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Migrating shorebirds as integrative sentinels of global environmental change

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Many shorebirds travel over large sections of the globe during the course of their annual cycle and use habitats in many different biomes and climate zones. Increasing knowledge of the factors driving variations in shorebird numbers, phenotype and behaviour may allow shorebirds to serve as 'integrative sentinels' of global environmental change. On the basis of numbers, timing of migration, plumage status and body mass, shorebirds could indicate whether ecological and climate systems are generally intact and stable at hemispheric scales, or whether parts of these systems might be changing. To develop this concept, we briefly review the worldwide shorebird migration systems before examining how local weather and global climatic features affect several performance measures of long-distance migrants. What do variations in numbers, phenotype and behaviour tell us about the dependence of shorebirds on weather and climate? How does data on migrating shorebirds integrate global environmental information? Documenting the dependencies between the population processes of shorebirds and global environmental features may be an important step towards assessing the likely effects of projected climate change. In the meantime we can develop the use of aspects of shorebird life histories on large spatial and temporal scales to assay global environmental change.

The world's environment is changing at great pace. At present, six billion humans consume 42% of the primary plant production, take 50% of the accessible water supply and dominate most of the fertile land (Vitousek *et al*. 1986, Pimm 2001). The pressure on the environment is increasing. In addition, humans may be responsible for a steep rise in the surface temperature of the Earth through the emission of CO_2 and other greenhouse gasses (IPCC 2001). Right now, we may be witnessing a speed of change in global climate that has only rarely been seen before. Of particular relevance to migratory shorebirds is the overwhelming presence of humans in all of the world's ecosystems. In addition to coping with the kind of changes in environmental conditions that have occurred in their evolutionary history, shorebirds have to cope with the erratic and unpredictable behaviour and actions of the ever-increasing human population.

Thus, human response to global change will determine its effects on the environment and for this reason we will not attempt to predict the future. Furthermore, we do not know enough about the ecological mechanisms that determine shorebird populations, and predictions of change in conditions putatively outside those witnessed within historical time are far too unreliable to be credible (Lindström & Agrell 1999, Tennekes 2001, and see Discussion). It is at present impossible to answer many of the questions of concerned scientists, policy-makers and conservationists. Questions about future population changes, especially those that require an understanding of how shorebirds use a series of (changing) sites during an annual cycle, are impossible to answer because they require a level of knowledge about long-distance migrating shorebirds far beyond what currently exists. Nevertheless, we can outline a programme of investigations that in due course may go some way towards addressing these scientific needs.

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Can shorebirds that embrace the entire globe within their flight paths provide us with information about environmental changes occurring over a large scale? How might variations in their number, phenotype and behaviour serve as biological 'integrators' of global environmental information in ways that no network of observers could realistically ever give us? Weather stations and analyses of land use can tell us about ongoing changes, but bird populations integrate this information in potentially insightful and surprising ways. What do we need to know about shorebird biology to be able to read the signs, and what additional efforts would be needed to keep a finger on the pulse of these integrative sentinels?

These are ambitious questions for a field that has seen little development. The world's shorebird populations and flyway structure (see below) are fairly well described (Davidson & Pienkowski 1987, Piersma *et al.* 1996, Piersma & Wiersma 1996, Davidson *et al.* 1998, Morrison *et al.* 2000, Wetlands International 2002, Stroud *et al.* 2004) and the population biology of a few species is known in detail. However, only a handful of long-term research programmes have provided the information that we need to link environmental parameters to shorebird 'performance' (phenotype and fitness related), leaving much to be understood. Our 'crown witnesses' are the high-arctic breeding and obligate marine wintering Red Knot *Calidris canutus* and the low-arctic/boreal breeding and inland wintering European Golden Plover *Pluvialis arenaria*. Before illustrating, season by season, the ways in which these and other shorebirds can be used to integrate various assessments of environmental conditions, we first summarize the structure of the world's shorebird flyways.

WORLDWIDE FLYWAYS

A 'flyway' is a geographical abstraction, comprising the composite of overlapping species- and population-specific migration routes (Hötker *et al.* 1998: p. 19, van de Kam *et al.* 2004). Most high-latitude migratory birds, including shorebirds, migrate southwards from their breeding grounds. The nine shorebird flyways that fan out in southerly directions from the tundra and taiga around the Arctic Ocean show considerable overlap, especially in the breeding areas (Fig. 1). For example, some species of shorebird that breed together in the Russian Arctic may spend the northern winter in places as far apart as western Africa and southeast Australia.

A clear characteristic of shorebird migration systems is that they link terrestrial, limnic (inland freshwater) and marine habitats together. During their life cycle high-arctic tundra breeding shorebirds are mostly associated with marine environments, both coastal and pelagic, whereas the low-arctic, boreal and temperate breeding birds are associated with limnic environments (Piersma 1997a, 2003). Thus, within their life cycles, shorebirds 'assemble and organize' information from geographically widely separated localities and combine environmental information from very different kinds of habitats (Piersma *et al.* 1996, Klaassen *et al.* 2001). In addition, shorebirds may spend a quarter of their life in transit between breeding and wintering grounds (Drent & Piersma 1990, Piersma & Davidson 1992), during which they have to cope with climatological features, especially wind. Although these factors could confuse rather than illuminate, we believe that performance measures such as numbers present, survival rate, juvenile percentages, timing of migration, body mass or body mass gains and extent of breeding plumage can provide useful information in relatively well-understood systems. Below are examples of interpretable correlations between performance measures of shorebirds and large-scale environmental variables.

THE WINTER

European Golden Plovers are common shorebird migrants in grassland areas of the northern Netherlands, where they show a clear preference for open landscapes, avoiding wooded and built-up areas (Jukema *et al.* 2001). The Golden Plovers that stage in The Netherlands in autumn, winter and spring breed in Scandinavian and northern Russian tundra. Most of those that arrive in The Netherlands in early autumn will winter in western France and the Iberian Peninsula in October and November, although some remain. In February, numbers in The Netherlands build up again, before the birsd depart northwards in April and May. The populations passing through in autumn and spring consist of the same individuals (Jukema *et al.* 2001). European Golden Plovers move to more southerly wintering areas chiefly as a result of frost and snow arriving from the northeast (Jukema *et al.* 2001). With lower December temperatures in The Netherlands, Jukema and Hulscher (1988) showed that between 1960 and 1985 Golden Plovers wintered further south (Fig. 2a), where they were more likely to find good frost-free feeding areas but where they were more likely to be shot by hunters. Winter
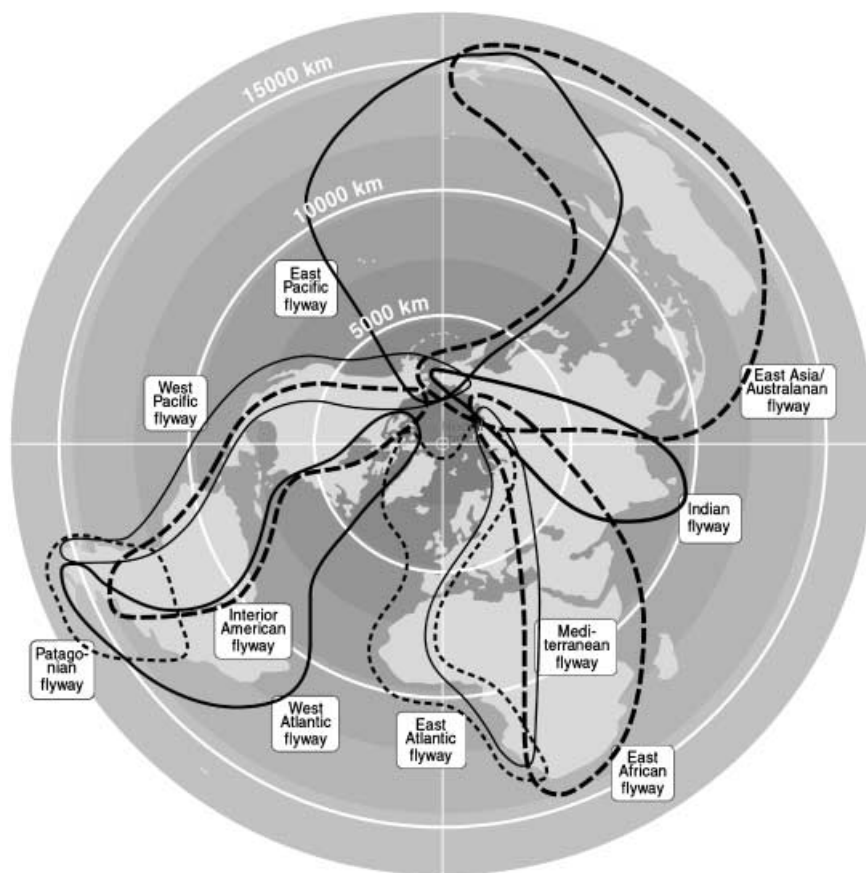
Figure 1. The worldwide pattern of nine shorebird flyways emanating from boreal to arctic latitudes to the south, and one that stretches from southernmost South America to the north (the Patagonian flyway). In this map, the world is projected from the North Pole (in the centre). From there, all directions are correct and map-distances to scale with real world great circle distances. From van de Kam *et al.* (2004).

severity and annual survival appeared to be negatively correlated (T. Piersma *et al.* unpubl. data). No severe winters have occurred since 1985/86; the relationship between winter weather and survival has become uncertain. This example illustrates how features of the winter climate may affect winter distributions and survival in a complex manner.

Similarly, numbers on the breeding grounds and survival rates can provide information regarding the conditions that the birds experience in their wintering areas. The number of breeding pairs of Purple Herons *Ardea purpurea* in The Netherlands, a long-distance migrant that spends the northern winter in the Sahel, correlates closely with the extent of winter drought in the Sahel region (Den Held 1981), apparently as a result of a correlation between annual survival and drought severity (Cavé 1983). Similar correlations have been described between winter wetness in the Sahel and the annual survival of

British and Dutch Sedge Warblers *Acrocephalus schoenobaenus* (Peach *et al.* 1991, Foppen *et al.* 1999) and the western population of White Storks C*iconia ciconia* (Kanyamibwa *et al.* 1993).

THE SUMMER

The yearly production of young shorebirds and geese breeding in the High Arctic is a striking example of a signal of biotic and abiotic environmental conditions being carried over enormous distances, away from the almost inaccessible Far North. Breeding success varies dramatically between years in a more or less cyclical manner (Roselaar 1979, Summers & Underhill 1987, Spaans *et al.* 1998, Bêty *et al.* 2001, 2002, Blomqvist *et al.* 2002), and the yearly variation in the production of arctic-breeding shorebirds and geese can be detected and evaluated by standardized monitoring programmes outside of the
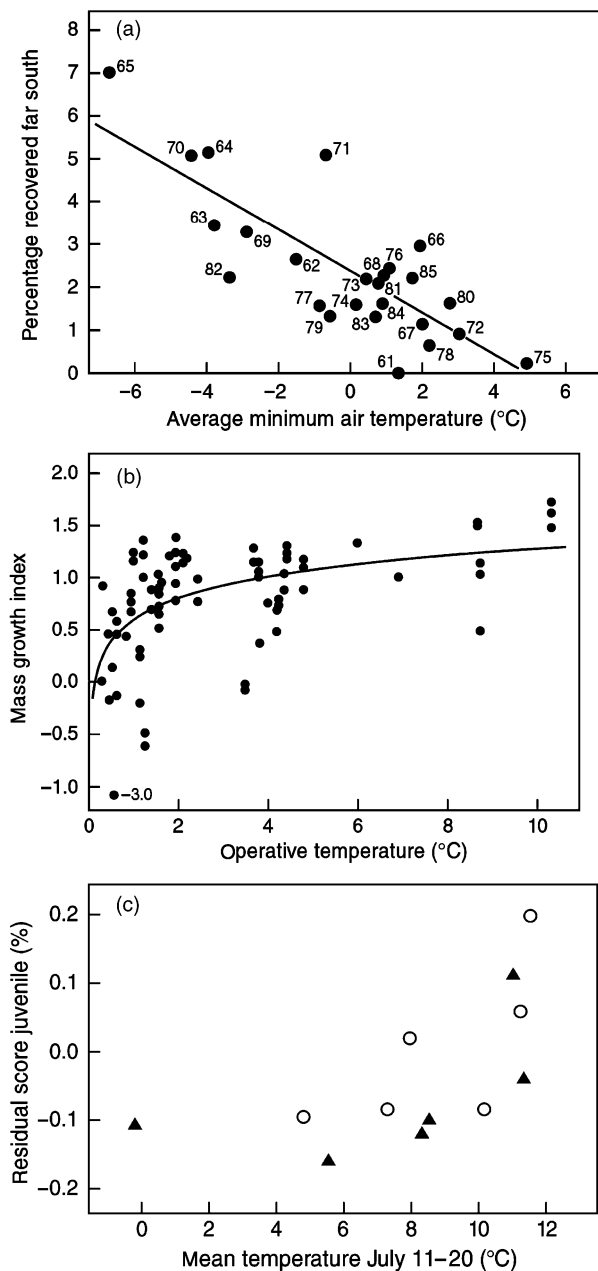
Figure 2. (a) The effect of average minimum air temperature in The Netherlands (measured at De Bilt) on the percentage of Golden Plovers recovered the same winter (November–March) in France, Spain, Portugal and Morocco (r^2 = 0.65). The numbers indicate the years in the 1900s from which the December temperatures are taken. Adapted from Jukema and Hulscher (1988). (b) Relationship between Red Knot chick growth index (growth observed divided by growth predicted at observed mass) and mean temperature on the Taimyr Peninsula, Russia (Schekkerman *et al.* 2003). (c) Relationship between mean summer air temperature (11–20 July) on the Taimyr Peninsula and the proportion of juveniles in the winter catches of Curlew Sandpipers in South Africa allowing for years of low (open circles) and medium (triangles) inferred predation pressure derived from assessments of Lemming abundance (Schekkerman *et al.* 1998).

Arctic (cf. Boyd & Madsen 1997, Lindström & Agrell 1999, Blomqvist *et al.* 2002), as far away as South Africa (Summers & Underhill 1987, Underhill *et al.* 1989, Schekkerman *et al.* 1998).

Two main factors seem to be responsible for the large and sometimes cyclical variation in High Arctic waterbird breeding success: Arctic lemming (*Dicrostonyx torquatus* and *Lemmus sibericus*) abundance and climate. Lemming abundance is often cyclical, although less so in North America than in Eurasia. Arctic Fox *Alopex lagopus* and the Snowy Owl *Nyctea scandiaca* largely feed on the easily depredated lemmings when their abundance is high. In lemming lows, the predators turn to alternative prey, such as the eggs, chicks and adults of shorebirds and geese. The variation in shorebird production follows interannual variations in lemming abundance closely. Successful reproduction occurs almost exclusively during peak Lemming years when snowmelt is early (Roselaar 1979, Summers & Underhill 1987, Blomqvist *et al.* 2002). Production of young is also affected by poor weather during the breeding season (e.g. Boyd 1992). Curlew Sandpiper *Calidris ferruginea* and Red Knot chicks (Fig. 2b) grow poorly during cold weather (Schekkerman *et al.* 1998, 2003) due to higher rates of energy expenditure, shorter foraging periods and reduced arthropod prey availability. Having accounted for variations in predation pressure, Curlew Sandpiper chick production measured on their South African wintering grounds was correlated with the mean air temperature on the Siberian breeding grounds between 10 and 20 July, the main hatching period (Fig. 2c).

THE MIGRATION PERIOD

The long flights between stopover areas that are few and far between not only necessitate intricate physiological mechanisms (e.g. Jenni & Jenni-Eiermann 1998), but also strategic flying with respect to water loss (Landys *et al.* 2000) and wind assistance en route (Alerstam 1978, Piersma & Jukema 1990, Piersma & van de Sant 1992, Liechti & Bruderer 1998, Green & Piersma 2003). The importance of wind assistance in enabling Red Knots breeding on the Taimyr Peninsula successfully to complete the first leg of their northward flight between the Banc d'Arguin, Mauritania, and the Wadden Sea in spring can be illustrated by their use of an 'emergency' stopover area (Smit & Piersma 1989) along the Atlantic coast of France, which is only used in years without the favourable tail-winds that allow the Wadden

Sea to be reached without this additional and time-consuming stop. All Red Knots stopping off in France had low body mass (Dick *et al.* 1987, D. Bredin unpubl. data) and in the German Wadden Sea body mass was also low in mid-May in the years that many birds stopped off in France (P. Prokosch unpubl. data). Thus, wind patterns along the northwest African coastline and over Iberia determine the use of particular staging sites and also the fuel storage schedules before the final flight to the Arctic breeding grounds. Breeding performance has been predicted (Ens *et al.* 1994, Weber *et al.* 1998) and shown (Drent *et al.* 2003) to decrease with delays and difficulties in fuelling.

During pair formation and mate selection, just after shorebirds have arrived on their breeding grounds, it is important for individuals to show their individual quality to ensure a high-quality partner. In many shorebirds both partners have input into mate selection (Piersma *et al.* 2001b) and it is likely that the extent to which individuals have been able fully to develop a nuptial plumage before and during the northward migration serves as an honest (quality) signal (Piersma & Jukema 1993, Piersma 1997b). The completeness of nuptial plumage during the spring stopover in the Wadden Sea among individual Bar-tailed Godwits *Limosa lapponica* correlates positively with body mass (Piersma & Jukema 1993) and local survival (Drent *et al.* 2003), and negatively with the amount of intestinal cestode parasites (Piersma *et al.* 2001b). What is true for individuals may also be true at a population level. Differences between years in the extent of the nuptial plumage of Red Knot along the East and West Atlantic flyways (T. Piersma & P.M. González, respectively, unpubl. data) suggest as yet unexplained environmental variations experienced by the birds. Unlike fat stores, nuptial plumages are not life-saving body structures. If nutrients are directed away from investment in such 'non-essential' tissues when energy is limited, nuptial plumages may be particularly sensitive indicators of the environmental conditions faced by individuals (Hill 1995). So far, scant attention has been paid to the potential uses of this informative badge.

These examples illustrate how the body mass and plumage values of shorebirds at stopover sites may provide us with information about the environmental conditions that they experienced earlier in their annual cycle. Whereas we may be able readily to interpret the signals of Red Knots staging in France, much work is still necessary before the variable plumages of Bar-tailed Godwits and other Red Knot populations can be fully interpreted.

DISCUSSION

Shorebird populations have been intensely studied over the last four or five decades, during which some of them have changed enormously in size. Morrison *et al.* (2001) reported that many North American shorebird populations, from different breeding areas, are in decline. The analysis of status and trends of African–Eurasian migratory shorebirds by Stroud *et al.* (2004) revealed three groups of populations of 'conservation concern' (i.e. with small and/or declining populations): (1) temperate European wet grassland breeding populations, pointing at a breeding ground change as the likely cause for the concern; (2) western Asian and Mediterranean dryland/ steppe breeding populations – here the dual pressure of increasing drought and desertification combined with increased human pressure causing land-use change are implicated; and (3) certain, but not all, populations wintering in West Africa, populations that come from different breeding areas, pointing at possible migration/staging area problems. Stroud *et al.* (2003) also note that the populations most highly dependent on the Wadden Sea as a staging area seem to be in decline. Despite some general attempts (e.g. Hughes 2000, Parmesan & Yohe 2003, Root *et al.* 2003), and a few focused on shorebirds (e.g. Zöckler 2002, Rehfisch & Crick 2003, G. Austin pers. comm.), in our judgement there are no cases where changes in demography, population size or distribution of shorebirds over the last 50 years could convincingly be attributed only to climate change. Instead, there are convincing data that implicate the key role of direct effects of human activities such as mechanical dredging (for shellfish and sand) and other fishery activities in shorebird population declines (Camphuysen *et al.* 1996, Piersma & Koolhaas 1997, Austin *et al.* 2000, Piersma *et al.* 2001a, Atkinson *et al.* 2003, Baker *et al.* 2004).

Of course, this does not imply that climate change does not matter to shorebird populations (it certainly has done over timescales of hundreds or thousands of years, as implied by the early Holocene population bottlenecks documented for Red Knots (Baker *et al.* 1994, Piersma & Baker 2000). It may merely demonstrate the lack of concerted effort to study complicated phenomena over long enough spans of time. Given the many complications, it does not come as a surprise that three sets of prediction suggest very different fates for High Arctic breeding Red Knots over the next 100 years or so. A modelling study on vegetation change in northern Europe by Cramer

(1997) offers little hope for Red Knots under a scenario that assumes that CO_2 levels become three times that of the 20th century average, a situation that may arise in 100–200 years, as the type of 'northern tundra' that these birds now breed on is reduced in size by almost 70%. In Eurasia, northern tundra would only remain on Novaya Zemlya and Spitsbergen, along with tiny patches in the mountains of Scandinavia (for additional discussion see Lindström & Agrell 1999, Jukema *et al.* 2001). By contrast, a map in Zöckler and Lysenko (2000) suggests that under a two-fold CO_2 scenario (80–100 years), very little of the tundra breeding grounds of Red Knots would disappear. Again in contrast, in that the timescale of predicted changes is very much shorter than in the Cramer (1997) study, an unpublished study by the US Navy suggests that within 30 years most of the summer ice of the Arctic Ocean would have melted away (MacKenzie 2002). As many Red Knots breed near this sea ice, which undoubtedly has a strong cooling effect on the nearby land, these changes would affect them strongly. During the first few years, warming of the tundra might be beneficial, as arthropod availability increases, leading to rapid growth rates and higher survival of chicks (Fig. 2b,c). This, however, is a transient state. Before long, habitat changes with respect to vegetation, food, predators and disease organisms would catch up and perhaps make Red Knot breeding success very low or zero (Lindström & Agrell 1999). Red Knots would then have to adapt to the new climatic regimes, move to the remaining suitable habitats to breed, or go extinct.

There will also be many changes on the habitats used by shorebirds for 10 months of the year outside of the breeding season. The global sea-level rise now under way is affecting the extent and quality of coastal intertidal habitats now (Galbraith *et al.* 2002) and in the future (Austin & Rehfisch 2003), and thus the fates of coastal wintering shorebirds. Some studies have tried to assess the likely impacts of loss of coastal habitat for the short-distance migrating Eurasian Oystercatcher *Haematopus ostralegus* (Goss-Custard *et al.* 1995a, 1995b; Durell *et al.* 1997), but no published assessments are yet available for northern breeding shorebirds that migrate over long distances. In addition to season- and habitat-specific effects, there may well be important cross-seasonal interactions. For example, in the Black-tailed Godwits *Limosa limosa islandica* that winter in England and breed in Iceland, the quality of spring fuelling areas appears correlated with the timing of arrival on the breeding grounds and with breeding success (Gill *et al.* 2001). In Red Knots there is evidence for density-dependent effects of overwintering numbers on breeding success (Boyd & Piersma 2001), and such density dependence could well come into effect through intraspecific competition for food or space on the spring or autumn staging grounds.

The foregoing discussion elaborates our starting point: that with the present knowledge of shorebird ecology and changing habitats (not only in the Arctic but also elsewhere), prediction is near impossible and almost pointless. Statements such as 'no tundra, no Red Knots or Curlew Sandpipers' can be made, but over what time period? Even with much greater knowledge, the large numbers of interacting and non-linear factors affecting the demography of shorebirds will make *precise* prediction impossible. But perhaps all we need are gross predictions.

Instead, we propose to use shorebirds as integrative sentinels of our changing world. Annual catches of 2000–3000 of the European Golden Plovers that make an autumn and a spring stopover in The Netherlands, for example, would enable us to monitor their breeding success (a likely function of body condition in spring, summer weather and predator densities), degree of stopover site philopatry (a function of the quality of the staging area in terms of food and predation risk), condition and moult in autumn (a function of food quality at the staging area that itself is partly weather dependent), timing of southward migration (possibly a function of the quality of the staging area and weather), wintering area (weather, food and predators further south), alternative staging sites in spring (weather and food), condition and moult in spring (weather, food and predation risk), and population size (a demographic function of 'everything' listed above; Jukema *et al.* 2001). With a relatively simple programme such as this, we can monitor a life cycle that integrates environmental factors from the whole of western and northern Europe. Even small changes in survival that occur over time periods of 3–5 years can be detected (K. Rogers & T. Piersma unpubl. data) and following such changes, detailed studies can be set up to identify the causes of the change in survival.

Such a programme would be even more informative if a series of migratory shorebirds were monitored in this way. For example, inclusion of Lapwing *Vanellus vanellus* and Ruff *Philomachus pugnax* in the comparison would enable us to distinguish between environmental changes on the breeding grounds (the three species breed in different habitats) and on

the wintering grounds (Lapwing and Golden Plover winter in Europe, Ruff in tropical Africa) or en route (they show considerable overlap in the staging areas). Inclusion of shorebird species frequenting intertidal staging areas such as Red Knots and Bar-tailed Godwits would further increase the scope for relevant comparisons and enable the rejection of more competing explanatory hypotheses. If Golden Plovers, Red Knots and Bar-tailed Godwits all showed population declines, but Ruffs and Lapwings did not, changes occurring in the northern dry tundra might provide a suitable explanation, especially if the percentage of juveniles was low. By contrast, if only Ruffs decreased we would seek changes in the environmental conditions in the Sahel region of Africa, especially if such a decline coincided with reduced survival rates, late arrival in spring and arriving birds that were lean with little development of nuptial plumage traits (cf. Jukema & Piersma 2000). Thus, in a comparative framework, the failures and fortunes of migrating shorebirds could be highly informative about the state of their world as well as ours (see also Baillie 1990).

In brief, we believe that precise predictions of the likely impact of climate change on the population viability of shorebirds will be difficult, if not impossible, to make. It will be difficult to disentangle the impacts of overall global change from those of climate change, although the former may be far more significant in the short to medium term. Nevertheless, considerable insight can be achieved with a two-tiered approach: (1) better knowledge of relevant land-use changes as a function of climate change and human activity, and (2) a better understanding of the interactions between shorebirds and the habitats that they use throughout the year. We propose that we could develop shorebird studies as an exciting tool to inform us in an integrated way about the current state of the world's ecology. This summary echoes an earlier plea by Boyd and Madsen (1997).

Possibly with the future of shorebirds at stake, increased knowledge will be helpful for conservationists. However, such knowledge can only be put to good use in a society that appreciates and values intriguing and fragile phenomena such as shorebird migrations, and that takes such 'uneconomical' considerations into account in land-use decisions. In this context, widely publicized and continuously developed public promotion of the factors affecting shorebirds worldwide could be of great and critical help in securing sensible long-term decisions at local, national and international levels.

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