REVIEWS

Why the most northerly breeding wader species do not winter in lowland freshwater habitats

*A long preoccupation with a most typical High Arctic-breeding wader (Knot) and the writing of wader texts for the Handbook of the Birds of the World perhaps may have primed the author, but reading Matt Ridley's 'The Red Queen: Sex and the evolution of human nature' (Viking, 1993) certainly inspired the rest of the following story..... In a Forum-contribution to the ecology journal **Oikos**, Theunis Piersma recently put forward a provocative hypothesis to explain why northerly breeding waders tend to winter in marine environments, and why boreal and temperate breeders winter in freshwater habitats. The hypothesis involves parasites, disease resistance, and physiological trade-offs between working hard and being immunocompetent. The paper is summarised here to invite comments and elaboration by fellow wader workers. Ed.*

Piersma, T. 1997. Do global patterns of habitat use and migration studies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? *Oikos* 80: 623-631.

The diversity of breeding shorebirds is highest in subarctic and arctic regions but the most northerly and climatically extreme parts of the Arctic are inhabited by few species. The Canadian Queen Elizabeth islands, North Greenland and the northern edge of Taimyr Peninsula, Severnaya Zemlya and the New Siberian Islands contain sizeable populations only of Ringed Plover, Grey Plover, Turnstone, Knot, Sanderling, and Purple Sandpiper. Strikingly, all these species are confined to marine shores outside the breeding period. Conversely, most of the tringine waders that breed in the northern boreal and subarctic climate zones, winter in inland, freshwater, wetland habitats.

Indeed, in the sandpiper subfamily Calidridinae, high arctic and alpine breeding species winter predominantly in marine environments; boreal/low arctic breeding species winter mainly in freshwater habitats (Table 1). A few species fell between these two extremes and they occupy marine as well as freshwater habitats during the nonbreeding season. The same pattern was found in congeneric pairs of plovers and sandpipers in which at least one species was restricted to (high) arctic breeding habitats. Ten of the 11 species-pairs showed the suggested association between arctic breeding and coastal wintering habitats (Table 2). Why would this be so?

Table 1. Interspecific associations between the types of breeding and wintering habitats of sandpipers (subfamily Calidridinae). 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. The sorting of the sandpiper species among the various types of breeding and wintering habitat was significantly different from random (Chi-square test, $X^2=20.5$, df=4, p<0.001).

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

Although high arctic tundra and marine shores seem to have little in common, both may be relatively 'healthy'. In fact, there is quite a lot of evidence that marine, arctic and alpine environments have reduced loads of parasites compared with boreal and temperate lowland freshwater habitats. Thus, in

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 examples from the Palearctic-African and American flyways, respectively. A ratio of 10 out of 11 is statistically significantly different from a random ration of 0.5 (two-tailed binomial test, p=0.001). Note that the difference even remained significant if a genus was counted only once (7 of 8; binomial test, p=0.03).

Northernmost breeder	More southerly breeder
Grey Plover *Pluvialis squatarola**	Golden Plover *Pluvialis apricaria*
Ringed Plover *Charadrius hiaticula**	Little Ringed Plover *Charadrius dubius*
Long-billed Dowitcher *Limnodromus scolopaceus*	Short-billed Dowitcher *Limnodromus griseus**
Bar-tailed Godwit *Limosa lapponica**	Black-tailed Godwit *Limosa limosa*
Hudsonian Godwit *Limosa haemastica**	Marbled Godwit *Limosa fedoa*
Whimbrel *Numenius phaeopus**	Curlew *Numenius arquata*
Greenshank *Tringa nebularia**	Marsh Sandpiper *Tringa stagnatilis*
Lesser Yellowlegs *Tringa flavipes**	Greater Yellowlegs *Tringa melanoleuca*
Little Stint *Calidris minuta**	Temminck's Stint *Calidris temminckii*
White-rumped Sandpiper *Calidris fuscicollis**	Least Sandpiper *Calidris minutilla*
Red/Red-necked Phalarope *Phalaropus fulicaria/lobatus**	Wilson's Phalarope *Steganopus tricolor*

the former habitat types, waders could in principle allocate their energetic and nutritional investments to sustained exercise and thermoregulation rather than to build-up and maintain disease resistance.

On the basis of these associations between the characteristics of breeding and wintering habitats and other comparative evidence (low apparent immunocompetence in marine wintering species, and very high levels of energy expenditure and fast growth in wader chicks in the High Arctic), a trade-off between investments in immuno-functioning (disease resistance) and sustained exercise (migration, thermoregulation) is suggested. For species restricted to parasite-poor habitats (high arctic tundra, exposed seashores) small investments in immunodefence mechanisms are sufficient. However, as such habitats are few and far between, this lifestyle necessitates long and demanding migratory flights in the course of an annual cycle. Also, the chosen habitats are often energetically costly to live in.

In summary, waders restricted to relatively parasite-poor habitats such as tundra and seashores would not invest in disease resistance. This would allow for high rates of energy expenditure without detrimental effects on survival. The lack of parasites would enable very high rates of energy expenditure before and during non-stop migration flights of 3,000-8,000 km, and for maintenance in cold and exposed habitats. Additionally, loss of immunodefence-related genetic diversity (*e.g.* MHC gene complex) might be of little consequence. For example, such species might quite easily survive extreme population crashes during climatic intervals with large habitat loss, something that may have happened repeatedly to Knots.

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Wetland Connectivity and Waterbird Conservation in the Western Great Basin of the United States

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INTRODUCTION

As scientists, managers and landowners, we have come to realize that to best understand the local and regional value of individual wetlands, we need to take a broad geographic, taxonomic, and management view. In December 1994, a symposium was held in Reno, Nevada that addressed this topic for shorebirds by bringing together researchers and managers from the Western Great Basin to discuss shorebird research and management in the region (Reed *et al.* 1997, *International Wader Studies 9*). In February 1998, a similar, but broader, symposium was held in Bend, Oregon that addressed wetland connectivity and waterbird conservation in the Western Great Basin. Over 100 participants spent one day listening to talks from waterbird researchers that focused on multi-scale habitat use and movements of birds in the region. From American Avocets *Recurvirostra americana* to White Pelicans *Pelcanus erythrorhynchos* we learned of phenomenal intra-season movements throughout the Basin and the value of collecting detailed data of this nature for representative waterbirds. We learned also about the National Shorebird Conservation Plan and spent the next day in discussion groups where future research and management priorities were outlined. These discussions were the first regional planning effort for the National Plan.

Western Great Basin wetlands stretch from Malheur National Wildlife Refuge in central Oregon to Mono Lake, California. This string of desert oases provides habitat to hundreds of thousands of waterbirds (shorebirds, wading birds, waterfowl, *etc.*) throughout the annual cycle. Over 48% (78/161) of North American waterbird species and 63% (29/46) of North American shorebird species commonly occur in the area. Furthermore, over 43% (9/21) of non-Arctic breeding shorebird species occur as breeders. Constant pressures for multiple use