Global-scale Shorebird Distribution in Relation to Productivity of Near-shore Ocean Waters

ROBERT W. BUTLER[1], NICK C. DAVIDSON[2] AND R. I. GUY MORRISON[3]

[1]Pacific Wildlife Research Centre, Canadian Wildlife Service, 5421 Robertson Road
Delta, British Columbia V4K 3N2 Canada
Internet: rob.butler@ec.gc.ca

[2]Wetlands International, PO Box 471, 6700 AL Wageningen, The Netherlands
Present address: Ramsar Convention Bureau, Rue Mauverney 28, CH-1196 Gland, Switzerland

[3]Canadian Wildlife Service, National Wildlife Research Centre, 100 Gamelin Boulevard
Hull Quebec K1A 0H3 Canada

Abstract.—The median density of shorebirds during their non-breeding season on the coast of South America was significantly greater in coastal zones with high primary productivity than in zones with moderate and low primary productivity. A world-wide review showed that sites harboring large numbers of wintering and migratory shorebirds corresponded significantly with regions of high coastal zone productivity. We suggest that the spacing of rich intertidal foraging habitats along the world's coastlines has been an important feature in the evolution of long distance migration by shorebirds. *Received 16 November 2000, accepted 20 December 2000.*

Key words.—Shorebirds, waders, coastal zone productivity, global shorebird distribution, evolution, migration.

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Identifying phenomena that explain the distribution and abundance of biota is a central theme of ecological theory. Biologists believe that food abundance is an important determinant of winter abundance and distribution of migratory birds, including shorebirds (Hockey *et al.* 1992; Davidson *et al.* 1992; O'Reilly and Wingfield 1995). Many of the world's 212 species of shorebirds (Charadriiformes: Haematopodidae, Recurvirostridae, Charadriidae and Scolopacidae) are among the most migratory vertebrates in the world. Some species make two annual journeys totalling 35,000 km between high latitude breeding regions and equatorial and southern hemisphere non-breeding habitats (Morrison 1984; Parish *et al.* 1987; Piersma *et al.* 1987; Summers *et al.* 1987; Gill *et al.* 1994). It has been argued that birds in general, and shorebirds in particular, have evolved traits in response to the long migrations between breeding and non-breeding quarters (Piersma and Baker 1999). These traits include accumulation of quantities of fuel in the form of lipid and protein that are expended during flight (Evans and Davidson 1990; Jenni and Jenni-Eiermann 1998), reduction of internal organ mass (Piersma 1998), and capacity for high altitude flights (Piersma and Jukema 1990; Marks and Redmond 1994; Butler *et al.* 1997). Long migrations often require shorebirds to make several rapid "refueling" stops which further requires abundant and readily available food at stop over sites. Migratory pathways of many shorebird species converge on sites with abundant prey, suggesting common selection factors might have shaped the migratory behavior of many species (Morrison 1984; Parrish *et al.* 1987; Piersma *et al.* 1987; Summers *et al.* 1987; Piersma and Davidson 1992). A relationship between shorebird density and productivity proposed for South America by Morrison and Ross (1989) was confirmed for Panama by Butler *et al.* (1998a; 1998b). In this paper, we demonstrate that the world-wide distribution of coastal dwelling shorebirds is positively related to regions of coastal zone primary productivity and we suggest that shorebird migration routes have evolved to take advantage of abundant food available in such regions.

METHODS

Data on shorebird distribution on the coast of South America were taken from Morrison and Ross's (1989) atlas, based on aerial surveys over 28,000 km of the South American coastline between 1982 and 1986. Numbers of shorebirds counted in 35 eco-units of the South American coastline (Fig. 2.2 and Table 3.2 in Morrison and

Ross (1989)) were divided by the length of coastline to obtain an estimate of the density of shorebirds in each eco-unit. Density estimates require information on the numbers of birds and the area of each beach. Beach area depends on its slope and the position of the tides. These data were not available so we divided the number of shorebirds counted in each eco-unit by the length of the beach. We calculated median densities because the data were skewed from a normal distribution. Morrison and Ross (1989) define an "eco-unit" as a geographical entity of broadly similar habitat. Ocean productivity was estimated for each of the 35 eco-units from satellite images throughout the year of coastal zone productivity summarized between 1978 and 1986 for the coast of South America (NASA 1999). The density of phytoplankton in these images is shown by different colors on the satellite images corresponding to the concentration of phytoplankton in the ocean where red $\cong 10$ mg.m^{-3}, orange $\cong 1.1$ mg.m^{-3}, yellow $\cong 0.8$ mg.m^{-3}, blue $\cong 0.2$ mg.m^{-3}, and so on. Eco-units that were adjacent to ocean areas that were predominantly red, orange, yellow or blue were designated as high, moderate, low and very low primary productivity, respectively. We compared the median densities of shorebirds calculated from Morrison and Ross's (1989) atlas because the data were skewed by a few sites with very large numbers of birds.

There is no world-wide convention on how shorebird abundance data are presented by researchers. Nevertheless, areas supporting 100,000 or more shorebirds at any one time are widely considered to be of major importance and we used this criterion to distinguish heavily used eco-units from those used by fewer birds. This criterion equates to that of the category "international sites" in the Western Hemisphere Shorebird Reserve Network (Morrison *et al.* 1991) and is five times greater than the minimum threshold of 20,000 birds using a site recognized for international importance under the Ramsar Convention on Wetlands (Ramsar Convention Bureau 2000). Such areas generally support both a high species diversity and several internationally important numbers of shorebirds from geographically separated breeding areas. Data on shorebird abundance on a world scale were obtained from published and unpublished sources. We subdivided the world into units by placing a ca. 250,000 km^2 scale grid over a map of the world. A total of 242 units were used, all of which included coastline south of the Arctic Circle. For each of these units we recorded the presence of high ocean productivity (*i.e.* red coastal regions on satellite images) or only lower productivity, and whether the unit held at least 100,000 shorebirds. The exception was where high ocean productivity spanned several units, but the exact unit in which large numbers of shorebird were present was not known. In these cases, we lumped adjacent units of continuous high coastal productivity with >100,000 shorebirds as if it was one unit rather than multiple units. We tested the null hypothesis that units holding >100,000 shorebirds were distributed equally between units of high and lower coastal zones productivity.

RESULTS

In South America, significantly higher densities of shorebirds occurred in areas of high coastal zone productivity than elsewhere (Table 1). The median density of shorebirds in eco-units where coastal zone productivity was high was 15.9 times greater than in eco-units where coastal zone productivity was very low. Moreover, the maximum density of shorebirds in eco-units with high coastal zone productivity was 293 times greater than in the eco-units with very low productivity. This finding supports the hypothesis that coastal zone primary productivity is a good predictor of non-breeding shorebird abundance and distribution on the coast of South America.

Worldwide, the data do not allow us to test how various levels of shorebird densities map on to coastal zone productivity, but the general trend for large numbers (≥100,000 shorebirds) to be found in regions of high coastal zone productivity concurs with the finding for South America (Fig. 1). As a general pattern, high productivity in north temperate coastal regions was more extensive, often encompassing much wider regions of the ocean than at low equatorial latitudes (NASA 1999). Nevertheless, south of Arctic regions the distribution of eco-units supporting over 100,000 shorebirds was closely associated with regions of high coastal zone productivity (Fig. 1). Eco-units holding ≥100,000 shorebirds occurred in 73 of 242 coastal units around the world's coastline. Seventy-one of these units

Table 1. Number of eco-units with shorebird densities above and below the overall median density (17.8 shorebirds/km of shore) and an index of ocean productivity at 35 coastal eco-units of South America.

	Index of ocean productivity		
Density	Very low + low	Moderate	High
Above median	1	8	9
Below median	8	7	2
N	9	15	11

Test for difference among medians: $\chi^2_3 = 13.5$, P< 0.01 (Zar 1984: 145-146).

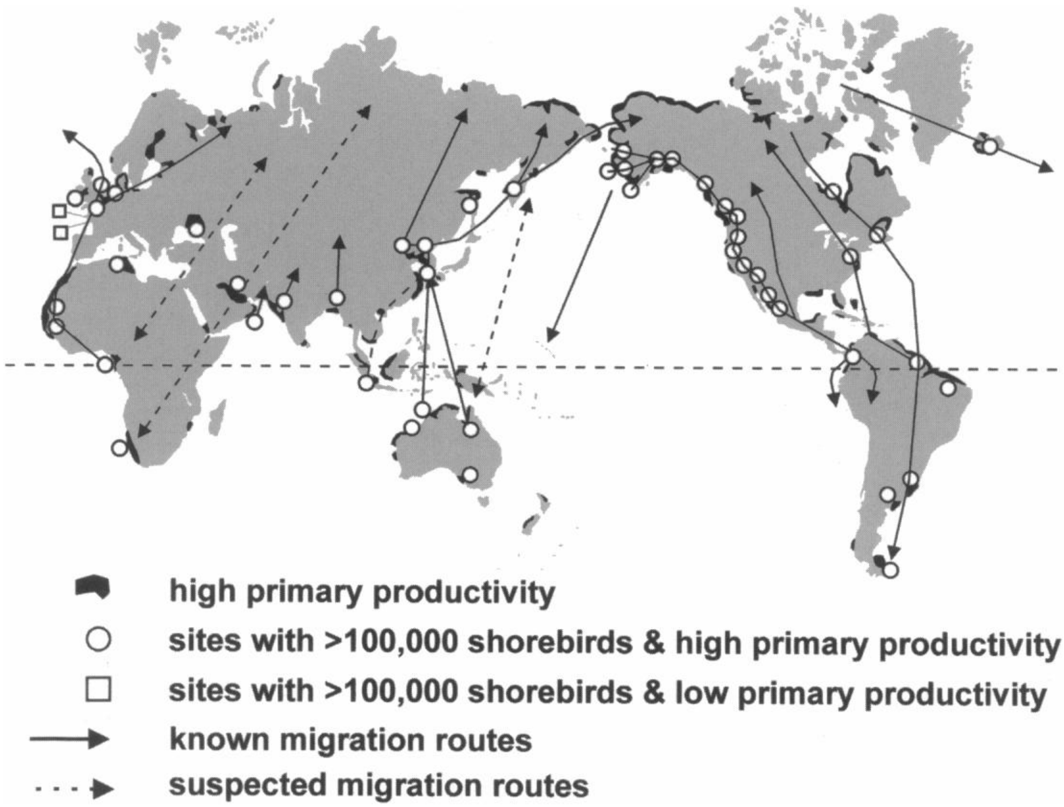

Figure 1. Generalized schematic of principal migration routes adapted from Hötker *et al.* (1998), coastal sites with >100,000 of shorebirds, and coastal zones with high productivity. Some neighboring sites were combined into a single open circle for clarity on the figure. Data sources are shown in Table 2.

were in regions of high productivity (i.e., red coastal regions on satellite images) and two units were in zones of moderate (orange) productivity. This distribution was highly significantly different from an expected distribution proportional to the number of units of high (117) and lower (125) coastal zone productivity $\chi^2_1 = 69.9$, $P < 0.001$). Therefore, we reject the null hypothesis that large flocks of shorebirds were distributed randomly along the world's coastlines. In comparison, 46 of the 169 coastal units that had low shorebird abundance (i.e., no known eco-units with <100,000 shorebirds) were in regions of high productivity and 123 were in regions with moderate or low productivity.

Our study focused on regions of the world that supported very large flocks of shorebirds, which happen to occur on soft sediments. However, the trend for higher densities of shorebirds to occur in areas of high coastal zone productivity might hold for rocky shoreline species as well. The Surfbird (*Aphriza virgata*) resides during the non-breeding season along rocky shorelines of the eastern Pacific and is seldom found on soft sediments (Hayman *et al.* 1986). Surfbirds were encountered along South American shores on twelve occasions during shorebird surveys by Morrison and Ross (1986), of which seven were on coastlines with high or moderate productivity and five were on low or very low coastal zone productivity beaches. The median density of Surfbirds on those twelve encounters was 0.32. The density of Surfbirds on high and moderately productive coastlines was above the grand median at five of seven locations, versus one of four locations on low and very low productivity coastlines. The power of the test is low and is not significant (Median Test $\chi^2_1 = 3.1$, n.s.), and larger samples are required to test the hypothesis that rocky shoreline species occur in greater density in regions with higher rather than lower coastal zone productivity.

DISCUSSION

Many of the areas of high coastal productivity were in Arctic regions where shorebirds occur only in the summer when they are widely dispersed over their breeding grounds. Environmental conditions, such as weather and ice-cover, make such regions generally unsuitable for shorebirds to use as migratory staging and wintering areas. Further south, other regions of high coastal zone productivity (e.g,. northern Scotland, Morocco, and the southern Red Sea) lack the extensive areas of tidal flats that are also a pre-requisite for the occurrence of large concentrations of shorebirds (Davidson *et al.* 1991): all eco-units listed in Table 2 are regions of extensive soft mudflats and sandflats. Furthermore, shorebird survey coverage is incomplete in some coastal regions, *e.g.* East Africa and south and east Asia. Our analysis suggests that it is reasonable to expect large concentrations of shorebirds in these regions. Only two oceanic coastal eco-units holding ≥100,000 shorebirds (Golfe du Morbihan and Baie de l'Aiguillon, France) were in lower (moderate) coastal productivity zones. Two other eco-units holding major concentrations of shorebirds are in enclosed seas in regions with high coastal zone productivity (Gulf of Gabes, Tunisia—Mediterranean Sea; Sivash, Ukraine—Black and Azov Seas).

An alternative explanation is that species of shorebirds that gather in large numbers are found on mudflat and sandflat habitats created by environmental processes that also produce highly productive coastal zones. Hence, it is not the coastal zone productivity *per se* that draws the shorebirds but the type of habitat that is present. We do not contend that coastal zone productivity alone draws large numbers of shorebirds, but instead suggest that the densities of shorebirds within a habitat type will be greatest in regions of high coastal zone productivity. We showed that the density of the Surfbird, a rocky shore specialist, tended to be greater in coastal regions of South America with moderate productivity than in zones with low and very low productivity. Studies from Panama also support our hypothesis that coastal zone productivity enhances mudflat habitats for shorebirds. Large flocks of shorebirds occupy mudflats in Panama (Morrison *et al.* 1998). The median density of calidridine shorebirds on 18 mangrove beaches with nearby upwelling was 197 times greater than on twelve mangrove beaches away from upwelling and significantly different (Butler *et al.* 1998b). The same comparison for mudflats without mangroves showed that 14.6 times as many shorebirds were present on ten mudflats in regions of upwelling than on three beaches without upwelling, but the difference is not statistically significant. In addition, some Brazilian mudflats that appeared to be good habitat, but were outside regions of high coastal zone productivity, supported correspondingly low densities of shorebirds (Morrison and Ross 1989, this study).

The positive and highly significant relationship between coastal zone productivity and shorebird abundance in South America supports the hypothesis that coastal zone primary productivity is a good predictor of non-breeding shorebird abundance over wide geographic scales. An inspection of the satellite images of ocean productivity in Panama lends support to these findings. The zone of highest ocean primary productivity (red and orange) in the eastern end of the Bay of Panama and lower levels (yellow and blue) elsewhere in the country correspond to respective high and low densities of shorebirds found there (Butler *et al.* 1998a, b).

Our results suggest that large numbers of the world's shorebirds gather during their non-breeding season in coastal regions of the world with high primary productivity. This finding concurs with a similar conclusion for the world's seabirds (Brown 1988; Hunt and Schneider 1987). The underlying reason for the association between high coastal zone primary productivity and shorebird abundance has not been explained. A probable explanation is that the combinations of topography, climate and water flow that concentrate nutrients along coastlines, and which induce the growth of phytoplankton, also produce conditions conducive to rapid growth of intertidal

Table 2. World-wide distribution of coastal eco-units that annually hold >100,000 shorebirds. An eco-unit was defined as a continuous or near continuous habitat type. Boreal season: Sp = spring, Su = summer, A = Autumn, W = winter.

Site and country	Total no. of shorebirds	Boreal season	Source
EUROPE			
Greater Thames Estuary, UK	300,000	W	International Waterbird Census (IWC) Wader database (unpubl. data)
Humber-North Norfolk Coast, UK	210,000	W	IWC Wader database (unpubl. data)
Liverpool Bay, UK	290,000		IWC Wader database (unpubl. data)
Breidafjordur, Iceland	>170,000	Sp	Gudmundsson & Gardasson (1992)
Wadden Sea, Netherlands, Denmark & Germany	2.2-2.6 million	A	Meltofte *et al.* (1994)
	0.9-1.2 million	W	
	1.8-2.2 million	Sp	
Sivash Gulf, Ukraine	0.98-1.24 million	A	Chernicko *et al.* (1991)
	0.90-1.13 million	Sp	
AFRICA			
Golfe de Gabes, Tunisia	300,000	Sp	Spiekman *et al.* (1993).
Namibian coast, Namibia	180,000	W	IWC Wader database (unpubl. data)
Banc d'Arguin/Baie d'Arguin, Mauritania	2.06 million	W	Zwarts *et al.* (1998a,b)
Archipelago dos Bijagos, Guinea Bissau	750,000	W	Zwarts (1988)
Cameroon/Gabon coast	100,000	W	R. West (pers. comm.); Schepers & Marteijn (1993)
Namibia/north-west South Africa	180,000	W	IWC Wader database (unpubl. data); Taylor *et al.* (1999)
MIDDLE EAST/INDIAN OCEAN			
Barr al Hickman, Oman	130,000	W	Green *et al.* (1994)
Arabian Gulf (Gulf States, Saudi Arabia and Iran	4 million	W	Zwarts *et al.* (1991)
Bangladesh coast	200,000-300,000	W	Kahn (1997)
Banyuasin Musi River Delta, Indonesia	110,000	?W	D. Watkins (pers. comm.)
EAST ASIA			
Moroshechnaya Estuary, eastern Russia	400,000	Sp	Gerasimov & Gerasimov (1998)
	1.0 million	A	
Shantar Islands, eastern Russia	200,000	Sp	Roslyakov & Roslyakov (1996)
Tongin Estuary, South Korea	120,000	Sp	M. Barter (pers. comm.)
Yalu Jiang, China	>150,000	Sp	Barter *et al.* (1998); Barter (1999)
Yellow River Delta, China	130,000	Sp	M. Barter (pers. comm.)
Shuangtaizahekou/Linghekou, China	100,000	Sp	M. Barter (pers. comm.).
Yancheng Nature Reserve/Dongsha Islands, China	140,000	Sp	M. Barter (pers. comm.)
AUSTRALIA			
Eighty Mile Beach, Australia	340,000	Sp/W	Parish *et al.* 1987
Roebuck Bay, Australia	170,000	Sp/W	Parish *et al.* 1987
The Coorong, Australia	240,000	W	Parish *et al.* 1987
Gulf of Carpentaria, Australia	250,000	W	Parish *et al.* 1987
NORTH AMERICA			
Central Yukon-Kuskokwim River Delta, USA	1-2 million	Sp/Su/A	Gill & Handel 1990
Port Heiden, USA	>100,000	Su/A	Harrington & Perry 1995
Nelson Lagoon, USA	>100,000	Sp	Gill & Jorgensen 1979, Gill *et al.* 1994
Izembek Lagoon, USA	>100,000	Su/A	Harrington & Perry 1995
Kachemak Bay/Mud Bay and Fox River Flats, USA	>600,000	Sp	Senner *et al.* (1981)
James Bay/Hudson Bay, Canada	>210,000	A	R. K. Ross & R. I. G. Morrison (unpubl. data)
Copper River Delta, USA	>500,000	Sp	Senner & Howe 1984

Table 2. (Continued) World-wide distribution of coastal eco-units that annually hold >100,000 shorebirds. An eco-unit was defined as a continuous or near continuous habitat type. Boreal season: Sp = spring, Su = summer, A = Autumn, W = winter.

Stikine River Delta, USA	>500,000	Sp	Gill *et al.* 1994
Fraser River Delta, Canada	500,000	Sp	Butler 1994
Bay of Fundy, Canada	350,000	A	Hicklin 1987
Grays Harbor, USA	>500,000	Sp	Senner & Howe 1984, Wilson 1993
Willapa Bay, USA	>100,000	Sp	Harrington and Perry 1995
Humboldt Bay, USA	150,000	W	Harrington and Perry 1995
San Francisco Bay, USA	>500,000	Sp	Senner & Howe 1984
Delaware Bay, USA	270,000	Sp	Clark *et al.* 1993
Laguna Atascosa, USA	500,000	Sp/A	Harrington & Perry 1995
Rio Colorado, Mexico	>100,000	Sp	Morrison *et al.* 1992
Laguna Ojo de Liebre, Mexico	>100,000	W	Morrison *et al.* 1992
Esteros Tobari and Lobos, Mexico	>100,000	W	Morrison *et al.* 1992
Culiacan-Los Mochis, Mexico	>100,000	W	Morrison *et al.* 1992
CENTRAL AMERICA			
Panama Bay, Republic of Panama	369,000	A	Morrison *et al.* 1998
SOUTH AMERICA			
North coast of Suriname, French Guiana, and Brazil	2.1 million	W	Morrison & Ross 1989
Maranhio Coast, Brazil	334,000	W	Morrison & Ross 1989
Bahia Samborombon, Argentina	100,000	W	Blanco & Canevari 1998

marine benthic organisms eaten by shorebirds. Shorebirds in general, eat many marine invertebrates such as polychaete worms, molluscs and crustaceans (Skagen and Oman 1996). It is well established that survival and reproduction of many seabirds is closely tied to food availability mediated through patterns of ocean upwelling (Duffy 1993). Widespread breeding failure and mortality during El Nino—Southern Oscillation (ENSO) events emphasizes this point (Duffy 1993). The widespread use of estuaries and freshwater habitats by shorebirds might confer a greater degree of immunity to the vagaries of ocean processes and therefore play a less important role in population regulation than among seabirds, but this topic has not been explored.

Our study suggests that the spatial distribution of productive regions of the world's oceans has played an important role in the evolution of shorebird migratory routes and strategies. Eight broad flyways are recognized in the world, along which shorebirds migrate between breeding and wintering grounds (Morrison 1984). Many shorebirds breeding in Alaska use the eastern Pacific flyway and stop at sites along the western shores of North, Central and South America and parts of the Caribbean, whereas shorebirds breeding in the low and mid-Canadian Arctic stop along the eastern shores of North and South America (Fig. 1; Morrison 1984; Davidson *et al.* 1992). Several species of shorebirds that breed in the northeastern Canadian high Arctic cross the Greenland icecap and stop in Iceland en route to wintering areas in western Europe. Species that breed in the Arctic region of western Asia stop in northern and western Europe, and west Africa. Some mid-Asian Arctic shorebirds stop at sites in Eastern Europe, the Middle East, east Africa and India, while others join eastern Asian Arctic shorebirds migrating along the western Pacific Coast to Southeast Asia and Australia. A few species make exceptionally long non-stop passages across vast regions of unproductive ocean to reach winter quarters on remote islands in the Pacific and beaches in Australia (Marks and Redmond 1994). In almost all cases, oceanic coastal locations that hosted large numbers of shorebirds corresponded with regions of high coastal zone productivity (Fig. 1).

Coastal eco-units holding more than 100,000 shorebirds occurred on all flyways. Four non-coastal sites supported over 100,000 shorebirds in the predominantly overland central American (Mississippi) Flyway (Skagen *et al.* 1999). There are major coastal concentrations of shorebirds that winter only on the Central Asian Flyway: birds on this flyway also migrate overland, to northern Asian breeding grounds. On all other flyways there are eco-units with major shorebird concentrations that are used as wintering areas and others as staging areas during migration (Fig. 1, Table 2). However, the number and distribution of major concentrations of shorebirds in areas of high coastal productivity differs substantially between flyways: for example, there only nine on the well-surveyed East Atlantic Flyway, twelve on the East Asian Flyway, but 17 just on the north American part of the Eastern Pacific Flyway. This implies that shorebirds using different flyways are following different migration strategies so as to capitalize on the different spacing and distribution of areas of high coastal productivity.

The observation that prey availability plays an important role in the local and regional distribution and abundance of wintering shorebirds (Morrison 1984; Hockey *et al.* 1992; Butler *et al.* 1998a) can be extended to a global scale to include the migration period. The major features associated with shorebird distribution and abundance in winter were the presence of suitable habitat and high biological productivity in adjacent coastal waters. As noted above, we suggest that the same environmental features that produce abundant phytoplankton blooms as reflected in the satellite imagery also provide suitable conditions for marine intertidal invertebrates eaten by shorebirds. Coastal environments enriched by nutrients from upwelled water from the ocean depths and run off from land have features known to attract large numbers of birds (Cloern 1982; Jarre-Teichmann 1998).

We suggest that the spatial distribution of productive zones in the world's oceans have probably been an important selective factor in the evolution of shorebird migration. Several lines of evidence support this hypothesis. First, migratory routes of shorebirds connect highly productive sites into migratory "stepping stones" that do not always take the most direct route. For example, some species follow the Atlantic coast of Africa to northern Europe and then fly eastwards to Siberia whereas others turn west, crossing the Atlantic to reach the Canadian Arctic (Fig. 1). Second, shorebird abundance at staging sites often corresponds to the abundance of their prey. For example, hundreds of thousands of shorebirds assemble in Delaware Bay, USA and in the Bay of Fundy, Canada when prey are available (Hicklin 1987; Burger *et al.* 1997; Tsipoura and Burger 1999) and occur in greatest number on mud flats where prey is abundant (Hicklin and Smith 1984). Third, shorebirds gather at coastal sites that are enriched by human sewage (Tubbs 1977; Impe 1985).

Many of the highly productive coastal zones in the world are separated by hundreds or thousands of kilometers of relatively marginal habitat with low productivity. Time minimization on migration (*sensu* Alerstam and Lindström 1990) is a common feature of shorebird migrations whereby natural selection is believed to have favored individuals that reduce the time spent on migration (Clark and Butler 1999). Rich foraging sites, where refueling can be quickly achieved, are widely and irregularly spaced across the earth's surface. Individuals best suited to fly between successive rich foraging sites should migrate faster and thereby reduce the chances of being caught by predators at stop-over sites, and arrive at the best time to choose mates and nesting sites on the breeding grounds. Thus, the spacing of productive foraging sites might have shaped the evolution of the great variety of behavior, physiology and morphology found among migrant shorebirds.

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