

Effects of salinity on rates of infestation of waterbirds by haematozoa

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A recent hypothesis suggested that migration patterns in waders and other birds could be shaped by the distribution of parasites and diseases. This hypothesis assumes a reduced exposure to parasites in species living in saline habitats. To test this assumption, the number of species of haematozoa and rates of infection reported for bird species living in fresh and salt-water habitats were compared. Species living in more saline habitats had fewer haematozoic parasite species than freshwater birds. Relative frequency of infection was also lower in saltwater species. Neither phylogeny nor the number of individuals examined for blood parasites in each species explained these differences. Thus, there is indeed evidence that birds living in saline habitats have a reduced risk of being parasitized by haematozoa, probably due to a reduced abundance of the invertebrate vectors.

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Different theories have proposed that parasites could shape the life-style of their hosts. The Hamilton and Zuk (1982) hypothesis on the relationship between plumage brightness and parasite resistance has been followed by several other hypotheses linking parasites and immunocompetence to general problems in evolutionary biology (e.g. Ridley 1993, Sheldon and Verhulst 1996). Recently, Piersma (1997) suggested that parasite and disease distribution could determine habitat use and avian migration strategies. He suggested that species breeding in the Arctic and wintering in marine habitats are less exposed to parasites and could afford to allocate more resources to thermoregulation or sustained exercise (e.g. migration) and less to immune defence mechanisms. Piersma's hypothesis was supported by a comparison of habitat characteristics in breeding and wintering areas of waders, and an apparent low immunocompetence in marine wintering species. Although treating parasites and disease in general, the actual data reviewed by Piersma (1997) largely dealt with blood parasites.

Although some large-scale analyses of geographical patterns on blood parasite distribution and abundance have been published (Greiner et al. 1975) and a number of studies suggest a reduced presence of blood parasites in birds of the Arctic (Greiner et al. 1975, Bennett et al. 1992a, Earlé and Underhill 1993), the presumed low presence of blood parasites in saline areas has not been evaluated in detail. A rigorous test of this hypothesis requires the comparison of a large number of taxa, taking into account the effect of host phylogeny. To test the hypothesis of a reduced presence of blood parasites in saline habitats, I analysed the diversity of haematozoa parasitizing saltwater and freshwater birds, controlling for the effects of the host's phylogeny.

Methods

Distribution maps and habitat descriptions in del Hoyo et al. (1992, 1996) were examined in order to identify pairs of phylogenetically related species with differences in their habitat preferences (freshwater or saltwater).

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Pairs of species were defined according to Morony et al. (1975) taxonomy, incorporating the changes made by del Hoyo et al. (1992, 1996). In the pairs chosen, differences in salinity were observed during the breeding or the non-breeding season, usually the latter. Each species pair was formed by one species living more in saltwater habitats than the species it was paired with. The first species was then considered a saltwater species, and the other a freshwater species, although the latter may have used saline habitats to a greater degree than saline species in other pairs. In the selection of the pairs I attempted to match species with similar breeding distributions and migratory behaviours. After a preliminary construction of the pairs, Bennett et al. (1982) and Bishop and Bennett (1992) host-parasite catalogues were consulted to determine the number of parasites reported for each species. If no information was available in the literature, I chose another species (usually in the same genus) with similar habitat preferences and with information about the occurrence of blood parasites. Data on parasite occurrence was recorded in this way for a total of 35 pairs, including species from 5 different orders (Table 1). Twenty-two pairs were formed by species in the same genus, 11 by species in the same family and 2 in the same order. By comparing pairwise data of phylogenetically related pairs of species differing only in the character of interest (in this case use of saline habitats), the statistical problem arising from non-independent data is avoided (Harvey and Pagel 1991). Additionally, pairwise comparison of sister taxa has the advantage of reducing the effects of other unknown confounding factors, because closely related species usually have a similar ecology and behaviour (Møller and Birkhead 1992). When more than one species pair was included from a single genus (the case of *Larus* gulls), each pair corresponded to an independent evolutionary change in habitat use, as judged from a detailed phylogeny of the group (Chu 1998). The number of different parasites reported in each host species was used as an index of the diversity of pathogens to be managed by the immune system. Given that in some cases only the genus but not the species of the parasite was reported, parasite diversity in each species was computed in two ways. First, I counted the total number of species, including only non-specific identifications when no other species of the same genus were reported for this host. Secondly, diversity of parasites was also estimated from the number of genera reported in each host species.

The relative number of parasitized birds (parasite prevalence), and the number of individuals examined from each species were obtained from Greiner et al. (1975), Peirce (1981), Bennett et al. (1992b), Ruiz et al. (1995) and Bosch et al. (1997). To compare the relative frequency of infection, only species with at least five individuals examined in these papers were considered. After these restrictions, data from eight pairs were considered for analysis (Table 2).

Means and standard deviations are reported. Statistical differences in parasite diversity were computed by Wilcoxon-matched pairs tests, because parasite diversity and prevalence were not normally distributed. Unless otherwise specified, one tailed probabilities were used since directional predictions were established prior to analysis.

Results

A higher number of parasite species was found in fresh than in saltwater waterbird species (2.6 ± 2.7 vs 1.2 ± 1.9 , $Z = 2.46$, $p = 0.007$). The same pattern appeared when comparing the number of parasite genera detected in freshwater and saline species (2.2 ± 1.9 vs 1.1 ± 1.5 , $Z = 2.29$, $p = 0.011$). To determine if this pattern was explained because of the higher tendency of researchers to study blood parasites in freshwater species, I compared the number of individuals examined for each species in the reviewed sources, without detecting any significant difference in the number sampled for parasites in both groups (freshwater 121.1 ± 294.9 , saltwater 110.1 ± 386.4 , $Z = -0.05$, two tailed $p = 0.96$, $n = 8$ pairs of species). Not only the number of species, but also the prevalences were higher in freshwater than in saltwater species (20.5 ± 26.9 vs 1.6 ± 3.0 , $Z = 1.99$, $p = 0.023$).

Discussion

The analyses performed suggest a lower presence of parasites in birds living in saline habitats, as judged by the number of genera and species of haematozoa reported in each host species, as well as the prevalences of haematozoic infections. The number of parasite species reported in a host species is positively correlated with the number of individuals sampled (e.g. Schall and Staats 1997). It might be possible that more individuals have been systematically sampled in freshwater habitats. Unfortunately the host-parasite catalogues (Bennett et al. 1982, Bishop and Bennett 1992) did not report the number of birds sampled, and do not cite most studies with negative results. Additionally, a publication bias is likely to occur, favouring the publication of positive surveys for blood parasites, and sometimes the original papers did not reflect the number of individuals sampled, but just refer to the number of infected individuals (see e.g. Table 1 in Peirce 1981). Nevertheless, an adhoc test performed over the number of individuals sampled in a few studies of some of the species analysed, do not reported significant differences in the number of individuals sampled in fresh and saltwater habitats.

Table 1. Number of parasite species and genera reported by Bennett et al. (1982), and Bishop and Bennett (1992) in the pairs of bird species analysed. For each pair the first species makes less use of saline habitats than the second.

Taxonomic level	Species in freshwater	Parasite		Species in saltwater	Parasite	
		Species	Genera		Species	Genera
Order Podicipediformes						
Family Podicipedidae	<i>Tachybaptus ruficollis</i>	1	1	<i>Podiceps auritus</i>	0	0
Order Pelecaniformes						
Family Pelecanidae	<i>Anhinga rufa</i>	3	3	<i>Sula sula</i>	0	0
Family Phalacrocoracidae	<i>Pelecanus rufescens</i>	1	1	<i>Pelecanus occidentalis</i>	0	0
	<i>Phalacrocorax africanus</i>	1	1	<i>Phalacrocorax pelagicus</i>	0	0
Order Ciconiiformes						
Family Ardeidae						
Subfamily Ardeinae						
Subfamily Nycticoracini	<i>Egretta alba</i>	5	5	<i>Egretta rufescens</i>	0	0
Subfamily Nycticoracini	<i>Nycticorax nycticorax</i>	12	6	<i>Nycticorax violaceus</i>	5	5
Family Ciconiidae	<i>Leptotilos crumeniferus</i>	4	3	<i>Leptotilos javanicus</i>	0	0
Family Threskiornithidae						
Subfamily Threskiornithinae	<i>Plegadis falcinellus</i>	0	0	<i>Eudocimus ruber</i>	3	3
Subfamily Plataleinae	<i>Platalea alba</i>	1	1	<i>Platalea ajaja</i>	2	2
Order Anseriformes						
Family Anatidae						
Subfamily Anserinae	<i>Anser fabalis</i>	2	2	<i>Anser brachyrhynchus</i>	0	0
	<i>Branta canadensis</i>	8	5	<i>Branta bernicla</i>	0	0
Subfamily Anatinae						
Tribe Tadornii	<i>Cairina moschata</i>	6	6	<i>Tachyeres brachypterus</i>	0	0
Tribe Anatini	<i>Tadorna ferruginea</i>	0	0	<i>Tadorna tadorna</i>	2	2
Tribe Aythyini	<i>Anas cyanoptera</i>	1	1	<i>Anas discors</i>	9	6
Tribe Aythyini	<i>Aythya affinis</i>	5	5	<i>Aythya marila</i>	3	3
Tribe Mergini	<i>Bucephala albeola</i>	2	2	<i>Melanitta perspicillata</i>	2	2
	<i>Mergus albellus</i>	1	1	<i>Mergus serrator</i>	5	3
Order Charadriiformes						
Suborder Charadrii						
Family Recurvirostridae	<i>Rostratula benghalensis</i>	2	2	<i>Dromas ardeola</i>	0	0
Family Burhinidae	<i>Himantopus himantopus</i>	1	1	<i>Recurvirostra avosetta</i>	0	0
Family Charadriidae	<i>Burhinus capensis</i>	1	1	<i>Esacus magnirostris</i>	0	0
Subfamily Charadriidae						
Family Scolopacidae	<i>Pluvialis apricaria</i>	0	0	<i>Pluvialis squatarola</i>	1	1
	<i>Charadrius dubius</i>	2	1	<i>Charadrius alexandrinus</i>	2	2
Subfamily Gallinaginae	<i>Scolopax rusticola</i>	8	6	<i>Phalaropus fulicarius</i>	0	0
	<i>Actitis hypoleucos</i>	6	5	<i>Arenaria interpres</i>	0	0
Subfamily Tringinae	<i>Limnodromus scolopaceus</i>	0	0	<i>Limnodromus griseus</i>	2	2
Tribe Numeniini						
Tribe Numeniini	<i>Limosa limosa</i>	2	2	<i>Limosa fedoa</i>	1	1
	<i>Bartramia longicauda</i>	1	1	<i>Numenius americanus</i>	1	1
Tribe Tringini	<i>Tringa glareola</i>	3	2	<i>Xenus cinereus</i>	1	1
Subfamily Calidrinae						
Subfamily Calidrinae	<i>Calidris minuta</i>	3	3	<i>Calidris canutus</i>	1	1
	<i>Micropalama himantopus</i>	0	0	<i>Limicola falcinellus</i>	1	1
Suborder Lari						
Family Laridae	<i>Larus canus</i>	3	3	<i>Larus audouinii</i>	1	1
	<i>Larus cachinnans</i>	1	1	<i>Larus hyperboreus</i>	0	0
	<i>Larus ridibundus</i>	2	1	<i>Larus genei</i>	1	1
Family Sternidae	<i>Sterna hirundo</i>	4	4	<i>Sterna dougallii</i>	0	0
	<i>Chlidonias leucoptera</i>	0	0	<i>Chlidonias niger</i>	0	0

Table 2. Number of individuals examined and number of individuals infected for eight different pairs of species. Source: Greiner et al. (1975), Peirce (1981), Bennett et al. (1992b), Ruiz et al. (1995) and Bosch et al. (1997).

Species	Freshwater		Species	Saltwater	
	Examined	Infected		Examined	Infected
<i>Anhinga rufa</i>	9	3	<i>Sula sula</i>	28	0
<i>Anas cyanoptera</i>	71	1	<i>Anas discors</i>	1607	118
<i>Burhinus capensis</i>	7	1	<i>Pluvialis squatarola</i>	18	1
<i>Actitis hypoleucos</i>	28	5	<i>Arenaria interpres</i>	44	0
<i>Tringa glareola</i>	6	1	<i>Numenius americanus</i>	10	0
<i>Calidris minuta</i>	5	0	<i>Calidris canutus</i>	9	0
<i>Larus cachinnans</i>	187	151	<i>Larus hyperboreus</i>	6	0
<i>Sterna hirundo</i>	587	0	<i>Sterna dougallii</i>	30	0

Bennett (1993) reported an absence of Haemoproteidae parasites in some primitive avian orders, some of which live in marine habitats. They suggested that parasites could have failed to successfully colonise some primitive bird groups over an evolutionary time scale. The present study is not intended to test this hypothesis, but it should be noted that this factor could not have affected the results presented here, because the parasitism in each saline species has been compared to another species from the same taxonomic group.

Two different factors could then explain the reported patterns. Haematozoa are transmitted by blood-sucking insects (Atkinson and van Riper III 1991). The lower diversity and presence of parasites in species using more saline habitats could be related to a reduced presence of vectors in these areas. Saline habitats are not very suitable for insects, given the permanent exposure at saline shorelines or open sea (Little and Earlé 1994, Piersma 1997), thus saline habitats could represent areas of low risk of infection by haematozoa due to scarcity of suitable vectors.

Alternatively, species living in saline habitats could have developed more effective immune systems. This does not seem a very suitable explanation for the reduced diversity and prevalence of parasites, since in most cases saltwater species maintained in captivity are highly vulnerable to disease and parasite infection (e.g. Bennett et al. 1993, Piersma 1997).

In conclusion, the results of the present study support one of the main assumptions of Piersma's hypothesis: birds living in saltwater habitats harbour a reduced diversity of parasites than their congeners in freshwater habitats. As Piersma (1997) suggested, a close look at the actual immune systems, and any interspecific differences in susceptibility to infection are necessary to further test his hypothesis.

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