1645/15-867

Ho J, Tumkaya T, Aryal S, Choi H, Claridge-Chang A (2019) Moving beyond P values: data analysis with estimation graphics. Nat Methods 16:565–566. https://doi.org/10.1038/s41592-019-0470-3

Kassambara A, Mundt F. (2020). factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R package version 1.0.7. https://CRAN.R-project.org/package=factoextra

Khalil LF, Jones A, Bray RA (1994) Keys to the cestode parasites of vertebrates. The Natural History Museum, London

Kindt R, Coe R (2005) Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF), Nairobi

Kinsella JM, Didyk AS, Canaris AG (2007) Helminths of Hudsonian godwits, *Limosa haemastica*, from Alaska and Manitoba. J Parasitol 93:716–717. https://doi.org/10.1645/GE-1133R.1

Magurran AE, McGill BJ (2011) Biological diversity: frontiers in measurement and assessment. Oxford University Press, Oxford

McDonald ME (1981) Key to Trematodes reported in waterfowl. Resource Publication US Fish and Wildlife Service.

Morand S (2015) (macro-) Evolutionary ecology of parasite diversity: from determinants of parasite species richness to host diversification. Int J Parasitol Parasites Wildl 4:80–87. https://doi.org/10.1016/j.ijppaw.2015.01.001

Nasir P, Diaz MT, Guevara DLDE (1970) Some avian digenetic trematodes of eastern Venezuela. Riv Parassitologia 31:107–112

Nunes Gomes S, Pesenti TC, Müller G (2016) Helminth parasites of the white-rumped sandpiper, *Calidris fuscicollis* (Aves: Scolopacidae), from Brazil. Neotrop Helminthol 10:163–168

O'Brien M, Crossley R, Karlson K (2006) The shorebird guide. Houghton Mifflin Harcourt, New York

Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020). Vegan: Community Ecology Package. R package version 2.5–7. https://CRAN.R-project.org/package=vegan

Piersma T (2003) "Coastal" versus "inland" shorebird species: interlinked fundamental dichotomies between their life- and demographic histories? Wader Study Group Bull 100:5–9

Poulin R (2011) Evolutionary ecology of parasites. Princeton University Press, Princeton

Thieltges DW, Amundsen PA, Hechinger RF, Johnson PT, Lafferty KD, Mouritsen KN, Preston DL, Reise K, Zander D, Poulin R (2013) Parasites as prey in aquatic food webs: implications for predator infection and parasite transmission. Oikos 122:1473–1482. https://doi.org/10.1111/j.1600-0706.2013.00243.x

Travassos L (1921) Trematodeos Novos IV. Brazil-Med 2:337

Travassos L (1928) Fauna helminthologica de Mato Grosso. Mem I Oswaldo Cruz 21:309–372

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL: https://www.R-project.org/.

Wong PL, Anderson RC (1991) Distribution of gizzard nematodes (Habronematoidea, Acuarioidea) of New World shorebirds (Charadriiformes), with special reference to localities of transmission. Can J Zool 69:2579–2588. https://doi.org/10.1139/z91-364

Yamaguti S (1963) Systema helminthum, vol 5. Acanthocephala, Intersci, New York