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Do global patterns of habitat use and migration strategies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure?

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On the basis of associations between the characteristics of breeding and wintering habitats, apparent immunocompetence, and chick energetics of shorebirds (Charadrii), trade-offs between investments in immunofunctioning on the one hand and growth and sustained exercise on the other are suggested, that determine the year-round use of particular types of habitat by long-distance migrating shorebirds. Some species appear restricted to parasite-poor habitats (high arctic tundra, exposed seashores) where small investments in immunomachinery may suffice and even allow for high growth rates. However, such habitats are few and far between, necessitate long and demanding migratory flights in the course of an annual cycle and are often energetically costly to live in. Species evolutionarily opting for parasite-poor habitats may be rather susceptible to parasites and pathogens as a result of investments in sustained exercise (including thermoregulation) rather than immunocompetence. Components of this general hypothesis are perfectly testable, and such tests may shed new light on several other biogeographical, energetic and evolutionary riddles.

hulst 1996), I will argue that the existence of diseases and parasites (i.e. all viral, bacterial and metazoan endoparasites and ectoparasites), and the costly immunological defences that they necessitate in potential hosts, may bear heavily on the functional interpretation of these scattered bits of natural history. Indeed, differences in the likelihood of parasitic infections between habitats, and differences in the investments in immunodefence between species, provide critical ingredients for a general hypothesis to explain several peculiarities of the distribution patterns of shorebirds and, indeed, other animals.

Biogeography of sandpipers (Calidrinae) and other shorebird species

During discussions about red knots (*Calidris canutus*), we have often wondered why a species that spends most of its time (10 months/yr) along north and south temperate and tropical shores takes the trouble to migrate all the way to the tundras of the high arctic to breed (Piersma and Davidson 1992, Piersma 1994, Harrington 1996). Why don't they forego many 1000 km of risky migration and just remain in the temperate zone, to breed in a Dutch meadow or in a Baltic marsh, as other shorebird species do? This seemed a 'good' question; i.e. nobody had a clue. Then there were other, seemingly unconnected and uninterpretable observations which related to interspecific differences in the incidence of infectious diseases in shorebirds held in captivity and to the metabolic capacity of growing shorebird chicks. As for so many other problems in evolutionary biology (e.g., Price 1980, Loye and Zuk 1991, Ridley 1993, Møller 1994, Lochmiller 1996, Sheldon and Ver-

The diversity of breeding shorebirds is highest in subarctic and arctic regions (Hale 1980, Hayman et al. 1986, Piersma et al. 1996a), but the most northerly and climatically most extreme parts of the Arctic are inhabited by a few species only. The Canadian Queen Elizabeth islands, North Greenland and the northern edge of Taymyr Peninsula, Severnaya Zemlya and Novosibirskiye Ostrova (New Siberian Islands) in Siberia contain sizeable populations of the following six shorebird species only: ringed plover *Charadrius hiaticula*, grey plover *Pluvialis squatarola*, ruddy turnstone *Arenaria interpres*, red knot *Calidris canutus*, sanderling *C. alba*, and purple sandpiper *C. maritima*. Strikingly, all these species are confined to marine shores outside the breeding period. Conversely, most of the tringine waders (Tringinae, family Scolopacidae) that breed in the northern boreal and subarctic climate zones winter in inland, freshwater, wetland habitats.

Table 1. Interspecific associations between the types of breeding and wintering habitats of sandpipers belonging to the subfamily Calidridinae based on the data presented in Appendix 1. The two species (*Calidris bairdii* and *C. melanotos*) mainly wintering in alpine freshwater environments in the Andes (and sometimes along seashores) were classified conservatively as wintering in "mixed" environments.

Breeding habitat	Wintering habitat		
	Marine	Mixed	Freshwater
High (/Low) arctic and Alpine	9	1	0
Low (/High) arctic	4	2	3
Boreal and Low arctic	0	1	4

The sandpiper subfamily Calidridinae (family Scolopacidae) contains 24 species of which the breeding and wintering (nonbreeding) habitats are summarised in Appendix 1 according to the most recent descriptions (Paulson and Erckmann 1993, Piersma et al. 1996a). As a first approximation, the breeding and wintering habitats of each species were assigned to one of three categories (Table 1), assuming that each species provided a statistically independent data point (note that the phylogeny of this close-knit subfamily has proved difficult to resolve; A. J. Baker pers. comm., see Baker 1992, Piersma et al. 1996a). Species breeding on alpine (mountain) tundra were ranked with those of high arctic tundra, as the two habitats have much in common in terms of exposure, seasonality, and climatic and biotic conditions during the breeding season (P. S. Tomkovich pers. comm.). It appears that high arctic and alpine breeding species winter predominantly in marine environments, and that boreal/low arctic breeding species winter mainly in freshwater habitats. A few species fall between these two extremes and they are most likely to occupy marine as well as freshwater habitats during the nonbreeding season. The sorting of the sandpiper species among the various types of breeding and wintering habitat is significantly different from random (chi-square test, $\chi^2 = 20.5$, $df = 4$, $p < 0.001$).

Table 2. Pairwise comparison between members of the same or closely related genera of plovers and sandpipers (Charadriidae and Scolopacidae). Each example consists of a species that breeds in the arctic, compared with a randomly chosen congener breeding more to the south. The species wintering in more marine habitats received an asterisk. The genera *Limosa*, *Tringa* and *Calidris* occur twice in the table with species-pairs from the Palaearctic-African and American flyways, respectively.

Northernmost breeder	More southerly breeder
Grey plover <i>Pluvialis squatarola</i> *	Eurasian golden plover <i>Pluvialis apricaria</i>
Common ringed plover <i>Charadrius hiaticula</i> *	Little ringed plover <i>Charadrius dubius</i>
Long-billed dowitcher <i>Limnodromus scolopaceus</i>	Short-billed dowitcher <i>Limnodromus griseus</i> *
Bar-tailed godwit <i>Limosa lapponica</i> *	Black-tailed godwit <i>Limosa limosa</i>
Hudsonian godwit <i>Limosa haemastica</i> *	Marbled godwit <i>Limosa fedoa</i>
Whimbrel <i>Numenius phaeopus</i> *	Eurasian curlew <i>Numenius arquata</i>
Common greenshank <i>Tringa nebularia</i> *	Marsh sandpiper <i>Tringa stagnatilis</i>
Lesser yellowlegs <i>Tringa flavipes</i> *	Greater yellowlegs <i>Tringa melanoleuca</i>
Little stint <i>Calidris minuta</i> *	Temminck's stint <i>Calidris temminckii</i>
White-rumped sandpiper <i>Calidris fuscicollis</i> *	Least sandpiper <i>Calidris minutilla</i>
Red/red-necked phalarope <i>Phalaropus fulicaria/lobatus</i> *	Wilson's phalarope <i>Steganopus tricolor</i>

A comparative method that may leave less to criticise than a comparison of subfamily members under the simplistic assumption of species' statistical independence (Felsenstein 1985, Brooks and McLennan 1991, Harvey and Pagel 1991) would be a comparison of the traits of closely related (e.g. congeneric) species-pairs (Møller and Birkhead 1992). I selected genera of plovers and sandpiper of the Charadriiform families Charadriidae and Scolopacidae (Piersma and Wiersma 1996, Piersma et al. 1996a), in which at least one species was restricted to (high) arctic breeding habitats (Table 2). Species-pairs from completely separate flyways (as in *Limosa*, *Tringa* and *Calidris*) were assumed to represent independent cases (a suggestion backed up for *Calidris* by the available phylogenetic reconstructions summarised by Székely and Reynolds 1995: Fig. 2). The tattler genus *Heteroscelus* and the turnstone genus *Arenaria* showed no variation in breeding and wintering habitat among species, and were therefore omitted from the analysis. For the entire sample of 11 species listed in Table 2, 10 species confirmed the suggested association between arctic breeding and coastal wintering habits, the dowitchers (*Limnodromus*) from the Americas providing a single exception. This ratio is statistically significantly different from 0.5 (two-tailed binomial test, $p = 0.001$; Siegel 1956: Table D). Note that the difference even remains significant if a genus is counted only once (7 of 8; binomial test, $p = 0.03$).

Geographical and habitat differences in the likelihood of parasitic infection

High arctic tundra and marine shores seem to have little in common, but both may be relatively 'healthy'. From personal experience I know that the likelihood of dangerous infections, even in the wet tropics, is low when one restricts movements to open water and intertidal areas. Similarly, it is hard to catch a cold in the high arctic, even when exposed to wet cold for long periods. But is there no better evidence that marine,

arctic and alpine environments have reduced loads of parasites?

Comprehensive distributional data on the prevalence of the great variety of parasites (including pathogens) in different climatic zones and habitats are hard to come by. This is not surprising given that the occurrence of parasites cannot be separated from the occurrence of suitable hosts and suitable vectors for parasite transmission, and that the study of each component of the system requires specialised sampling and recording techniques. Perhaps the best evidence that the likelihood of parasitic infection is reduced at high latitudes comes from studies of blood parasites (haematzoa) of birds (Laird 1961, Greiner et al. 1975, Bennett et al. 1992a, Borg 1992, Earlé and Underhill 1993). In a study of blood smears of 57 026 individual birds of 388 species representing 55 different families from all over North America, Greiner et al. (1975) found that only a few percent of the individuals from the high arctic carried haematzoa, whereas 30–60% of birds from the other, climatically more congenial, regions carried them. Bennett et al. (1992a) found that tundra-nesting individuals of rock ptarmigan *Lagopus mutus* and horned larks *Eremophila alpestris* lacked blood parasites, even though conspecifics from the boreal forest zone did carry them. A low prevalence of parasites (or parasite-transmitting vectors) in montane habitats is suggested by the example of endemic Hawaiian honeycreepers (Drepanidae). The honeycreepers have become extinct in lowland forests due to several avian diseases carried by newly introduced night mosquitoes and are now confined to high altitudes where these mosquitoes are absent (Warner 1968, van Riper et al. 1986).

In the study of Greiner et al. (1975), only 0.9% of the 1159 shorebirds (25 species of Scolopacidae) harboured blood parasites, the four carriers all being species breeding at rather low latitudes and/or being found in freshwater habitats (spotted sandpiper *Actitis macularia*, long-billed dowitcher *Limnodromus griseus*, American woodcock *Scolopax minor* and solitary sandpiper *Tringa solitaria*). Of the 13 species of scolopacid waders from Western Europe examined for blood parasites (Peirce 1981), the four species infected were exactly those more or less confined to freshwater habitats (green sandpiper *Tringa ochropus*, common sandpiper *Actitis hypoleucos*, Eurasian woodcock *Scolopax rusticola* and common snipe *Gallinago gallinago*). Something similar was reported for birds in sub-Saharan Africa (Bennett et al. 1992b). Of the 10 species of Scolopacidae screened for blood parasites, the only three showing infections were rather southerly-breeding migrants wintering mainly in freshwater habitats (*A. hypoleucos*, wood sandpiper *Tringa glareola* and *G. gallinago*).

That strictly marine habitats give a small exposure to parasites and/or their vectors is indicated by the finding that none of the 528 examined individual alcids (razor-

bill *Alca torda*, black guillemot *Cepphus grylle*, puffin *Fratercula arctica* and common guillemot *Uria aalge*) carried haematzoa (Greiner et al. 1975). The kentish plover *Charadrius alexandrinus*, a shorebird species restricted to saline shoreline habitats, contained no haematophagous parasites either (Figuerola et al. 1996). This relative poverty of (blood) parasites may be partially linked to a paucity of suitable vectors such as blood sucking insects. Insects, as a rule, do not occur in marine environments. As a consequence, parasites (e.g., bacteria, viruses) other than haematzoa but also dependent on flying vectors are scarce in marine environments. With regard to ectoparasites, most of them are insects too (Marshall 1981), and thus cannot endure unprotected exposure at saline shorelines or at sea. Being adapted to live near warm bird skins, ectoparasites may face additional difficulties when carried by their migrating hosts into severely cold arctic environments. For example, fleas (Siphonaptera) are mainly temperate in distribution, and their diversity and abundance decrease both latitudinally and altitudinally (Marshall 1981). Fleas are not found in the upper montane and high arctic climatic zones.

With an increase in latitude and altitude, the incidence of parthenogenesis (asexual reproduction) in insects increases, even within species (Suomalainen 1950). According to a quote in Ridley (1993) 'there are ticks and lice, bugs and flies, moths, beetles, grasshoppers, millipedes and more, in all of which males disappear as one moves towards the poles from the tropics'. Loss of sexual reproduction at high altitudes and latitudes has been interpreted as a consequence of the decreasing levels of parasite infections (Glesener and Tilman 1978), and may represent a release from the evolutionary arms race between pathogens and hosts (Ridley 1993).

Susceptibility to infection under captive conditions

At least six species of sandpipers (redshank *Tringa totanus*, red knot, sanderling, western sandpiper *C. mauri*, dunlin *C. alpina* and ruff) have been kept for research purposes under long-term captive conditions, all at research facilities at north temperate latitudes. I was able to gain personal experience with four of the six captivity situations. In our own studies with red knots (e.g., Piersma 1994), we have had difficulty with keeping the birds free from viral infections such as avian pox, which tended to occur together with secondary infections of bacteria and infestations of feather lice. Only very clean and regularly disinfected cages and a constant exposure to seawater (flowing over the bottom of the cage) solved the disease problems. This suggested not only that red knots are rather susceptible

to these common avian pathogens, but also that reconstructing a 'marine environment' helped to reduce, at least the external signs of, infections. A contrast is provided by the ruff, an antipode to red knots with respect to its habitat choice during breeding and wintering (Appendix 1). Ruffs held in The Netherlands and in Canada (Ontario and British Columbia) never gave much disease problems, not even when kept at rather high densities in cages with only self-polluted freshwater around their feet. The remaining two species, western sandpiper and dunlin, seem to hold the middle ground, both with respect to habitat choice (Appendix 1) and disease problems in captivity.

Even though this comparison is not based on a carefully controlled experiment, the cage environments are roughly comparable over all four species with respect to space and climatic conditions. If the conclusion that some species are more likely to catch a disease than others is robust, there is a correlation between the degree to which species occur in relatively parasite-poor habitats (at high altitudes/latitudes and marine) and their susceptibility to avian diseases common to domestic birds.

So, why are high arctic breeders seashore-winterers?

I propose that the life histories of high arctic and alpine breeding shorebirds represent the outcomes of evolutionary 'paths of least resistance' generated by nutritional and energetic trade-offs between physical peak performances (during growth, during long-distance migration and for thermogenesis [shivering] during exposure in cold and open habitats) and investments in the immune system. The use of relatively parasite-poor but energetically costly breeding habitats (Piersma and Morrison 1994, Wiersma and Piersma 1994) would go hand in hand with low general immunocompetence, and a restriction to marine, seashore environments in the nonbreeding season. Species breeding under more congenial climatic conditions would be able to invest in better immune systems allowing them to winter at parasite-rich inland freshwater areas.

Costs of immunodefence and energetics of growth

Extensive studies on time budgets, thermoregulation and overall energetics of the chicks of shorebirds breeding at temperate latitudes have shown that during the first few days of their life shorebird chicks are thermolabile and, depending on size and ambient temperature, have to be heated up at regular intervals by brooding parents (Beintema and Visser 1989, Visser and Ricklefs

1993). Recently, we collected comparable data for the chicks of red knots on high arctic tundra at Taymyr Peninsula, Siberia (Schekkerman et al. 1996). Red knot chicks remained active and maintained growth at air temperatures where chicks of similarly sized or larger meadow-breeding shorebird species such as redshank and black-tailed godwit *Limosa limosa* require continuous brooding by one of the parents, thus preventing them from feeding and growing. The greater activity at lower temperatures led red knot chicks to have daily rates of energy expenditure (measured by the turnover of doubly-labelled water, $^2\text{H}_2^{18}\text{O}$) that were 1.5 times as high as measured in temperate-breeding shorebird chicks of the same mass. Yet, their growth rates were among the highest measured in shorebirds. Why are these red knot chicks able to continue feeding at such low ambient temperatures, expend so much more energy and grow at faster rates than their southerly meadow-breeding family members? Is food more abundant and is their instantaneous rate of energy intake higher? Probably not, since indices of arthropod abundance in the two study areas (prey size and numbers captured per day by standardised trap systems) are similar in tundra and meadow (H. Schekkerman and I. Tulp unpubl.).

Studies of a large variety of (growing) animals (Chandra and Newberne 1977, Glick et al. 1981, 1983, Gershwin et al. 1985, Klasing 1988, Lochmiller et al. 1993, Milonoff et al. 1993) have experimentally demonstrated interactions between food quality, indices of the developing immune system and growth rate. The development of an effective immunodefence machinery is always repressed in nutritionally starved groups. This development may therefore be rather costly. Could it be that red knot chicks are able to perform at such high energetic and nutritional levels *because of* a paucity of pathogens and parasites on the tundra? Red knots do not have to invest heavily in the development of an immune system. Conversely, the rates of growth and energy expenditure of shorebird chicks in temperate meadows may be restricted in view of nutritional commitments to the development of immunodefence in a parasite-rich environment. These immuno-investments do not directly show up in their energy expenditure. But high levels of expenditure may only be possible without negative fitness effects (see Daan et al. 1996) in relatively germ-poor environments, as is suggested by recent studies by sport physiologists and exercise-immunologists.

Long-distance migratory flights and immunofunction

Heavy endurance exercise routinely performed by marathon runners may lead to injuries of the fibres in

the active skeletal muscles (Evans and Cannon 1991, Smith 1991). In such cases macrophages and other phagocytic cells invade the injured muscle cells and remove them, and therefore part of the immune system becomes occupied. It follows that during intense bouts of exercise the immune system is not able to fully respond to new infections, which would explain why heavily exercised humans and rats have reduced immunocompetence, and are more likely to catch a cold, than lightly or non-exercised subjects (Mahan and Young 1989, Fitzgerald 1991, Hoffman-Goetz and Pedersen 1994, Nieman 1994, Nieman and Nehlsen-Cannarella 1994, Shek et al. 1995).

The long-distance migrations carried out by shorebirds necessitate a whole array of physiological preparations related to the storage of fuel and the successful execution of the many 1000-km long uninterrupted flights, often at high altitudes (e.g., Butler and Woakes 1990, Ramenofsky 1990, Jenni-Eiermann and Jenni 1992, Piersma et al. 1996b). Such preparations may have much in common with the physiological changes resulting from heavy endurance training in humans. The intense sustained endurance exercise before and during the migratory flights (red knots and other sandpipers remain in continuous flight for several days) might lead to similar kinds of tissue damage (bar-tailed godwits *Limosa lapponica* lose 25–30% of their muscle and organ tissue during the 5300 km northward flight from Africa to Europe; Piersma and Jukema 1990), and make them susceptible to parasitic infections. The argument could then be turned around: the preparation for long-distance flights under time-stress and the recovery from such demanding flights can only be successfully carried out by birds that do not have to simultaneously operate a large immune system (Saino and Møller 1996). During the wintering period in exposed seashore habitats especially at northern latitudes, rates of energy expenditure (Wiersma and Piersma 1994) approach those during sustained peak performance in humans (Westerterp et al. 1986, Westerterp and Saris 1991) and may have similar immunological implications. Thus, as in bumble bees (*Bombus terrestris*; König and Schmid-Hempel 1995), there may be a trade-off between immunocompetence and endurance exercise levels in shorebirds.

Longevity of shorebirds

In spite of high basal metabolic rates (Kersten and Piersma 1987), and field metabolic rates as well (Piersma et al. 1991, Piersma and Morrison 1994, Wiersma and Piersma 1994), sea- and shorebirds tend to live long lives; they have long maximum lifespans (Goede 1993). Goede (1993) hypothesised that this high 'lifespan energy potential' was caused by the high levels

of selenium found in these avian groups. Selenium-containing enzymes are capable of neutralising free radicals, and this antioxidation effect may ensure a smaller accumulation of DNA-defects and thus postpone death (see Ricklefs and Finch 1995). I like to additionally argue that a life in relatively parasite-poor environments may also be a factor contributing to the high survival of shorebirds. In this context it is striking that marine Charadriiformes and Procellariiformes have a lifespan energy potential that is 43% higher than that of non-marine Charadriiformes (Goede 1993: Table 2), a difference that apparently is also correlated with selenium content.

It should be kept in mind that for stable populations a higher adult survival necessarily goes together with a lower recruitment. The latter may represent the survival cost of growing up in remote and climatically extreme habitats including the costs associated with making mistakes in habitat choice by inexperienced fledglings. The fact that 2 of 88 carefully examined red knots from normal seashore habitats were infected (and detrimentally affected) by a freshwater trematode (Underhill et al. 1994) illustrates the health hazard to high arctic breeding shorebirds of even briefly visiting inland habitats. Indeed, this is rarely done by adults, but more often by juvenile red knots on their first lonely voyage south (pers. obs.).

Testable assumptions and predictions

The hypothesis that there exist critical trade-offs between investments in immunofunctioning on the one hand and sustained exercise and growth on the other, trade-offs that determine the year-round use by long-distance migrating shorebirds of particular types of habitat differing in their prevalence of parasitic infection, is based on a number of assumptions that need testing. The hypothesis also generates a number of predictions and these can be tested too. The main assumption is that high arctic and alpine and marine habitats give a much lower parasite burden than boreal, temperate and tropical freshwater habitats. Although some empirical evidence was put forward to support these claims, much work remains to be done to really quantify environmental gradients in the likelihood of different types of parasitic infections. The wealth of data that no doubt exists on the distribution of unicellular parasites and viral pathogens of birds and mammals could be analysed in ways explored for haematzoa (notably by Greiner et al. 1975).

The hypothesis generates a large number of predictions. Species-differences in susceptibility to infection need testing under standardised conditions. The possibility that chicks of temperate meadow-breeding shorebirds have rather restricted metabolic scope and growth

potential at low air temperatures compared to chicks of high arctic sandpipers because they are investing heavily in their immunodefence machinery offers various avenues for experimental testing. One would predict that species confined to parasite-poor environments do not invest as much in bodily structures involved in the immune response, as species continuously exposed to large batteries of parasites (Glick 1986). Alternatively or additionally, species of parasite-poor habitats might show lower heterozygosity for genes in the major histocompatibility complex (MHC: coding for glycoproteins that serve as specific receptors binding antigens for cell-surface presentation to T-lymphocytes, and thus, destruction; e.g. Potts et al. 1997) than species of parasite-rich habitats. Chicks of high-arctic breeding shorebirds are bound to have smaller bursi of Fabricius (an organ that plays a role during the development of immunocompetence) than chicks of more southerly breeding species. Also, the immune response of temperate and arctic shorebird chicks can be compared directly, and chicks of both types of species can be exposed to various combinations of artificial environmental and climatic regimes, including exposure to either environmental sterility or disease vectors. As a matter of fact, in a comparative study Møller and Erritzøe (1997) demonstrated, by paired comparisons of closely related bird species belonging to several different orders, that the size of two immune defence organs (the bursa of Fabricius and the spleen) was consistently larger in the migratory species. A final prediction would be that, all things being equal except the likelihood of parasitic infection, species of seashore habitats would be able to store nutrients at faster rates than species of freshwater habitats because of the trade-off between investments in immunofunctioning and sustained exercise.

General discussion

Comprehensive reviews of habitat selection and spatial behaviour in shorebirds (Myers 1984) and of the ecological factors driving the evolution of seasonal migration of birds in general (Alerstam and Högstedt 1982), dealt with the interacting effects of conspecific competitors, food and predators. None of these reviews touched on parasitism and immunodefence. In the light of the foregoing discussion, parasitic infections are predicted to additionally play an important role in patterns of habitat selection and spatial behaviour, including long-distance migration.

The existence of parasites may not only play an influential role in the ecology and evolution of the migration patterns of shorebirds and other birds, but may represent an underrated factor in the rest of the behavioural ecology of birds as well. For example, many sandpiper species, and especially the arctic/

marine species, show seasonal plumage shifts in both sexes, changing from a dull grey plumage type to a much more contrasting plumage with rusty-red or black underparts during the breeding season (Hayman et al. 1986, Piersma et al. 1996a). This breeding plumage may be a sexually selected trait indicating either disease resistance (the standard explanation offered in the mushrooming literature on this subject; e.g., Hamilton and Zuk 1982, Borgia and Collis 1990, Boyce 1990, Hillgarth 1990, Zuk et al. 1990, Dufva and Allander 1995, Saino and Møller 1996), or rather, the owner's ability to avoid being infected due to careful habitat selection and migratory performance (an alternative based on the arguments put forward in the present paper; and see Pruett-Jones et al. 1990 for a rather similar suggestion). In bar-tailed godwits staging in the Wadden Sea during their northward migration to the arctic breeding grounds, the degree of breeding plumage is not only correlated with arrival time, body mass and extent of additional plumage-improvements (Piersma and Jukema 1993), but also with the degree of intestinal parasitic infections (T. Piersma et al. unpubl.).

The importance of parasites on the population dynamics of their hosts is widely recognised and well studied (e.g., Anderson and May 1986), but several recent ecology textbooks fail to mention the potential large-scale biogeographical consequences (Begon et al. 1990, Ricklefs 1990). Yet, the mammal literature offers some good examples of the large impact of parasites on the distribution of potential hosts. A major pandemic of viral rinderpest that swept through east Africa in the late 1800's left vast areas uninhabited by several ungulate species for decades (Price 1980, Dobson 1995). Tsetse flies and the sleeping sickness (trypanosomiasis, caused by the blood parasite *Trypanosoma evansi*) that they carry still make large areas of African savannah inhospitable for humans and their livestock (McNeill 1976). Cornell (1974) put forward an interesting model to explain distributional gaps between closely related bird species over apparently suitable habitat. He postulated that gaps are maintained by pairs of species-specific parasites to which the regular host is adapted but which is highly pathogenic to the other. Occupation of the gap by one adapted population is then prevented by the pathogen (transmitted by a vector) from the other, and vice versa.

One kind of physiological adaptation (a relative lack of immunological investments) may have allowed some shorebird species to occupy a global niche (the use of widely dispersed but relatively parasite-poor and reasonably food-rich habitats) that allows/necessitates high overall rates of energy expenditure (for growth and sustained exercise during maintenance and migration). This 'immunological specialisation' must have gone hand-in-hand with specialisations with respect to prey detection and foraging mode, to make the few suitable

habitat patches profitable from a purely energetic perspective (Piersma 1994). Occupation of the niche of arctic/marine habitats is an evolutionary success, and has probably been around since the very first ice ages at the start of the Pleistocene epoch, even though today the population sizes of these arctic/marine shorebird species are rather lower (Piersma 1986: Table 4) than those of possibly more immunocompetent species occupying freshwater habitats.

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Appendix 1

Species list of the sandpiper subfamily Calidridinae (family Scolopacidae) with a crude typing of the habitats occupied during the breeding and nonbreeding (wintering) periods (based mainly on Piersma et al. 1996a). If more than one type is regularly used, the two are separated by a slash; habitats of minor importance are given in parentheses.

Nr.	Common name	Latin name	Breeding habitat	Wintering habitat
1	Surfbird	<i>Aphriza virgata</i>	Alpine	Marine
2	Great knot	<i>Calidris tenuirostris</i>	Alpine	Marine
3	Red knot	<i>Calidris canutus</i>	High arctic/Alpine	Marine
4	Sanderling	<i>Calidris alba</i>	High arctic	Marine
5	Semipalmated sandpiper	<i>Calidris pusilla</i>	Low/High arctic	Marine (Freshwater)
6	Western sandpiper	<i>Calidris mauri</i>	Low arctic	Marine (Freshwater)
7	Red-necked stint	<i>Calidris ruficollis</i>	Alpine	Marine (Freshwater)
8	Little stint	<i>Calidris minuta</i>	Low/High arctic	Marine/Freshwater
9	Temminck's stint	<i>Calidris temminckii</i>	Low arctic/Boreal	Freshwater
10	Long-toed stint	<i>Calidris subminuta</i>	Boreal	Freshwater
11	Least sandpiper	<i>Calidris minutilla</i>	Boreal/Low arctic	Freshwater
12	White-rumped sandpiper	<i>Calidris fuscicollis</i>	High/Low arctic	Marine (Freshwater)
13	Baird's sandpiper	<i>Calidris bairdii</i>	High arctic/Alpine	Alpine-Freshwater (Marine)
14	Pectoral sandpiper	<i>Calidris melanotos</i>	Low arctic	Alpine-Freshwater
15	Sharp-tailed sandpiper	<i>Calidris acuminata</i>	Low arctic	Freshwater (Marine)
16	Curlew sandpiper	<i>Calidris ferruginea</i>	High/Low arctic	Marine (Freshwater)
17	Purple sandpiper	<i>Calidris maritima</i>	High arctic/Alpine	Marine
18	Rock sandpiper	<i>Calidris ptilocnemis</i>	Low arctic/Alpine	Marine
19	Dunlin	<i>Calidris alpina</i>	Average: Low arctic	Marine (Freshwater)
20	Spoon-billed sandpiper	<i>Eurynorhynchus pygmeus</i>	Low arctic	Marine
21	Broad-billed sandpiper	<i>Limicola falcinellus</i>	Low arctic/Boreal	Marine/Freshwater
22	Stilt sandpiper	<i>Micropalama himantopus</i>	Low arctic	Freshwater
23	Buff-breasted sandpiper	<i>Tryngites subruficollis</i>	Low arctic	Freshwater
24	Ruff	<i>Philomachus pugnax</i>	Boreal/Low arctic	Freshwater