

Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide

Theunis Piersma

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Abstract Shorebirds, or waders, form an ecologically (but not phylogenetically) homogenous group of birds that, despite this homogeneity, exhibits clear correlated contrasts in habitat use and migration distance between closely related species pairs. In addition, within species there is distinct variation in breeding and wintering latitudes, i.e. migration distance. I examine here such contrasts at different taxonomic levels and evaluate what we can learn about selective forces on habitat selection and the evolution of migration strategies in birds. My primary example is the worldwide migration system of the Red Knot *Calidris canutus*. These sandpipers breed only on high arctic tundra (65–83°N), but they move south from their disjunct, circumpolar breeding areas to nonbreeding sites on the coasts of all continents (except Antarctica), between latitudes 58°N and 53°S. Due to their specialized sensory capabilities, Red Knots generally eat hard-shelled prey found on intertidal, mostly soft, substrates. As a consequence, ecologically suitable coastal sites are few and far between, so they must routinely undertake flights of many thousands of kilometres. In contrast to prediction, Red Knots at tropical intertidal sites have lower fuelling rates than birds at more southern or northern latitudes. This leads to greater time–

stress in the southernmost wintering populations that not only have to cover over 14,000 km in single migrations, but also cannot rely on tropical regions to make refuelling stops. Rapid human-caused losses of the food-base in staging areas during both north- and southward migrations have been demonstrated to have caused rapid declines in several Red Knot populations. Detailed worldwide eco-demographic research on these extreme long-distance migrants, as embodied in, for example, the recently established Global Flyway Network, yields a two-pronged benefit: (1) on the basis of the unintended large-scale experiments carried out by humans, we rapidly come to grips with the selection pressures moulding the migration strategies of migrant birds, and (2) in applied contexts, the work gives instantaneous feedbacks on the conservation consequences of man-made alterations to wetland environments at the relevant global spatial scales.

Keywords Annual cycle · Conservation · Flyways · Foraging · Migration · Seasonal schedules · Waders

Introduction: comparisons are the backbone of biology

Biodiversity is the wellspring for comparisons, and insightful comparison is the basis for much of our understanding in biology (Wilson 1992). The development of biological research fields as divergent as genetics, functional morphology, nutrition, communication, behavioural and other kinds of ecology is based on comparison: comparisons between (aspects of) individuals, between groups and populations living in different places and different environments, between species and between higher taxa, between habitats (e.g. Schmidt-Nielsen 1964; Krebs and Davies 1987; Avise 1994; Wainwright and Reilly 1994;

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T. Piersma (✉)
Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands
e-mail: theunis@nioz.nl

T. Piersma
Department of Marine Ecology and Evolution,
Royal Netherlands Institute for Sea Research (NIOZ),
P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

Klasing 1998; Marler and Slabbekoorn 2004). Needless to say, “the comparative approach... was Darwin’s favoured technique” (Harvey and Pagel 1991).

Birds, so visible, audible and ubiquitous, so variable yet structurally uniform, so inspiring in numbers and behaviour and so inviting to study, have been exceptionally well studied compared with other vertebrate groups and have thus become a major focus for comparative work on life histories and mating systems (Bennett and Owens 2002). Among the birds of open landscapes, the shorebirds—or waders—form an ecologically quite homogeneous guild, but not a monophyletic clade, within the order Charadriiformes (Paton et al. 2003). The approximately 217 shorebird species belonging to 14 families (Jacanidae, Rostratulidae, Dromadidae, Haematopodidae, Ibidorhynchidae, Recurvirostridae, Burhinidae, Glareolidae, Pluvianellidae, Charadriidae, Scolopacidae, Pedionomidae, Thinocoridae and Chionidae) have received a great deal of scientific attention (see relevant chapters in del Hoyo et al. 1996), at least the common species living in parts of the world with an ornithological tradition (Piersma et al. 1997). Shorebirds exhibit great variability, both within and between families, in the degree of sexual size and plumage dimorphism and in mating system (van de Kam et al. 2004), and this has invited several comparative analyses of sexually selected traits in relation to ecology, migration and mating system (Pitelka et al. 1974; Figuerola 1999a; Jukema and Piersma 2000; Piersma and Baker 2000; Székely et al. 2004, 2006).

The plovers Charadriidae (with 66 species and 105 distinct populations or subspecies) and the sandpipers Scolopacidae (with 86 species and 134 subspecies units) are not only the two most diverse families among shorebirds, they also show the greatest diversity with respect to migration propensity and migration distance. There are plover and sandpiper species where individuals never move more than several 100 m away from their natal areas (see, for example, Miskelly 1999), but the plovers and the sandpipers also count among their ranks champion seasonal migrants that cover entire ocean basins in single flights (see, for example, Johnston and McFarlane 1967; Gill et al. 2005). Rather than providing a wide-ranging comparative analysis of ecological correlates of migration behaviour among shorebird species (in fact, I believe that at present this is not the best taxonomic level for insightful analyses), I will build on the considerable intraspecific variation in migration distances among extant populations of the Red Knot (*Calidris canutus*) to investigate how ecological factors may have moulded migration distance. Of course, these ecological, season-specific selection pressures will shape all aspects of the annual cycle, i.e. fuelling, flight and moult (Buehler and Piersma 2007). Several such selection

pressures have recently been brought to light as a consequence of rapid, man-made alterations of habitats, and these will be discussed. However, it is their use of very specific habitats year-round that we first have to consider: why do Red Knots and other migrant birds breeding in the High Arctic tend to winter in marine or saline habitats?

Covariation between breeding and wintering habitat: a life-history gradient generated by differential disease pressures?

Red Knots breed in the high arctic, about as far north as one can get. Outside the breeding season, one finds Red Knots only in marine coastal habitats, usually large wetlands with extensive intertidal foreshores (Piersma et al. 2005). Red Knots are also particular because they are a specialized molluscivore (see below) but shift to eat surface arthropods during the summer months on high arctic tundra. Thus, as they are able to live off intertidal bivalves as well as surface arthropods, there is no obvious reason based on their trophic specialization why Red Knots should restrict themselves to tundra during the breeding season (they should be able to find such arthropod prey in temperate meadows as well; see Schekkerman et al. 2003) and coastal intertidal habitats during the nonbreeding season (they should also be able to use freshwater wetlands with shellfish resources, such as the Niger floodplains in Mali; Zwarts et al. 1999, 2005).

Expanding the comparison, other high arctic breeding shorebirds, such as Grey Plover (*Pluvialis squatarola*), Sanderling (*Calidris alba*), Purple Sandpiper (*Calidris maritima*) and Bar-tailed Godwit (*Limosa lapponica*) also winter in marine coastal wetlands, a striking contrast with their more southerly breeding congeners (respectively, for example, Eurasian Golden Plover *Pluvialis apricaria*, Temmick’s Stint *Calidris temminckii*, Dunlin *Calidris alpina* and Black-tailed Godwit *Limosa limosa*) that tend to additionally, or uniquely, rely on freshwater wetlands during the nonbreeding season. Piersma (1997) put these interspecific associations to formal statistical tests and was able to confirm the empirical linkages between the degrees of northerly breeding and the use of marine or coastal nonbreeding habitats. However, this association does not stop at shorebirds. Comparisons among gulls, terns and allies (Lari), ducks, Anatidae and passerines (Table 1) all suggest that the far-northern breeders tend to use coastal or saline habitats, re-emphasizing that the biogeographic pattern is not coupled to some sort of trophic specialization. Then and now, the only relevant covariate that I could dream up is the possibility of a relative paucity of disease organisms or their vectors in both arctic and marine habitats (Piersma 1997, partially inspired by Ridley 1993).

Table 1 Evidence for linkages between latitude of breeding and degree of coastal/marine wintering habitat in various groups of birds

Group	Evidence for linkage
Sandpipers Calidridinae	Significant association between breeding latitude and relative use of marine wintering habitats
Shorebirds Charadrii	In 11 pairwise, within-genus comparisons, ten cases confirmed the association between arctic breeding and marine wintering
Gulls and allies Lari	Obligate open sea wintering skuas (Stercorariidae) all breed in boreal and arctic habitats, whereas the closely related tern family (Sternidae), especially species with a more southerly breeding distribution, also use nearshore and inland freshwater wetlands (e.g. to roost)
Sternidae	The two northernmost and the southernmost breeding tern species (respectively, Arctic <i>Sterna paradisaea</i> , Aleutian <i>Sterna aleutica</i> and Antarctic tern <i>Sterna vittata</i>) only winter in marine habitats
Laridae	The northernmost breeding gulls (Glaucous Gull <i>Larus hyperboreus</i> , Ivory Gull <i>Pagophila eburnea</i> , Ross's <i>Rhodostethia rosea</i> and Sabine's Gull <i>Xema sabini</i>) are all limited to marine environments in the nonbreeding season
Ducks and geese Anatidae	The two most northerly breeding species of duck (Long-tailed Duck <i>Clangula hyemalis</i>) and goose (Brent <i>Branta bernicla</i>) strictly winter in marine and coastal habitats
Songbirds Passeriformes	The two most northerly breeding passerines (Snow Bunting <i>Plectrophenax nivalis</i> and Lapland Longspur <i>Calcarius lapponicus</i>) tend to especially use coastal and saline wintering habitats

The shorebird examples are from Piersma (1997)

High arctic breeding species may represent one end of a continuum of decreasing investments in immunity, a strategy that would ecologically be enabled by low disease pressure and which in turn makes it possible for the birds to show high levels of energetic performance (high growth, storage and thermoregulatory rates).

There is an increasing body of evidence indicating that disease organisms—blood parasites in particular—and/or their vectors are indeed relatively sparse in both high arctic and marine/saline habitats compared to temperate and tropical freshwater habitats (e.g. Bennett et al. 1992; Figuerola 1999b; Jovani et al. 2001; Mendes et al. 2005). However, any of the contrasts in overall immune investments, or aspects of immunity, between high arctic/marine species and with lower latitude/freshwater species—contrasts that would logically follow from the differential exposure to disease pressures during either the egg- or chick-phase or later during life—have as yet proven to be difficult to investigate and to confirm (Mendes et al. 2006a, b).

A corollary of the disease-based covariation hypothesis of Piersma (1997) is that drastic historic population bottlenecks, ones extreme enough to lead to the loss of genetic variation in the genes coding for the immune system (i.e. genes coding for antigen recognition sites and for natural antibodies; see O'Brien and Evermann 1988), would have been tolerated by species under relaxed disease pressures—i.e. the high arctic breeders and marine wintering ones (Piersma 2003). During periods of rapid climate change (disappearance of tundra, loss of intertidal wintering habitats during fast sea level changes), these species would be

especially susceptible to habitat loss and population bottlenecks (Piersma 2003). Consistent with this, Red Knots indeed show quite low levels of neutral genetic variation, Dunlin (an intermediate species) has been reported to show intermediate levels of genetic variation and Ruff (*Philomachus pugnax*, quite southerly breeding and a marine averse calidrid sandpiper), supposedly show high levels of genetic variation (Segre et al. 1970; Baker et al. 1994; Avise 2000; Buehler and Baker 2005).

On this basis, I suggested that there might be historical feedbacks in the generation of contrasts between the low and high end of the immunity/habitat selection gradient (Piersma 2003). As shown in Fig. 1, if an increased susceptibility to disease has indeed restricted the range of suitable habitats [e.g. birds having to avoid areas with ample food but many (vectors for) debilitating diseases, such as mosquitoes carrying avian malaria], we have a system with a strong positive historical feedback link. This is rather more exciting than a system where historical ecological constraints have simply led to a loss of genetic variation for disease resistance; that is, lowered disease resistance being just a *consequence* (and not also a cause) of population bottlenecks due to temporary restrictions in habitat availability.

In this scenario then, habitat selection, population size, migration strategies and disease resistance are all linked in one historical web of causality. In fact, there are several additional biological contrasts that may be relevant: the more pronounced seasonal plumage dimorphism in the high-latitude breeding species (Jukema and Piersma 2000) and their greater apparent organ flexibility (Piersma 1998) as well as

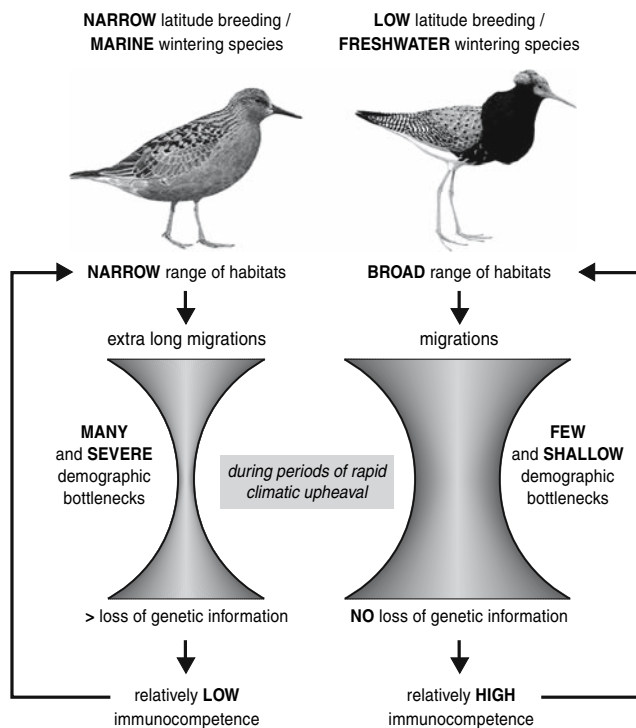


Fig. 1 Schematic overview of the contrasts between latitudinal migrant shorebird species that breed at high latitudes and spend the winter in marine (saline) habitats and those that breed at lower latitudes and spend the winter in freshwater (including grassland) habitats and the possible consequences and positive feedbacks induced by population bottlenecks. Based on Piersma (2003)

the finding that freshwater species first migrate northwards from the circa-tropical wintering areas at earlier ages than the coastal species (D.I. Rogers, personal communication). Also, freshwater species of shorebirds appear to have a lower ‘lifespan energy potential’ (spend less energy per maximum lifetime) than marine species (Goede 1993).

Intraspecific comparisons: introducing a long-distance migrating, molluscivore shorebird

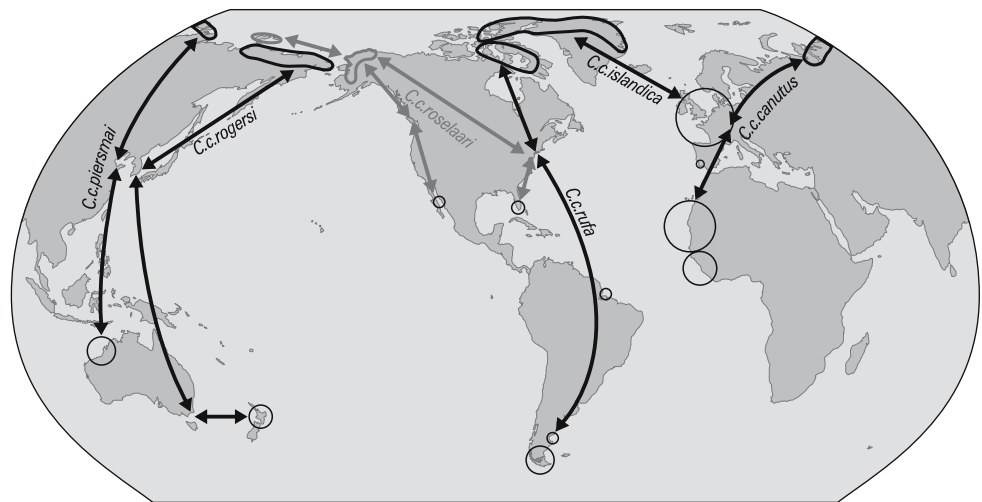
Returning to the point made at the start of the previous section—that Red Knots uniquely breed on high arctic tundra and only use extensive coastal wetlands during the nonbreeding season—I can now add spatial and temporal details. The discontinuous circumpolar breeding range of Red Knots incorporates breeding areas of at least six populations (Fig. 2), populations that are morphologically sufficiently distinct to count as subspecies (Roselaar 1983; Tomkovich 1992, 2001). The subspecies certainly are distinct when it comes to their migratory trajectories and the seasonal timing of their movements (Piersma and Davidson 1992; Piersma et al. 2005; Buehler and Piersma 2007). The populations show little (Tomkovich and Riegen 2000) or

no overlap at the final wintering¹ destinations, and only limited overlap during south and northward migration. The subspecies *islandica* and *canutus* co-occur in the Wadden Sea during the southward migration (Nebel et al. 2000) and less so during the northward migration (Prokosch 1988). The subspecies *piersmai* and *rogersi* coming from wintering areas in northwest Australia and southeastern Australia/New Zealand, respectively, both migrate through the Yellow Sea in spring (Battley et al. 2005; Piersma et al. 2005). Red Knots wintering from Georgia to northern Brazil are distinct from the *rufa* knots wintering in southernmost South America (Baker et al. 2005; Atkinson et al. 2005) and may represent an eastern group of *roselaari* birds, or an undescribed separate population that co-occurs with *rufa* knots during the northward migration in Delaware Bay (Atkinson et al. 2005, 2007). Another population of *roselaari* knots is now known to connect wintering areas in northwestern Mexico and staging areas in southwestern Alaska (R.E. Gill Jr, P.S. Tomkovich, H.P. Sitters and N.A. Clark, personal communication). In the case of *canutus*, a previously existing transequatorial wintering area in southern Africa seems to have been abandoned from the 1990s onward (R.W. Summers and L.G. Underhill, personal communication). Arguably the most fascinating aspect of the whole substructuring of the world’s Red Knots is the suggestion, based on genetics, that all of the world’s six or seven subspecies have diversified recently from a single founder population that survived the last glacial maximum of approximately 20,000 years ago (Baker et al. 1994; Piersma 1994; Buehler and Baker 2005; Buehler et al. 2006); if true, the subspecies of Red Knots have very shallow phylogenetic roots.

Although, as we have seen, the apparently strict non-breeding habitat requirement of Red Knots (extensive and open coastal intertidal areas) may relate to the avoidance of pathogens, it may also relate to the avoidance of predators (Piersma et al. 1993a, b; van den Hout et al. 2007), and it certainly relates to their trophic specialization. Studies on their diet have revealed that Red Knots eat hard-shelled molluscs (Prater 1972; Piersma 1991; Piersma et al. 1993b, 1994; González et al. 1996; van Gils et al. 2005c), sometimes supplemented with easily accessed softer prey, such as crustaceans (Alerstam et al. 1992; van Gils et al. 2005b) and even polychaetes (P.M. González, personal communication). This is not because Red Knots necessarily prefer hard-shelled molluscs (in fact, they do not when given the choice; van Gils et al. 2005a), but because they are specialized in finding and processing such prey, even at the detriment of being able to find actively crawling soft-

¹ Taking a knot-o-centric view (i.e. that of a bird born in the northern hemisphere in summer), I see only benefits in talking about *wintering* areas, even if wintering takes place during the southern summer.

Fig. 2 Global distribution of the six recognized subspecies of Red Knots during the breeding and nonbreeding season, with schematic south- and northward migration routes, and information on migration distances and approximate population sizes. The contours in the Arctic delimit the approximate breeding areas and circles indicate wintering areas. The size of the circle indicates the relative number of birds using the respective ‘wintering’ areas. This figure is modified after Buehler and Piersma (2007) and is an update of the original synthesis by Piersma and Davidson (1992)



	<i>C. c. piersmai</i>	<i>C. c. rogersi</i>	<i>C. c. roselaari</i>	<i>C. c. rufa</i>	<i>C. c. islandica</i>	<i>C. c. canutus</i>
Total migration distance (km)	10400	15000	7500	15000	4650	9000
Max. single flight distance (km)	6300	6500	5600	8000	2830	5100
Breeding latitude	75–78°N	67–70°N	65–75°N	64–76°N	76–85°N	75–80°N
Population size	30000	100000	35000	30000	400000	300000

bodied worms and small crustaceans that other sandpipers specialize on (Gerritsen and Meijboom 1986). In fact, Red Knots have a unique sensory capacity—which to date has not described for any other animal—that uses self-induced pressure gradients around hard objects in wet soft sediments (Piersma et al. 1998; Fig. 3). The “remote detection” of buried hard-shelled prey is probably enabled by their bill-tip organ, the dense conglomerations of pressure sensors (Herbst’ corpuscles) clustered in forward pointing “sensory pits” in the outside surfaces of the tips of both upper and lower mandible (Piersma et al. 1998).

Unlike molluscivore shorebirds that remove the flesh from the shell with their stout bill, such as oystercatchers Haematopodidae (Hockey 1996), but just as molluscivore diving ducks (Kehoe and Ankney 1985; Barnes and Thomas 1987; Goudie and Ryan 1991), Red Knots ingest their prey whole, crushing the shell in the muscular part of the stomach, the gizzard (the glandular stomach is rudimentary; Piersma et al. 1993c). Crushed shell material is not usually voided as pellets (as is the habit of a related shorebird, the Dunlin *Calidris alpina*; Worrall 1984), but as faeces (Dekinga and Piersma 1993). As a consequence of

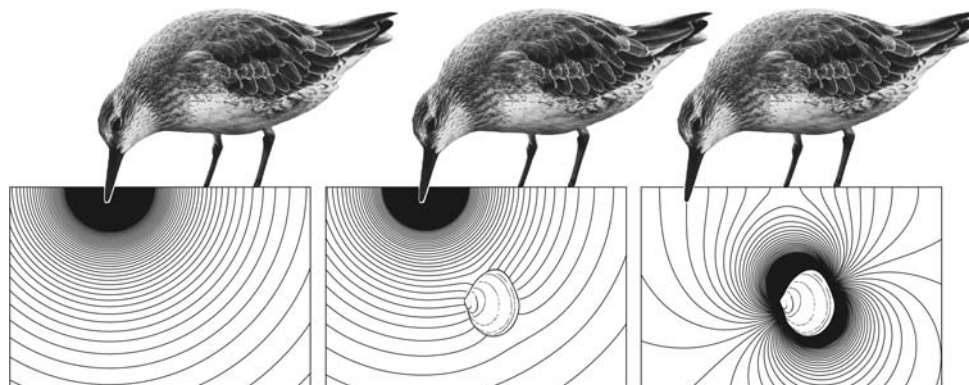


Fig. 3 Cross section through a tidal flat showing hypothetical pressure fields created when a Red Knot probes the upper surface of the wet sediment. In the *left-most* cross section there are no hard objects present to disrupt the pressure field. In the *middle* cross section, a buried bivalve prevents the interstitial water from rapidly moving away from the pressure exerted by the repeatedly probing bill.

This results in an increased water pressure around the bivalve that allows the knot to detect it from several centimetres away (cross section at *right*, showing contours of pressure differences between the ideal spherical pressure landscape on the *left* and the disturbed pressure landscape in the *middle*). Based on Piersma et al. (1998)

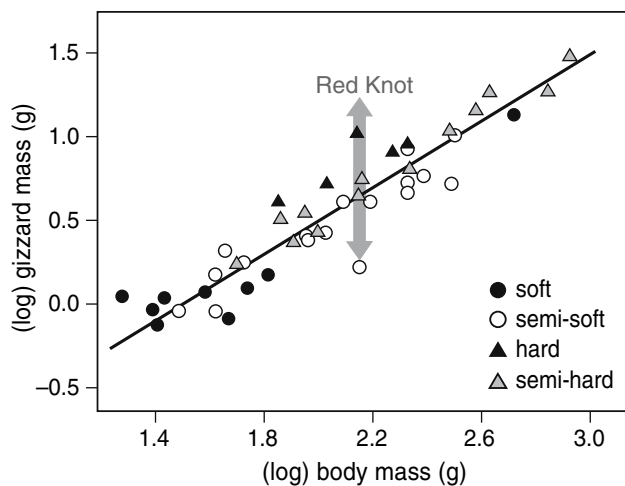


Fig. 4 Allometry of the fresh gizzard mass in 41 species of shorebird from four different families, assigned to four different diet 'hardness' categories. For the Red Knot, the vertical line additionally indicates the great variation in gizzard mass that can occur even within individuals. After Battley and Piersma (2005)

the work that the gizzard and intestine have to do on the shell material, and perhaps to prevent wear and tear inflicted by shell fragments on the sensitive intestinal wall, both gizzard and intestine are relatively heavy in hard-shelled-prey-eating shorebirds (Battley and Piersma 2005). In an allometric comparison among 41 shorebirds, the Red Knot came out as the species with the largest gizzard for its body mass (Fig. 4). Experimental work has shown that gizzard size determines the shell-processing capacity of a bird and thereby limits instantaneous food intake rates (van Gils et al. 2003).

A heavy digestive tract is a burden for well-travelled birds that would best be off with low flight costs, and it is therefore no surprise that at every stage of the annual cycle, Red Knots seem to keep the gizzard to the locally possible minimum (Piersma et al. 1999a, b; van Gils et al. 2003, 2005c, 2006a) When fed soft trout-food pellets in captivity, wild-captured Red Knots, which had eaten bivalves up to that point, lost half of the gizzard mass within about 1 week (Dekinga et al. 2001). This loss could be reversed by a return to a diet of hard-shelled mollusc prey. Building on an extensive set of dedicated laboratory experiments, gizzard mass in free-living Red Knots (measured non-invasively by ultrasound; Dietz et al. 1999; Starck et al. 2001) can be predicted quite accurately for different months, years and sites (Fig. 5) on the basis of energetic requirements, the length of the working day, the quality (the flesh to shell mass ratio) of the prey and whether birds are trying to maintain energy balance (*satisficing*) or rather fuel as fast as they can (*net rate maximizing*; van Gils et al. 2003, 2006a) This gives us a context to examine gizzard mass, prey quantity and quality requirements and energy

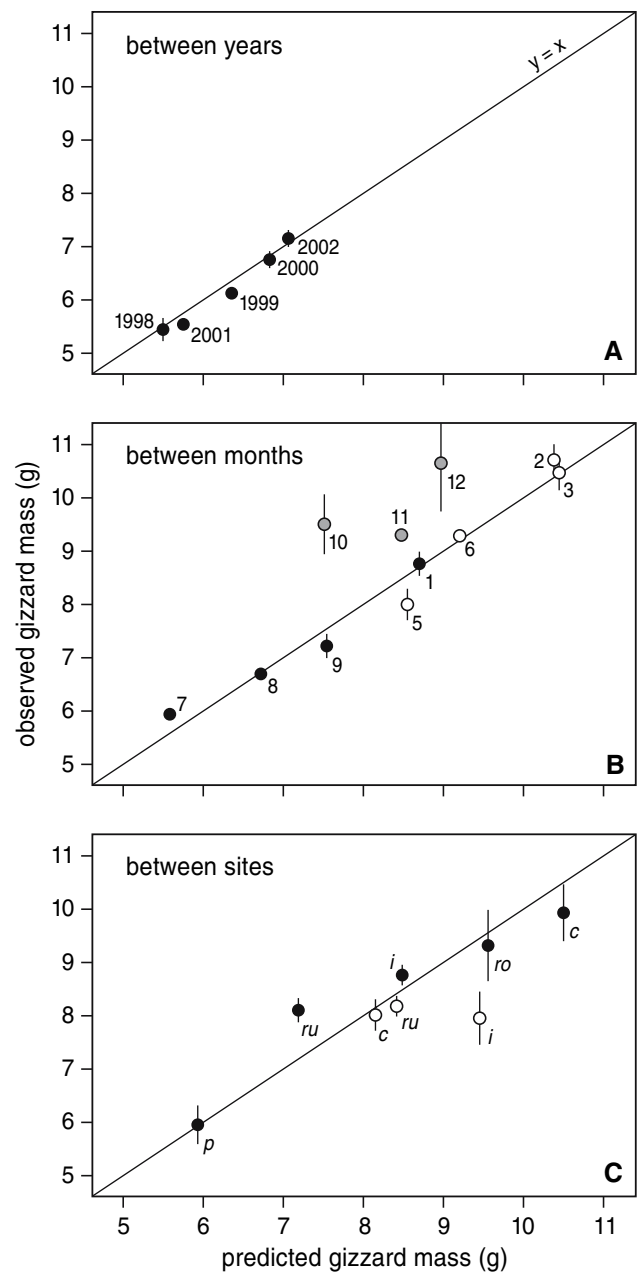


Fig. 5 Relation between observed gizzard mass and predicted gizzard mass at various temporal and spatial scales: **a** between years (Dutch Wadden Sea during late summer), **b** between months (Dutch Wadden Sea; 1–12 indicate the months January–December), **c** between sites (worldwide; letter indicates subspecies: *c* *canutus*, *i* *islandica*, *p* *piersmaei*, *ro* *rogersi*, *ru* *rufa*). In all plots, black dots indicate samples from wintering periods when *satisficing* gizzards are predicted; in **b,c** open dots indicate fuelling periods when *rate-maximizing* gizzards are predicted; additionally, in **b**, grey-filled dots (underestimations by 1.6–2.0 g) indicate those months in early winter (October–December) when Red Knots were assumed to be *satisficing* but actually were building up a small peak in body mass. Diagonal lines give $y = x$ and bars give standard errors. From van Gils et al. (2006a)

requirements as factors potentially constraining the fuelling and migration performance of Red Knots (Battley et al. 2005; van Gils et al. 2006b).

Do ecological constraints shape seasonal plumage changes and other annual cycle characteristics?

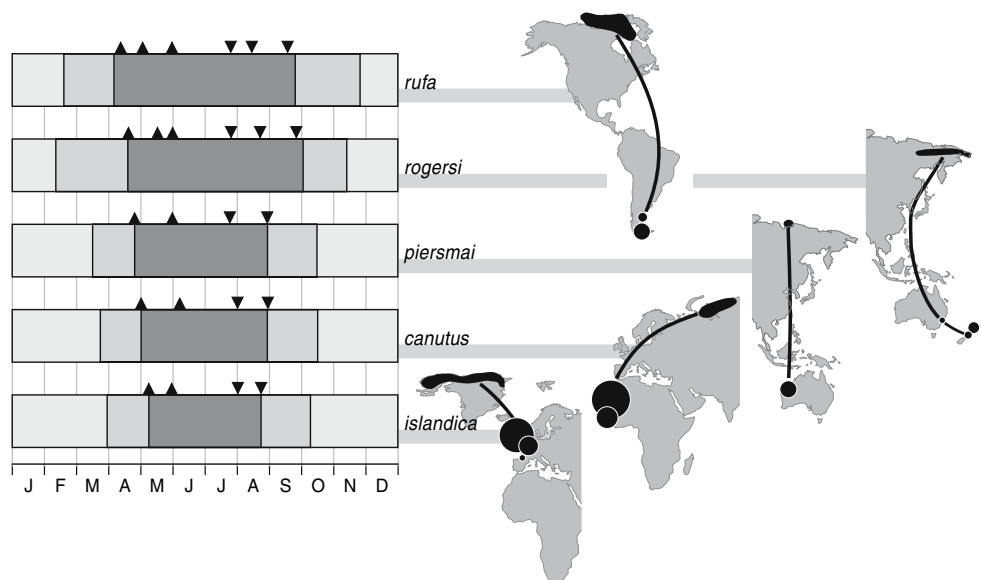
An examination of the seasonal timing of moults and long-distance flights of the five best-known subspecies (Fig. 6) indicates two groups with similar patterns. The two subspecies *rufa* and *rogersi*, which both winter south of the Equator, make three non-stop northward and three non-stop southward flights and carry the alternate (breeding) plumage for no fewer than 6–7 months (Piersma et al. 2005). The first northward flights do not take them very far from the wintering areas—*rufa*, from Tierra del Fuego to northern Patagonia (Baker et al. 2001); *rogersi*, from New Zealand to eastern Australia (Battley 1997; Battley and Piersma 1997). In both subspecies, this is followed by very long flights across the Equator to north temperate staging grounds in eastern North America and around the Yellow Sea, respectively. The three subspecies *piersmai*, *canutus* and *islandica*, which winter in or north of the tropics, each make two non-stop north- and two southward flights and carry the alternate (breeding) plumage for a shorter time, 3–4 months. In all subspecies, much of the moult from the basic to the alternate plumage takes place before the first northward flight, i.e. on the wintering areas (although some subspecies, especially *rufa*, do a fair amount of ‘touching-up’ at the staging sites during the northward migration, and some moult back to the basic plumage at stopover sites during southward migration; González et al. 2006; personal observation).

Note that the ordering in two “migration-types” does not reflect what we currently know about their phylogenetic relatedness (Buehler and Baker 2005; Buehler et al. 2006). For example, *piersmai* (“northern” winterer, two flights, short alternate plumage season) and *rogersi* (transequatorial,

three flights, long alternate plumage season) would be more closely related to each other than to either *canutus* or *rogersi* (of respectively either type). Similarly, *rufa* (the transequatorial champion) appears to be the closest relative of *islandica*, the only subspecies wintering in the north-temperate zone. The suggestion that migration schedules of Red Knots are not deeply rooted in their phylogeny echoes similar findings of evolutionary lability of migration in passerines, where closely related species or subspecies may also show stark divergences in migratory versus sedentary behaviour (Helbig 2003; Outlaw et al. 2003; Outlaw and Voelker 2006; Pérez-Tris et al. 2004; Winker and Pruett 2006).

Apart from this timing-of-moults-and-flights correlate of migration distance, the extent and relative intensity of the rusty-redness of the alternate plumage of each subspecies is also correlated with migration distance (Fig. 7; Buehler and Piersma 2007). The subspecies that winter in or north of the tropics (*canutus*, *islandica* and *piersmai*) are the ‘darker’ subspecies, whereas the transequatorial *rogersi* and *rufa* have lighter bellies than both *roselaari* and *piersmai*; *rufa* is also the palest of all in overall plumage. This relatively lower investment in melanin-based colouration of contour feathers by the transequatorial wintering subspecies may indicate that they cannot invest so much energy in moult. For both *rogersi* and *rufa*, we know that the wintering grounds offer relatively rich food resources (P.F. Battley, unpublished data; G.B. Escudero et al., unpublished data), a feature of their environment that is actually reflected in their decent fuelling rates before northward departure (Piersma et al. 2005). The *piersmai* subspecies, wintering just south of the Equator in north-western Australia, shows slow rates of fuelling before northward migration (Piersma et al. 2005), and it migrates

Fig. 6 Timing of plumage changes and of the northward (upward pointed triangles) and southward flights (downward pointed triangles) in the five best known subspecies of Red Knot, along with approximate migration routes and the relative population size of the wintering populations. In these diagrams, the time that Red Knots carry the grey-coloured basic plumage is indicated by the light shading, the time they carry the rusty-red alternate plumage is indicated by the darkest shading and the periods that they moult contour feathers to go from one to the other plumage type by the intermediate shading



very late (Battley et al. 2005). In view of these arguments, it seems most likely that lack of time at the southern wintering grounds curtails investments in this—sexually selected (Jukema and Piersma 2000; Piersma and Jukema 1993; Battley et al. 2006)—trait. The subsequent increased survival of individual *rufa* birds showing a ‘touch-up’ contour feather moult during their stopover in San Antonio Bay, northern Patagonia, in March 1998 relative to that of non-moulting individuals (González et al. 2006) suggests that relative plumage redness within populations is a honest quality signal, perhaps correlated with health, disease resistance and/or age (Piersma et al. 2001a, b; Drent et al. 2003; Battley 2007). Note that as male Red Knots of all subspecies are usually somewhat brighter and more extensively rufous than females (personal observation), females may not have as much need to advertise their quality.

In this context one wonders why Red Knots that winter as far south as Tierra del Fuego (*rufa*) and New Zealand (*rogersi*) do not, or hardly, use tropical coastal wetlands as stopovers; after all, such areas are found en route. For example, why do *rufa* not make the time to refuel at the Maranhão coast in northeastern Brazil (see Baker et al. 2005), an area used by “eastern *roselaari*” (Fig. 2)? I believe that an answer is suggested by the very low rates of fuelling before northward flights in tropical wintering areas (Piersma et al. 2005). The fuelling rates of 1 g/day or less at wintering sites in West Africa and in north-western Australia were surprising because, everything else being equal, the warm climates and low maintenance costs at such tropical sites (Wiersma and Piersma 1994) should enable higher rather than lower fuelling rates. Tropical constraints may relate to both the high ambient heat loads during the fuelling period (preventing hard work; Battley et al. 2003) and the mediocre quality of the prey (van Gils et al. 2005c). In summary, I propose that although tropical coastal wetlands with reasonable shellfish stocks can be used as wintering areas (because birds have the time to get away again; Zwarts et al. 1990), they fall short of providing the conditions for rapid en route refuelling by the transequatorial migrants. This means that the ultra-long, transequatorial migrants face the severest time constraints in carrying out seasonal functions, such as the moults, which are then reflected in their phenotype (Fig. 7).

The identification of selection pressures in a rapidly changing world

Perhaps more than any other habitat, wetlands suffer at the hands of ever-expanding and affluent human populations (Boere et al. 2006). In many parts of the world water

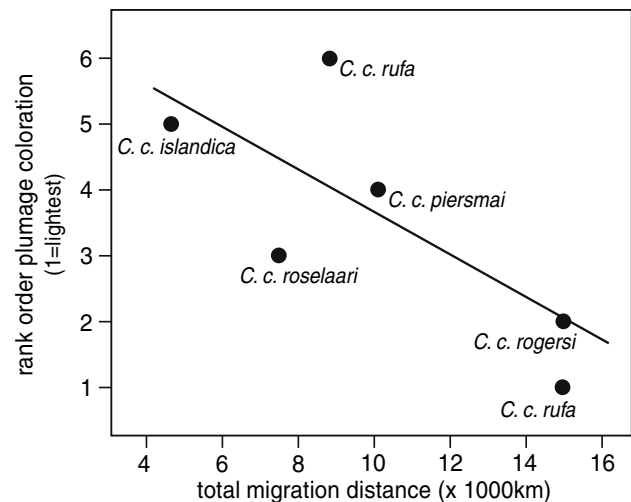


Fig. 7 Intraspecific correlation based on subspecific averages between the colouration of the alternate (breeding) plumage coloration and the overall migration distance for a one-way journey in Red Knots. Here, for breeding plumage, a six signifies the darkest colouration [taking into account both overall extent of redness and depth of colour (after Buehler and Piersma 2007; plumage data from Tomkovich 1992, 2001)]. Pearson correlation $r = 0.751$; $P = 0.04$, one-tailed test

resources are taken away from the wetlands to sustain agriculture. The preservation of wetlands has not been helped by a long-standing mindset that wetlands are mere wastelands. In coastal regions, wetlands were—and are still—reclaimed to satisfy increasing demands for harbour, industrial, housing and agricultural space; that most of the world’s humans live close to the coast intensifies the conflict, as does the demand for the marine resources harvested from the remaining areas. In this light it is no surprise that a recent survey by the international Wader Study Group showed that of 207 shorebird populations with known population trajectories (out of a total of 511 known shorebird populations), almost half (48%) were in decline, whereas only 16% were increasing (International Wader Study Group 2003; Stroud et al. 2006). With threefold more populations in decline than increasing, shorebirds belong to the most globally endangered segment of the migrant birds of the world.

We can, and should, lament the loss of wetland habitat and the migrant birds that make use of these wetlands. Equally, and as part of the scientific underpinning of conservation efforts, we can use well-studied cases of habitat modification to decipher the selection pressures that mould the variety of migration strategies just described for a single highly specialized migratory shorebird species, the Red Knot. As it happens, all populations of Red Knots are now in decline (Wetlands International 2006, personal observation) and, in a few cases, direct causal links have been established between human-induced habitat changes

at wintering and stopover sites and changing bird numbers at the population level. What do these cases tell us?

The first case concerns *rufa*, the southernmost wintering subspecies. The non-breeding population in Tierra del Fuego was over 67,000 birds in surveys carried out 1982–1985, but declined to around 18,000 in January–February 2005–2007 (Morrison et al. 2004; R.I.G. Morrison, personal communication). The decline was particularly steep from 2000 to 2002, with wintering numbers in Tierra del Fuego dropping from 51,000 to 27,000. In the absence of evidence for great changes in either the wintering or southern stopover areas, or from the Arctic breeding grounds, all of the evidence suggests a serious refuelling problem in the major staging site during northward migration, Delaware Bay, at the New Jersey–Delaware coast of northeastern USA (Baker et al. 2004). Here Red Knots feed and fuel on a single prey type, the eggs of horseshoe crab *Limulus polyphemus* (Tsipoura and Burger 1999; Haramis et al. 2007), which are superabundant and easily accessed in May when the horseshoe crabs come to spawn at the bay's beaches in great numbers. However, from the early 1990s onwards, the harvesting of horseshoe crabs for bait and the biomedical industry underwent an order of magnitude increase (Walls et al. 2002) and, consequently, the large masses of spawning crabs that characterized so many beaches around Delaware Bay (Myers 1986) became a pretty rare and localized sight. From 1997 to 2002, an increasing proportion of knots failed to reach threshold departure masses of 180–200 g. Reduced nutrient storage, especially in late-arriving birds, possibly combined with reduced sizes of intestine and liver during refuelling, had severe fitness consequences for adult survival and the recruitment of young in 2000–2002 (Baker et al. 2004); problems of food availability have become even more serious since (Atkinson et al. 2007). From 1997 to 2002 known survivors in Delaware Bay were heavier at initial capture than birds never seen again, and annual survival of adults decreased by 37% between May 2000 and May 2001 (Baker et al. 2004); annual survival showed the decline a year later for the segment of birds stopping over in San Antonio Bay, northern Patagonia (González et al. 2006). As they began to leave Delaware Bay for the breeding grounds with suboptimal stores, breeding success of Red Knots was also impoverished, with the number of second-year birds found in wintering flocks declining by 47% from 2000 to 2001 (Baker et al. 2004).

The decline of *rufa* knots around at the turn of the millennium can thus clearly be attributed to a food—or rather a fuelling—constraint acting on the last stopover site before the flight into the breeding grounds, the ‘launching pad’ so to speak. The studies that span research workers and areas at the two American continents have thus demonstrated how critical it is for these migrants to reach

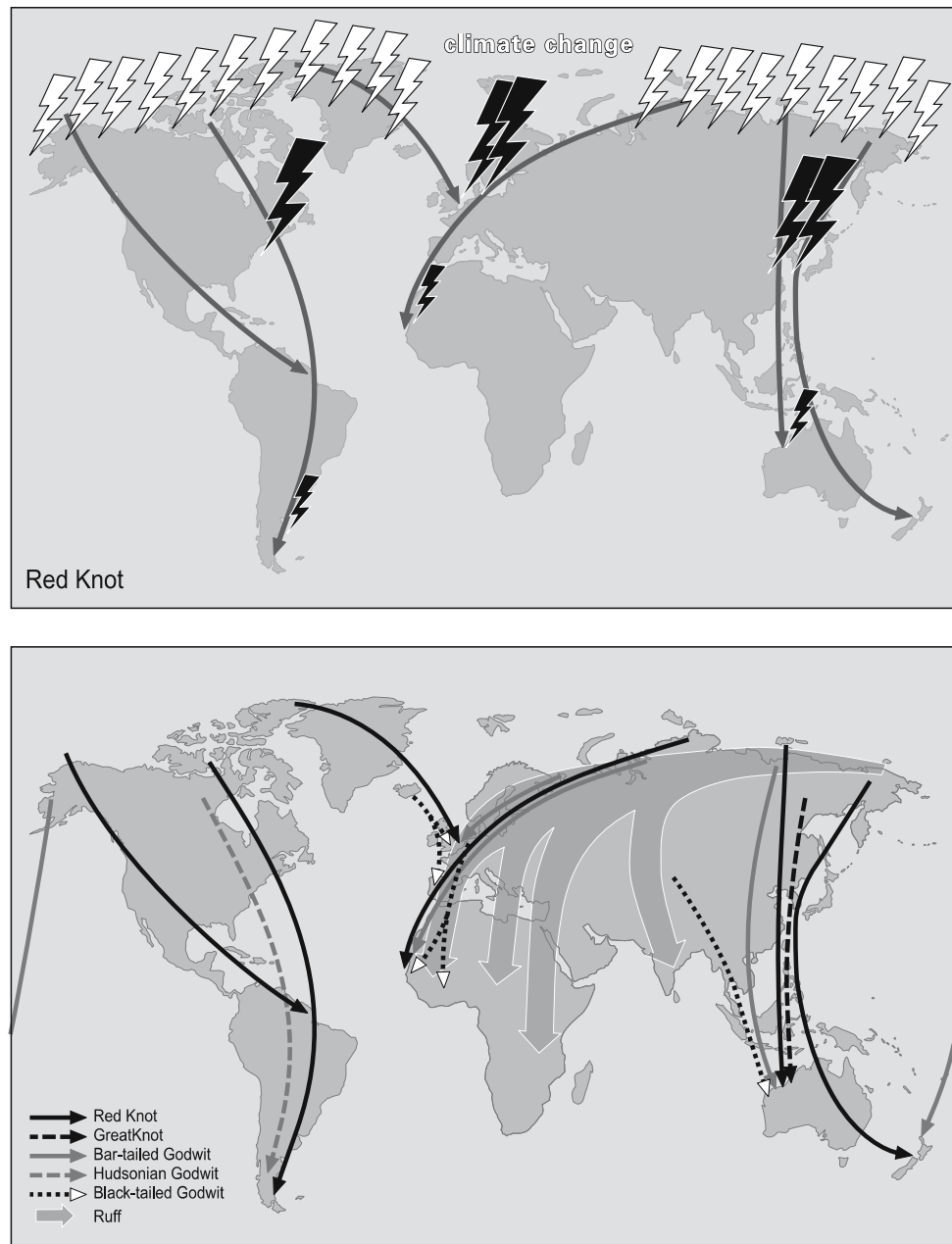
high threshold body masses at departure to the breeding grounds (compare Morrison et al. 2005). Threshold mass levels can be reached by fast fuelling on a reliable and abundant food supply, or by arriving early enough to compensate. The latter, as we have seen, is likely to be a problem for a time-stressed migrant such as *rufa* that comes from the far end of the other hemisphere and, in fact, late arrivals in recent years may also represent individual adjustments to local fuelling difficulties encountered in previous years (Atkinson et al. 2007).

In summary, for the case of the *rufa* subspecies encountering serious refuelling problems during its stopover before the direct flight to the breeding grounds, we now have hard evidence that below average mass gains at staging sites during northward migration negatively impacts subsequent survival. As predicted (e.g. Piersma 1987; Gudmundsson et al. 1991), fuelling performance and speed of migration are selected for. Similarly, after early summers in the early 1970s, when *islandica* knots ran into icy conditions on the breeding grounds, the heaviest birds during stopover in Iceland had the greatest chance to survive (Morrison 2006; Morrison et al. 2007).

Implicit in this whole argument is the issue of inter-seasonal carry-over effects: birds that encounter problems during some stage of the annual cycle may only come to pay the reproductive or survival price at some later stage (Piersma 1987; Piersma and Baker 2000). In the case of *rufa* knots, those that were captured light or late in the San Antonio Oeste area in northern Patagonia were less likely to ever be encountered again (González et al. 2006).

How factors acting in subsequent seasons can determine the fate of individuals can also be demonstrated with research on *islandica* knots that arrive in late summer in the Dutch Wadden Sea to moult and spend the winter (van Gils et al. 2006c). In this particular case, the returning Red Knots in 1998–2003 encountered serious declines in both prey quantity and quality as a result of the destructive mechanical harvesting of edible cockles *Cerastoderma edule* in the best feeding areas (Piersma et al. 2001a, b; van Gils et al. 2006c; Kraan et al. 2007). From 1998 to 2002, the fraction of the 250-km² of intertidal flats in the western Dutch Wadden Sea that was too poor for Red Knots to obtain a threshold intake rate of 4.8 W (based on food requirements at that time of year; Piersma et al. 1995) increased from 66 to 87% (van Gils et al. 2006c). Diet quality declined by 11.7% per year and to compensate for such reductions in prey quality the knots increased gizzard mass. Despite this increase in gizzard size over the years, resightings of individually colour-banded birds in which the gizzards were measured before release with ultrasonography (Dietz et al. 1999) demonstrated that individuals not seen again in our study area had undersized gizzards; individuals that we subsequently did see again had gizzards

Fig. 8 a Summary of the currently recognized ecological problems encountered by the various subspecies of Red Knots worldwide (see text), including major problems (*big lightning bolts*), such as overharvesting of benthic resources in Delaware Bay and the Dutch Wadden Sea and reclamations around the Yellow Sea, and smaller problems (*smaller bolts*) related to increased disturbance by humans in wintering areas in Patagonia, Mauritania and northwestern Australia, as well as the imminent habitat changes following from global warming (*repeated lightning bolts over the Arctic*). **b** A sentinel system for the world's long-distance migrant shorebird, the Global Flyway Network, that combines all research efforts to follow the demographics of a comprehensive set of long-distance migrating shorebird populations (see Table 2) in the context of studies on the ecological conditions at their wintering and staging grounds



large enough for a balanced daily energy budget (van Gils et al. 2006c). Local annual survival rate (calculated from resighting rates of colour-ringed birds) increased with year-specific food quality. Individually colour-ringed knots that disappeared from the western Dutch Wadden Sea may have died or, perhaps more likely for a wide-ranging migrant, emigrated to other areas, such as the estuaries in the UK. Here they probably paid a mortality cost due to the extra travel and/or due to uncertainties in the food supply at their new destination. Whatever happened to them, the steep decline in numbers of Red Knots wintering in the Dutch Wadden Sea can be explained satisfactorily by these documented population- and individual-level effects of

declining food conditions (van Gils et al. 2006c). The local disappearance from the western Dutch Wadden Sea accounted for much of the 25% decline of the entire NW European wintering population over the same period.

This example, then, shows that birds arriving from the tundra breeding areas with a gizzard that was too small needed more time to adjust their gizzard than their remaining energy stores allowed them: they would face starvation unless they left the area promptly. Were they to have left the tundra at higher body masses, with bigger gizzards, or not have encountered opposing winds en route, they would have found ways to survive and adjust to a Dutch Wadden Sea where food conditions had become

Table 2 Summary table of the long-distance migrating shorebird species and subspecies studied in concerted ways within the context of the Global Flyway Network and in combination with the areas where they are presently studied most intensively (i.e. where marking

and resighting efforts are concentrated), two ecological characteristics (habitat and diet types used), and an indication of whether the populations are currently on a trajectory of increase or decline

Species	Subspecies	Core study site(s)	Habitat	Diet	Population change
Red Knot <i>Calidris canutus</i>	<i>canutus</i>	Mauritania	Coastal	Molluscs	Negative
Red Knot	<i>piersmai</i>	NW Australia	Coastal	Molluscs	Negative
Red Knot	<i>rogersi</i>	New Zealand	Coastal	Molluscs	Negative
Red Knot	<i>roselaari?</i>	NW Brasil	Coastal	Molluscs	Negative
Red Knot	<i>rufa</i>	Argentina & USA	Coastal	Molluscs	Negative
Red Knot	<i>islandica</i>	Netherlands	Coastal	Molluscs	Negative
Great knot <i>Calidris tenuirostris</i>		NW Australia	Coastal	Molluscs	Negative
Bar-tailed Godwit <i>Limosa lapponica</i>	<i>lapponica</i>	Netherlands	Coastal	Worms	Positive?
Bar-tailed Godwit	<i>taymyrensis</i>	Netherlands & Mauritania	Coastal	Worms	Negative
Bar-tailed Godwit	<i>menzbieri</i>	NW Australia	Coastal	Worms	Negative
Bar-tailed Godwit	<i>baueri</i>	New Zealand	Coastal	Worms	Negative
Hudsonian Godwit <i>Limosa haemastica</i>		Argentina	Coastal	Worms	Stable?
Black-tailed Godwit <i>Limosa limosa</i>	<i>limosa</i>	Netherlands	Inland	Worms	Negative
Black-tailed Godwit	<i>islandica</i>	Iceland, UK, France	Coastal	Worms & molluscs	Now stable
Ruff <i>Philomachus pugnax</i>		Netherlands	Inland	Arthropods	Negative
Sanderling <i>Calidris alba</i>		Ghana, Mauritania, Netherlands, Iceland	Coastal	Worms & arthropods	Variously stable and negative

A graphical representation of the research network is provided by Fig. 8b

poor due to human economic activities². The encounter of such conditions is part of the migrants' life story. I would argue that the extent and the rapidity of human-caused changes (often for the worse, and certainly not helped by any drastic climate change; Fig. 8a) enable us to pin down ecological cause–effect relationships (if we bother to study the processes).

Conservation-relevant prospects: widening the scope of the comparisons

Based on the preceding arguments, I feel very encouraged that sustained efforts in studying the varying fates of some of the world's long-distance migrant shorebirds will continue to yield fundamental biological insight and at the same time provide precisely the information that well-meaning governmental and non-governmental organizations need to galvanize efforts to protect these very migratory phenomena and the networks of wetlands on which they depend. It would be particularly rewarding to

extend the comparisons among the world's populations of a shellfish-specialist dwelled on here to comparisons between subspecies in differently tropically specialized species (e.g. the worm-eating Godwit *Limosa*) and between different ecologically specialized species themselves (shellfish specialists, such as the two knot species versus the three godwit species that have a much more varied diet, notably polychaete worms). Returning to the contrast between high Arctic/marine versus lower latitude/freshwater species, comparisons between the ecology and demographics of, on the one hand, pure freshwater habitat specialists as the Ruff and the *limosa* subspecies of the Black-tailed Godwit (*Limosa limosa*) and, on the other hand, species only using coastal marine nonbreeding environments might prove very insightful.

Luckily for science and conservation, shorebirds worldwide have, for a long time, attracted considerable attention from researchers working in both amateur and professional capacities (Piersma and Baker 2000). To bring the dreams just outlined to practice, we have endeavoured to amalgamate many of the existing demographic research initiatives into a truly *worldwide observatory* of the changing fates of the world's shorebird populations and their habitats (Fig. 8b). We have named this the *Global Flyway Network, the shorebird ecological demographics and conservation initiative*. The programme intends to combine and coordinate the efforts of a worldwide

² Ironically, the intertidal mud- and sandflats in the Dutch Wadden Sea belong to the best formally protected areas in The Netherlands, having received multiple conservation agreement assignments. Despite this, the government issued permits for novel industrial forms of shellfish harvesting on the basis of the argument that these represented extensions of old fishing rights.

consortium of well-established shorebird scientists that over the past decade have demonstrated productive collaborations at several different levels. Covering all major flyways, it is our aim to cover the changing world with a system of continuous critical observations on the ecology, demography, body condition, health status and relevant genetic variability in 16 (or more) distinct populations of long-distance migrant shorebirds.

The objectives of the Global Flyway Network are to make important contributions of three different kinds: (1) to provide an instantaneous sentinel service for the global conservation community, i.e. an early warning system of flyway populations under threat, the early identification of populations in decline and in need of recovery action as well as the monitoring of the fates of populations known to be in dire straits; (2) to help generate the stories that need to be told to fuel the imagination and the good will of people who can make a difference to the fate of the habitats and populations under threat; (3) to further the science, including an understanding of the historical background and the current demographic processes and ecological, genetic and immunological constraints that determine whether populations flourish or flounder. The species selected (Table 2) cover all major flyway systems, have a tenfold range in body size, represent declining as well as (a few) increasing or stable populations and show contrasts in sensory and ecological specializations and in general habitat use. From a conservation point of view, this sentinel system covers declining populations and others under threat (those using geographical flyways under siege from overexploitation or habitat destruction, e.g. staging areas around the Yellow Sea, Wadden Sea and Delaware Bay, wintering areas in Sahel).

In summary, detailed worldwide eco-demographic research on these extreme long-distance migrants, as embodied in the Global Flyway Network, yields a two-pronged benefit: (1) on the basis of the unintended large-scale experiments carried out by humans, we rapidly come to grips with the selection pressures moulding the migration strategies of migrant birds, and (2) in applied contexts, this type of work gives instantaneous feedbacks on the conservation consequences of man-made alterations to wetland environments at the relevant global spatial scales.

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