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Barriers and distances as determinants for the evolution of bird migration links: the arctic shorebird system

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We analysed migratory connectivity between different winter quarters and breeding sectors in the circumpolar tundra region for arctic shorebirds, in relation to migratory distances and ecological barriers. Total distances and barriers were calculated and measured for all potential migratory orthodrome links between 10 selected winter regions and 12 breeding sectors. The migratory segment between the northernmost stopover site and the breeding area, associated with the entry to and exit from the tundra during spring and autumn migration, respectively, was also identified and measured for each potential link.

The analysis indicated that the evolution of migratory links among arctic shorebirds is constrained not by distance as such but by distance across ecological barriers, possibly because of the complex adaptations required for barrier crossing and extensive detour migration (and in a few cases because barrier distances exceed the birds' theoretical flight range capacity). A particularly pronounced barrier effect of the Arctic Ocean, as apparent from a sharp decline in migratory connectivity between the opposite sides of the Arctic Ocean, may reflect a crucial importance of favourable entry and exit conditions for successfully occupying different sectors of the tundra breeding area by shorebirds from winter regions situated at widely different total distances in both the southern and northern hemispheres.

Keywords: biogeography of migration; migratory connectivity; migration distance; barriers to migration

1. INTRODUCTION

It is commonly accepted as a fact that one of the ultimate factors that limits species ranges is ecological barriers that prohibit dispersal (Cox & Moore 2000). For many long-distance migratory bird species though, and particularly for the Arctic shorebird group, where long non-stop migratory flights across deserts, mountains and oceans are known to occur, ecological barriers may appear to have little or no great effect on range extension.

Instead, it has been proposed that range limitations for long-distance migratory species are primarily attributable to other biological/ecological (e.g. Brown *et al.* 1996), historical (e.g. Pielou 1979; Kraaijeveld & Nieboer 2000) and genetic factors (Böhning-Gaese *et al.* 1998; Bensch 1999), and even to increased dispersal itself that dilutes adaptation in the range periphery (Kirkpatrick & Barton 1997).

Many arctic shorebirds are capable of very long non-stop flights (e.g. Williams & Williams 1991; Pennyquick & Battley 2003). Because the energy, time, and safety costs associated with migration ought to increase roughly in proportion with migratory distance (e.g. Alerstam & Lindström 1990; Houston 1998; Lank *et al.* 2003) we would still however, expect an effect of both migratory distance and barriers on the evolution of migratory links between different potential breeding and wintering regions.

The evolutionary significance of ecological barriers for migration routes has been recognized in many birds and the effects have been described to vary both between

groups of birds and migratory systems. (e.g. Moreau 1972; Berthold 1993; Kerlinger 1995; Fujita *et al.* 2004; Irwin & Irwin 2005). The shorebirds rely on quite specific coastal or wetland habitats. Several types of landforms where there are no or few such habitats can therefore constitute severe barriers to migration and hence influence migratory routes and distribution of these species. We expect that migration routes are influenced by ecological barriers because of the extra cost they add to migration. Traversing a barrier requires an extra energy and safety cost resulting from the carrying of heavy fuel loads. Likewise, circumventing a barrier also entails increased costs primarily in time and energy (but also in safety) associated with the longer flight distance of the detour route (Alerstam 2001). Thus, any continuous distance along a potential migratory route that is made up of landforms where fuelling options are unavailable may involve a significant barrier effect and affect the evolution of migratory routes and hence, render certain areas inaccessible as breeding or wintering areas.

Another important limitation to the evolution of routes linking certain winter and breeding regions is probably posed by the geographical configuration of suitable high-quality northernmost stopover sites that provide access to the different sectors of the circumpolar Arctic (Alerstam *et al.* 1986). It is possible that these northernmost staging sites may be of particularly critical importance for the breeding distribution of birds from different winter regions. When the birds arrive at these northern latitudes in spring the nutrient resources on the tundra are still quite limited and the climate conditions may be quite harsh. Because of the advantage it involves for a bird to arrive at

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the breeding ground at the right time and in good condition (e.g. Marra *et al.* 1998; Drent *et al.* 2003), birds whose breeding destinations are relatively close to these final stopover sites in spring may have a selective advantage over those whose breeding grounds are more remote (Alerstam *et al.* 1986).

As the feeding conditions in the Arctic regions deteriorate as the summer season progresses, access to these northern major stopover sites may be of critical importance also during autumn migration.

In this study we investigate the large-scale patterns of migratory connectivity of shorebird populations between major winter regions and the different Arctic regions, and we aim to analyse (i) whether and to what degree these are influenced by the total migration distance and the geographical configuration of continents and major landforms. More precisely, we ask whether the total distance of potential links between winter and breeding regions affect the degree to which they are existing links in the migration systems of the different shorebird species. We also ask whether continuous stretches of landform types such as open oceans, deserts, mountains, glaciers or pack ice along these potential links have a barrier effect on migration and thereby also on connectivity.

We also test (ii) whether the location of major northernmost staging areas ('entry sites') used by the shorebirds on spring migration before their final flights to the tundra breeding destinations are of particular critical importance in providing access to the tundra regions. The focus is on spring migration rather than autumn migration because the Arctic shorebirds are assumed to be under the strictest pressure then as food availability may be severely limited at northerly latitudes at this time of the year.

Finally (iii), we compare the distance and barrier relationships for connectivity between a specific winter region and different breeding regions with the corresponding relationships for connectivity between a specific breeding region and different winter regions. The asymmetry between these two perspectives on migration links is important for understanding the different evolutionary situations for birds in a given winter and breeding region, respectively.

2. MATERIAL AND METHODS

Spatial information about the global breeding and wintering ranges of 30 Arctic shorebird species was compiled from ornithological literature sources and digitally mapped in an ARCVIEW 3.2 GIS (ESRI 1992–2000) project (for procedure and sources about the species' ranges and for the spatial definition of Arctic tundra biome see Henningsson & Alerstam 2005). The 30 species selected for this study have breeding ranges that are primarily contained in the Arctic tundra biome. More precisely, the species are the Arctic members included in the genera: *Arenaria*, *Calidris*, *Charadrius*, *Eurynorhynchus*, *Limicola*, *Limnodromus*, *Limosa*, *Philomachus*, *Pluvialis* and *Tryngites*.

We also selected 10 different winter 'hotspot' regions, with a high abundance and diversity of wintering shorebird species (figure 1).

Each species' breeding range was denoted as present or absent in each of 36 Arctic sectors (34 with Arctic tundra) based on a longitudinal 10° sector division of the circumpolar Arctic (figure 1).

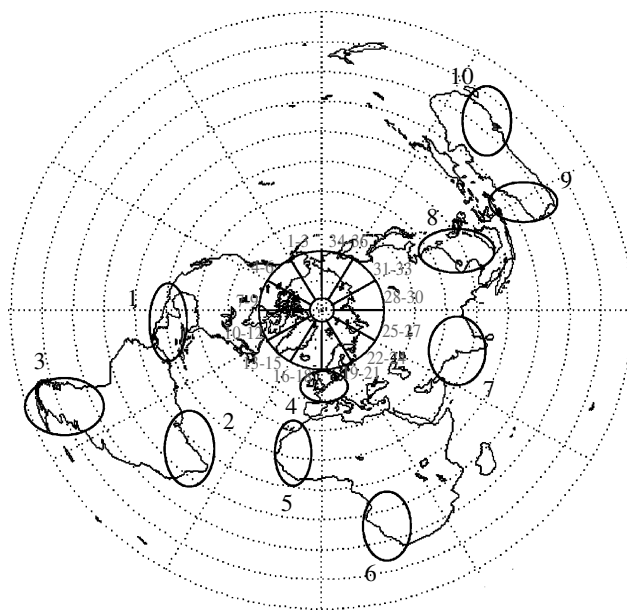


Figure 1. Azimuthal equidistant projection of the Earth centred at the North Pole. The schematic positions of 10 major wintering regions for shorebirds are encircled and numbered. The longitudinal division of the Arctic into 36 sectors (34 contain Arctic tundra) is indicated with numbers. The links between the 10 winter regions and 12 equally spaced tundra sectors were used for barrier measurements.

The connectivity between the 34 different breeding sectors and the 10 major winter regions was compiled for each of the 30 species of shorebirds from literature sources (sources in Henningsson & Alerstam 2005). The number of species migrating between each Arctic sector and each of the different winter hotspot regions were mapped so to present the structure of the broad-scale migratory connectivity of the Arctic shorebird system.

The orthodrome (great circle) distances between each of the 10 winter regions and every third Arctic sector (i.e. 12 Arctic locations; 120 total orthodrome links) were calculated according to the formula in Gudmundsson & Alerstam (1998b). The orthodrome links were analysed by placing a transparent string along each link on a large globe of the Earth (showing topographical features) and measuring distances occupied by different landform categories within a 250 km wide corridor along each of the 120 orthodrome links. The landforms categories were: inland, coast, ocean, mountain range, glacier and desert.

We are aware that not all migratory routes always follow exact great circle routes, but have assumed these as approximations because there are indications that many shorebird migration routes resemble great circles and also because for many species the routes are not known in sufficient detail that would allow for analysis of exact actual routes for each species.

The northernmost major shorebird staging area located nearest each of the 120 orthodrome links was identified (14 different such major staging areas between 39° N and 64° N described in the literature; Morrison & Myers 1987; Parish *et al.* 1987; Piersma *et al.* 1987; Summers *et al.* 1987; Wetlands International RSDB 2001) and the associated entry links from that staging site to breeding locations were measured separately. The direct routes were calculated between the final major staging site and each of the 12 Arctic breeding locations, and the landform attributes associated with each

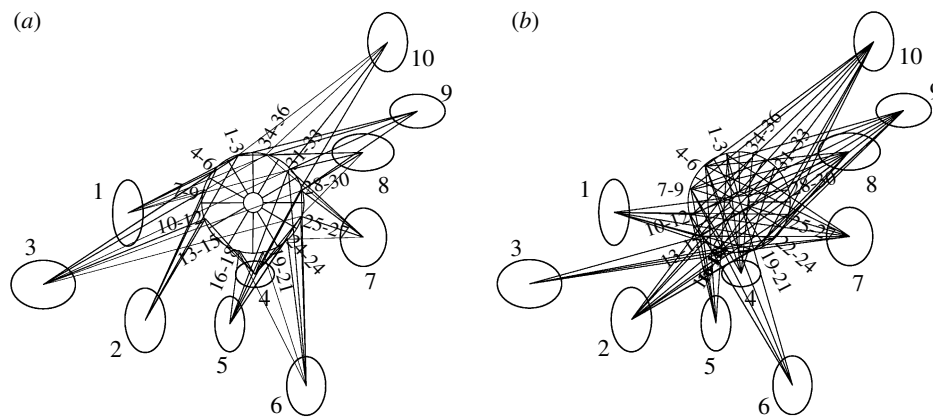


Figure 2. Schematic diagram representing the broad-scale patterns of migratory connectivity of shorebird populations between different breeding sectors in the Arctic and major winter regions for (a) occupied links and for (b) unoccupied links. Breeding sectors and winter regions are drawn according to the azimuthal equidistant map projection (figure 1) with geographic features removed to enhance clarity of connectivity pattern.

Table 1. Correlation coefficients between species occupancy and distances of barriers and other habitats associated with (a) each total link and (b) entry link.

(Number of links in both (a) and (b) are 120 and asterisks indicate levels of statistical significance (* $p < 0.05$; ** $p < 0.01$).)

(a) total link		(b) entry link	
variable	Pearson's r	variable	Pearson's r
inland	0.08	inland	0.04
coast	0.15	coast	-0.19*
ocean	-0.25**	ocean	-0.28**
mountain range	-0.22*	Arctic ocean	-0.34**
glacier	-0.22*	glacier	-0.19*
desert	-0.12	sum barriers	-0.43**
sum barriers	-0.39**	total distance	-0.36**
total distance	-0.15		

entry link were measured on the globe as for the total links. The landform categories for the entry links were: inland, coast, Arctic Ocean and pack ice, other ocean, and glacier.

We tested whether the number of species from a given winter region that occupy a certain area in the Arctic, from here on referred to as species occupancy, is affected by the total distance of the associated migratory link and the segment distances of the different landforms and geographical barriers along the link. More precisely, we analysed the correlations between species occupancy and the distance of total links and of the separate landforms constituting the links ($n = 120$).

The combined effect on species occupancy of the total link variables was investigated using backward multivariate linear regression analysis.

Similarly, the correlations between species occupancy and the entry links (total distance and landform distances) were analysed ($n = 120$). The combined association between species occupancy and the entry landform covariates was also investigated using backward multivariate linear regression analysis.

In order to test whether these entry links are particularly crucial in providing access to the different tundra regions we also analysed the relative effects of entry links and the remaining part of each total link in a combined multivariate regression model. Two sets of staging sites were analysed in

parallel with one set including sites used particularly during spring (entry migration to the tundra) and one including the typical autumn sites (exit migration from the tundra). Many of the northernmost stopover sites were the same during spring and autumn migration, and the two sets of staging sites were thus highly similar. Because the two sets of analyses yield almost identical results we have chosen to focus on the set representing the spring situation and the part of the migratory link that provide entry to the tundra regions. However, we would like to point out that the importance of the northernmost parts of the migration links could also reflect constraints to the exit routes away from the tundra zones during autumn migration.

The univariate correlations and linear regressions between species occupancy and distance and barrier extent of total links were also analysed within winter region and breeding location, respectively. Hence, from the winter region perspective there are 10 different correlation and regression coefficients, each based on the 12 potential links associated with each winter region. Conversely, from the breeding area perspective, there are 12 different correlation and regression coefficients, each based on the 10 potential links associated with each breeding location.

3. RESULTS

(a) Connectivity patterns

All potential links (120) between the 12 arctic sectors and the 10 winter regions were organized in matrices representing occupied and non-occupied links (and the number of species associated with an occupied link), the orthodrome distances as well as the landform distances constituting the links. Of these 120 links 54 are occupied and 38 of these are occupied by more than one species. The maximum number of species occupying a link is 8 and these are birds wintering in northwest Australia and breeding in sectors 32 and 35 in eastern Siberia. The occupied and non-occupied links are schematically depicted in figure 2. It is notable that unused links often tend to run across the polar region while used links rarely do this.

(b) Correlations

There are significantly negative correlations between species occupancy and each of the four different types of

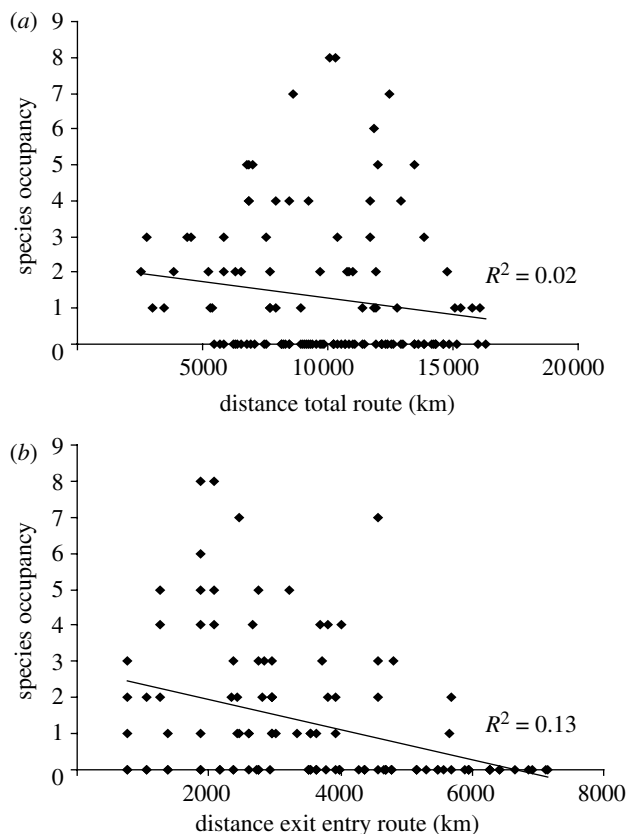


Figure 3. Scatterplot of the relationship between species occupancy of links and (a) the total distance of the links and (b) the distance of the entry parts (the distance between the tundra breeding areas and the northernmost major stopover sites associated with each link).

barrier (i.e. ocean, mountain range, glacier and desert) measured along the total links, and when the distances of these barriers are considered together (sum barriers) the correlation is quite strong. In contrast, there is no significant correlation between species occupancy and total link distance (sum barriers + inland + coast; table 1a and figure 3a).

There are also significant negative relationships between species occupancy and each of the barriers associated with the entry part of the links. Entry distances across oceans, and particularly Arctic Ocean have relatively strong negative effects on species occupancy (table 1b). The combined negative effect on species occupancy by the different landform barriers (sum barriers) associated with the entry part of the links is even slightly stronger than for the total link. Total distance of the entry links also has a negative effect on species occupancy which is not the case for the total distance of the total links (table 1a,b; figure 3a,b).

(c) Multivariate linear regression

Three different multivariate linear regression models were calculated with species occupancy of the different migratory links as dependent variable ($n=120$; table 2). Model 1a refers to the total route and includes all total link covariates (independent variables: inland, coast, ocean, glacier, desert and mountain range). This model explained about 26% of the species occupancy variation. Stepwise removal of the least significant covariate until all covariates included met a significance criterion of $p < 0.05$ yielded

Table 2. Multivariate regression models for species occupancy of links in relation to distances of different types of barriers and other habitats.

(The contributory value of each barrier covariate to each model is indicated by the standardized regression coefficient (β) and significance value. The explanatory value for each model on the variation in species occupancy of links is represented by the model R^2 value. R^2 values for the final models (1b, 2b, 3b), after excluding non-significant variables by backward elimination, are indicated in bold figures. (Model 1a) total route, initial variables; (1b) total route, final variables; (2a) exit/entry route, initial variables; (2b) exit/entry route, final variables; (3a) combined 1b and 1a, initial variables; (3b) combined 1b and 1a, final variables. Ocean₁, including Arctic Ocean and pack ice; ocean distance for total routes; ocean₂, excluding Arctic Ocean and pack ice; ocean distance for exit/entry routes; ocean₃, excluding Arctic ocean and pack ice; ocean distance for total routes.))

model	variables	β	signifi- cance	model R^2
1a	inland	0.065	0.498	0.26
	coast	0.168	0.047	
	ocean ₁	-0.392	0.000	
	glacier	-0.143	0.098	
	desert	-0.200	0.030	
	mountain	-0.327	0.000	
1b	ocean ₁	-0.350	0.000	0.20
	glacier	-0.204	0.016	
	mountain	-0.332	0.000	
2a	inland	-0.099	0.026	0.22
	coast	-0.170	0.058	
	glacier	-0.049	0.608	
	ocean ₂	-0.230	0.012	
	Arctic ocean	-0.347	0.000	
2b	coast	-0.175	0.039	0.21
	ocean ₂	-0.221	0.010	
	Arctic ocean	-0.340	0.000	
3a	glacier _{totroute}	-0.127	0.124	0.28
	mountain _{totroute}	-0.320	0.000	
	ocean _{3totroute}	-0.252	0.004	
	coast _{entryroute}	-0.241	0.003	
	Arctic ocean _{entryroute}	-0.296	0.000	
3b	ocean _{3totalroute}	-0.249	0.005	0.27
	mountain _{totalroute}	-0.319	0.000	
	coast _{entryroute}	-0.257	0.002	
	Arctic ocean _{entryroute}	-0.327	0.000	

model 1b, with three remaining covariates (ocean, glacier and mountain) that together explained about 20% of the species occupancy (table 2).

Entry links were analysed in an analogous way, with model 2a including all initial entry link covariates (inland, coast, glacier, Arctic Ocean and other ocean). This model accounted for 22% of the variation in species occupancy of the 120 different migratory links. Model 2b included only entry link covariates with a significant ($p < 0.05$) contribution to the model (coast, Arctic Ocean and remaining ocean).

A combined model initially including the significant covariates from the final entry link model and the significant covariates associated with the remaining part of the total link (model 3a; table 2) had an R^2 value slightly higher than any of the separate models 1b and 2b, respectively. The stepwise removal of the covariates that

Table 3. Correlation (r) and regression coefficients (B ; per 10^6 m) for the relationships between the number of species associated with each link and both the total distance and the summed barrier distances of that link when links are analysed separately based on winter region origin ($n=10$) and breeding region origin ($n=12$), respectively.

(For each winter region, r and B are calculated for the 12 possible links to the different breeding sectors, and the table shows the mean and scatter for these values for the 10 different winter regions. Similarly, for each breeding sector, r and B are calculated for the 10 possible links to the different winter regions, and the mean and scatter for these values are shown for the 12 different breeding sectors.)

		total distance				sum barriers				n
		mean	min	max	s.d.	mean	min	max	s.d.	
r	within winter region	-0.41	-0.81	0.38	0.37	-0.64	-0.75	-0.48	0.11	10
	within breeding sector	-0.27	-0.63	0.11	0.26	-0.38	-0.76	-0.006	0.21	12
B	within winter region	-0.54	-1.3	-0.04	0.37	-0.62	-1.00	-0.40	0.2	10
	within breeding sector	-0.10	-0.28	0.06	0.1	-0.24	-0.50	-0.07	0.15	12

were not significantly contributing to the model here yielded model 3b (table 2) that included ocean, mountain, coast (of the entry link) and Arctic Ocean as independent variables. Two of the variables in model 3b thus refer to the entry part of migration and two to the remaining part of the total migration link. Furthermore, the explanatory power of this model (27%) exceeded that of models 1b and 2b, showing that the entry parts of links do not alone account for all of the barrier effect on species occupancy because there are also important barrier elements associated with the remaining parts of the total links (table 2).

(d) Winter region versus breeding region perspective

The negative relationships between species occupancy and total distance and barrier as calculated within each separate winter region (winter region perspective) are generally stronger than the corresponding relationship within each separate breeding sector (breeding area perspective). This holds for both total links and entry links (table 3; figure 4). The mean correlation coefficients and the mean slopes for the linear regressions between both species occupancy and sum barrier extent as well as species occupancy and total distance show much stronger negative relationships for the winter region perspective than for the breeding sector perspective. In general, within each of the different winter regions, the number of species using the migratory links tends to decrease sharply with increased total distance of the potential links (figure 4a). On average, within winter regions the number of species drops by 0.54 for an increase of 1000 km in total distance of migratory links (table 3; figure 4a). However, this decline occurs at widely different absolute distances for the different winter regions, giving as a result a lack of significant overall correlation with total distance when species occupancy is analysed across all winter regions (cf. table 1; figure 3a). In contrast, when considering the relationships of species occupancy versus total distance within the different breeding sectors, the number of populations is generally declining very slowly or not at all with the total distance of the potential links (figure 4b). On average, the decline is only 0.10 species per 1000 km increase in distance (table 3), over approximately the same distance ranges between 5000 and 15 000 km for the different breeding sectors (figure 4b). The differences in regression coefficients between the winter region and breeding region perspectives are statistically significant for

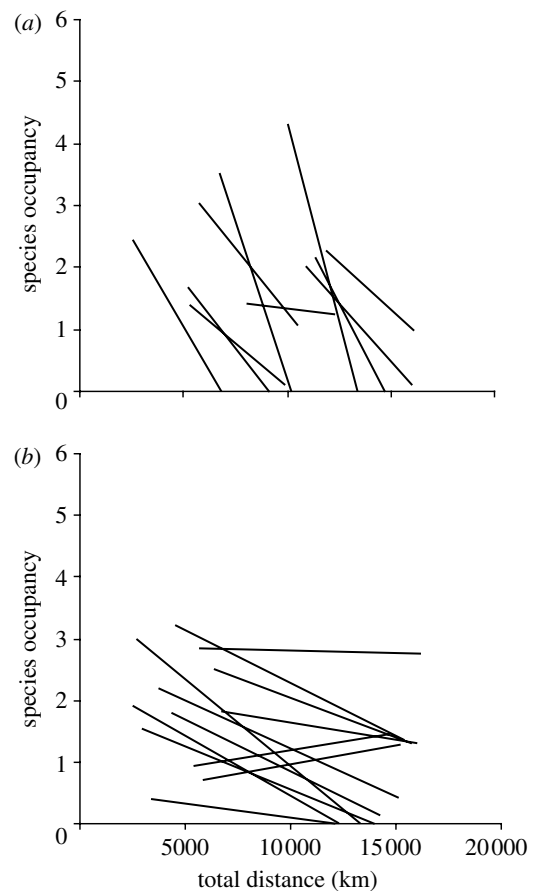


Figure 4. Linear relationships between species occupancy and total distance for (a) links from the same winter region (10 different winter regions; 10 regressed lines) to all 12 tundra sectors and for (b) links from the same tundra sector (12 different tundra breeding sectors; 12 regression lines) to all 10 winter regions.

both the relationship of species occupancy versus total distance and that of species occupancy versus sum barrier distance (Mann-Whitney U -tests $p < 0.01$ for both total distance and sum barriers; cf. table 3).

4. DISCUSSION

Our results show that there is no distinct overall effect of total distance on the utilization of migratory links for the arctic shorebirds (figure 3a; table 1a). We had expected that links involving shorter overall flight distances, and

thereby lower cost of migration, would have evolved more frequently, and that the number of species using a link would decline with increased distance.

A possible interpretation of these results is that some birds have much to gain from wintering in regions further south. For many birds, the advantage of spending the winter in austral summer conditions apparently outweighs the extra cost of the long migratory journey. Hence, there is a trade-off situation such that a bird can either choose to spend the winter on northerly wintering grounds and experience less benign winter survival conditions yet have the advantage of short migration with early arrival both at the breeding ground (Drent *et al.* 2003) and at the wintering ground (Salomonsen 1955). Alternatively, a bird can choose to over-winter in the southern hemisphere and enjoy the austral summer resource peak at these latitudes and thereby increase winter survival probability while perhaps also being relieved of some of the competition pressure they would otherwise have experienced from other migrants and residents at more northerly winter sites. In return, these birds have to adapt their annual time, energy, and safety budget to cope with the increased migration costs. Because of this trade-off between long- and short-distance migration, the migratory patterns of the Arctic shorebird system may reflect a balance, ultimately competition driven (Salomonsen 1955), between the different wintering scenarios which result in a fairly even representation of populations in all categories of migration distances.

In contrast to the lack of correlation between connectivity and total distance, there is a distinct negative correlation between connectivity and the amount of ecological barriers encountered along a direct route of that link. That is to say, links that are interrupted by extensive segments of open oceans and, to lesser degree, mountain ridges and glaciers are less likely to become established than links with a geographic configuration primarily along coasts or across lowlands (tables 1a and 2).

Essentially, there are three main potential explanations behind the distinct negative effects of ecological barriers on migration links. Links would not be expected to evolve across barriers if (i) the distances of the barrier crossings exceed the birds' theoretical flight range. In our analysis however, this factor cannot account for much of the avoidance of ecological barriers, as most of these barriers entail distances well within the possible flight ranges of the shorebirds (Gudmundsson *et al.* 1991; Hedenström & Alerstam 1992; Pennyquick & Battley 2003). As a matter of fact, only 15 of the 120 links contain a continuous barrier of more than 5000 km (the longest continuous barrier measured is a 7740 km stretch over the Atlantic Ocean between northeast South America and Iceland). Links entailing large barriers may evolve less frequently also because of (ii) the extra time, energy and safety costs of transporting large fuel loads required for barrier crossing (or the extra time, energy and safety cost associated with increased distance of detours; Alerstam 2001). However, this seems somewhat paradoxical considering that, as discussed above, the extra costs associated with long distance migration apparently do not constrain the evolution of migration links for these birds. This indicates that barriers involve costs that do not merely correspond to an added distance but may be of a qualitatively different kind. Perhaps more importantly

(iii) there may be particular evolutionary constraints to the establishment of migration routes across or around ecological barriers. In contrast to mere extensions of the total migratory distance, extensive non-stop flights across different types of barrier require particular physiological and behavioural adaptations (e.g. ability to store and carry large fuel loads, ability to cope with extreme temperature conditions or extreme altitudes etc.) and detours may require particular adaptations to orientation programmes (Gwinner & Wiltchko 1978; Berthold 1993; Gwinner 1996; Alerstam *et al.* 2003).

The barrier effect is exceptionally pronounced in the northern parts of the links close to the breeding regions, i.e. the Arctic Ocean appears to contribute substantially as a barrier in preventing certain links becoming established (tables 1b and 2). It is surprising that a possible winter region that is located on the opposite side of the pole with respect to a certain Arctic sector is never occupied by birds from that sector even if the total distance is shorter than to some of the winter regions that are occupied and that lie on the same side of the pole. For the 120 potential links, only one is occupied that connects a region in the Arctic with a winter region located at the opposite side of the pole and furthermore, among the species considered in this analysis, only one species is represented in this link (figure 2a). This highly unusual case is that of the central Siberian populations of *Calidris melanotos*, where at least the majority of the birds seem to still migrate to their ancestral winter quarters in southern South America (Mead 1983; Haig *et al.* 1997; Sutherland, 1998). However, there are also other known cases of extensive barrier flights in the Arctic region. For example, a link across the Greenland icecap, used by at least three species of shorebirds (*C. canutus*, *Arenaria interpres*, *Charadrius hiaticula*) between the Canadian Arctic and Iceland and northwest Europe, is indicative of the capability of some migrants to traverse extensive and severe barriers when this is adaptive.

Gudmundsson & Alerstam (1998a) conducted tracking radar studies of transpolar bird migration in the central polar basin during the summer of 1996. They observed, in stark contrast to the peripheral areas of the Arctic Ocean, an absence of bird migration from the zone near the North Pole. Their observations confirm the patterns of migratory connectivity that are revealed for the shorebird system in our present study (figure 2a,b). As pointed out by Gudmundsson & Alerstam (1998a), there is, with the present geographic configuration of continents, no tundra sector where the nearest potentially suitable winter region is associated with a transpolar route. However, as there are populations that travel to the southern hemisphere beyond seemingly potential options located much closer, the distance factor does not provide the full explanation. As discussed earlier, evolution might favour migratory routes that avoid extensive and costly non-stop flights, which require special temporary physiological and behavioural adaptations. Arctic Ocean crossing in particular may be an unfeasible option, as the tundra environment may not provide the resources required for such a feat. In addition to being of little evolutionary value for birds to perform trans-Arctic Ocean migrations, Gudmundsson & Alerstam (1998a) proposed that severe orientation complications in regions close to the North Pole may provide yet another explanation to the negligible

migratory activity observed across the Arctic Ocean interior.

It appears from the present analysis that the migration segments that link the breeding grounds with the last and first northernmost stopover site in spring and autumn respectively, generally have had disproportionately large effects on the migration connectivity (tables 1 and 2). This is surprising as the entry links usually constitute relatively small segments of the total routes (with the exception of some of the links connecting the west European winter regions with certain tundra areas where the northernmost stopover sites are in or near the Wadden Sea, and where the 'entry route' therefore equals the total route). The mean proportion of the entire links that are entry segments is 40% (the proportions range between 6 and 100% for the 120 different migratory links in this analysis).

Much research on avian migration stresses the particular importance of the quality and location of the last stopover site on the birds' arrival condition at breeding grounds and subsequent breeding success (e.g. Alerstam *et al.* 1986; Farmer & Wiens 1999; Drent *et al.* 2003). Our results support the possible key importance of these staging sites and their function in providing entry and exit to and from the tundra zones.

The asymmetry regarding distance and barrier effects between breeding region perspective and winter region perspective in this analysis is probably reflecting the effect of the Arctic Ocean barrier in particular. Of the 12 links from one and the same winter region to the different sectors in the Arctic, the links with the longest distances are always those connecting to the sectors on the remote side of the Arctic Ocean. As discussed earlier, there is a connectivity pattern that is essentially devoid of migratory links between winter regions and tundra sectors on the opposite side of the North Pole (figure 2). Because of this, negative relationships between both total distance and the summed barrier distances emerge prominently when links from each winter region are considered separately, but are deflated when links are considered from a breeding sector perspective. The fact that occupied links from a breeding sector do not include extensive Arctic Ocean crossings but still vary in both total distance and extent of other barriers, supports the conclusions that total distance in itself is less important for the establishment of the shorebird migration links and that there are particular evolutionary constraints associated with migration across the Arctic Ocean.

According to this view the migratory connectivity for the shorebirds is thus adapted to present day topography and geography of the continents. An alternative possibility is that historical climatic events such as the cycles of Quaternary glaciations have influenced the establishment of present migration routes (Engelmoer & Roselaar 1998; Moreau 1972; Williams & Webb 1996). The links from one breeding region may be associated with particular winter regions even if these are somewhat suboptimal under present day schemes both because of genetic constraints slowing down migratory direction change (e.g. contemporary populations trace ancestral routes; Kerlinger 1995) or social constraints (e.g. populations expand into new areas and acquire, by social transference, the migration routes already established by the native populations at a time when conditions were different). As the shorebirds' tundra breeding zone probably underwent more dramatic changes during glacial and interglacial

periods compared to their winter habitat on lower latitudes, there is a possibility that historical factors may thus provide an additional explanation why links appear to be more adaptive from a winter region perspective than from a breeding region perspective.

The major northernmost stopover sites, because of their critical importance in providing access for the shorebirds to the tundra breeding regions, are of great conservation concern especially in the light of future climate change and other rapid habitat deteriorations. Rapid climatic changes are thus not only a threat to the shorebird populations on the tundra breeding grounds but may also affect the migratory stopover sites with severe consequences for the migratory connectivity patterns in the Arctic.

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REFERENCES

- Alerstam, T. 2001 Detours in bird migration. *J. Theor. Biol.* **209**, 319–331. (doi:10.1006/jtbi.2001.2266.)
- Alerstam, T. & Lindström, Å. 1990 Optimal bird migration: the relative importance of time, energy, and safety. In *Bird migration: the physiology and ecophysiology* (ed. E. Gwinner), pp. 331–351. Berlin: Springer.
- Alerstam, T., Hjort, C., Högstedt, G., Jönsson, P. E. & Karlsson, J. 1986 Spring migration of birds across the Greenland inland ice. *Meddelelser om Grønland, Bioscience* **21**, 1–38.
- Alerstam, T., Hedenström, A. & Åkesson, S. 2003 Long distance migration: evolution and determinants. *Oikos* **103**, 247–260. (doi:10.1034/j.1600-0706.2003.12559.x.)
- Bensch, S. 1999 Is the range size of migratory birds constrained by their migratory program? *J. Biogeogr.* **26**, 1225–1235. (doi:10.1046/j.1365-2699.1999.00360.x.)
- Berthold, P. 1993 *Bird migration: a general survey*. Oxford, UK: Oxford University Press.
- Brown, H. H., Stevens, G. C. & Kaufman, D. M. 1996 The geographical range: size, shape, boundaries and internal structure. *Annu. Rev. Ecol. System.* **27**, 597–623. (doi:10.1146/annurev.ecolsys.27.1.597.)
- Böhning-Gaese, K., Gonzales-Guzman, L. I. & Brown, J. H. 1998 Constraints on dispersal and the evolution of the avifauna of the Northern Hemisphere. *Evol. Ecol.* **12**, 767–783. (doi:10.1023/A:1006538414645.)
- Cox, C. B. & Moore, P. D. 2000 *Biogeography an ecological and evolutionary approach*, 6th edn. Oxford, UK: Blackwell Science Ltd.
- Drent, R., Both, C., Green, M., Madsen, J. & Piersma, T. 2003 Pay-offs and penalties of competing migratory schedules. *Oikos* **103**, 274–292. (doi:10.1034/j.1600-0706.2003.12274.x.)
- Engelmoer, M. & Roselaar, C. S. 1998 *Geographic variation in waders*. Dordrecht, the Netherlands: Kluwer Academic Publishers.
- Farmer, A. H. & Wiens, J. A. 1999 Models and reality: time–energy trade-off in pectoral sandpiper (*Calidris melanotos*) migration. *Ecology* **80**, 2566–2580.
- Fujita, G., Hong-Liang, G., Ueta, M., Goroshko, O., Krever, V., Ozaki, K. & Mita, M. 2004 Comparing areas of suitable habitats along travelled and possible shortest routes in migration of white-naped cranes *Grus vipio* in East Asia. *Ibis* **146**, 461–474. (doi:10.1111/j.1474-919X.2004.00286.x.)

- Gudmundsson, G. & Alerstam, T. 1998a Why is there no transpolar bird migration? *J. Avian Biol.* **29**, 93–96.
- Gudmundsson, G. & Alerstam, T. 1998 Optimal map projections for analysing long-distance migration routes. *J. Avian Biol.* **29**, 597–605.
- Gudmundsson, G., Lindström, Å. & Alerstam, T. 1991 Optimal fat loads and long-distance flights by migrating knots *Calidris canutus*, sanderlings *Calidris alba* and turnstones *Arenaria interpres*. *Ibis* **133**, 140–152.
- Gwinner, E. 1996 Circadian and circannual programmes in avian migration. *J. Exp. Biol.* **199**, 39–48.
- Gwinner, E. & Wiltchko, W. 1978 Endogenously controlled changes in migratory direction of the garden warbler *Sylvia borin*. *J. Comp. Physiol.* **125**, 267–273. (doi:10.1007/BF00656605.)
- Haig, S. M., Gratto-Trevor, C. L., Mullins, T. D. & Colwell, M. A. 1997 Population identification of western hemisphere shorebirds throughout the annual cycle. *Mol. Ecol.* **6**, 413–427. (doi:10.1046/j.1365-294X.1997.t01-1-00203.x.)
- Hedenström, A. & Alerstam, T. 1992 Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *J. Exp. Biol.* **164**, 19–38.
- Henningsson, S. S. & Alerstam, T. 2005 Patterns and determinants of shorebird species richness in the circum-polar Arctic. *J. Biogeogr.* **32**, 383–396. (doi:10.1111/j.1365-2699.2004.01204.x.)
- Houston, A. I. 1998 Models of optimal avian migration: state, time and predation. *J. Avian Biol.* **29**, 395–404.
- Irwin, D. E. & Irwin, J. H. 2005 Siberian migratory divides—the role of seasonal migration in speciation. In *Birds of two worlds—the ecology and evolution of migration* (ed. R. Greenberg & P. Marra), pp. 27–40. Baltimore, MD: Johns Hopkins University Press.
- Kerlinger, P. 1995 *How birds migrate*. Mechanicsburg, USA: Stackpole books.
- Kirkpatrick, M. & Barton, N. H. 1997 Evolution of species range. *Am. Nat.* **150**, 1–23. (doi:10.1086/286054.)
- Kraaijeveld, K. & Nieboer, E. N. 2000 Late quaternary paleogeography and evolution of arctic breeding waders. *Ardea* **88**, 193–205.
- Lank, D. B., Butler, R. W., Ireland, J. & Ydenberg, R. C. 2003 Effects of predation danger on migration strategies of sandpipers. *Oikos* **103**, 303–319. (doi:10.1034/j.1600-0706.2003.12314.x.)
- Marra, P. P., Hobson, K. A. & Holmes, R. T. 1998 Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**, 1884–1886. (doi:10.1126/science.282.5395.1884.)
- Mead, C. 1983 *Bird migration*. Fletham, UK: Country Life Books.
- Moreau, R. E. 1972 *The Palaearctic–African bird migration systems*. London: Academic Press.
- Morrison, R. I. & Myers, J. P. 1987 Wader migration systems in the New World. *Wader Study Group Bulletin* 49 Suppl. IWRB Special Publications 7, 57–69.
- Parish, D., Lane, B., Sagar, P. & Tomkowiak, P. 1987 Wader migration systems in east Asia and Australasia. *Wader Study Group Bulletin* 49 Suppl. IWRB Special Publications 7, 4–14.
- Pennyquick, C. J. & Battley, P. F. 2003 Burning the engine: a time-marching computation of fat and protein consumption in a 5420-km non-stop flight by great knots, *Calidris tenuirostris*. *Oikos* **103**, 323–332. (doi:10.1034/j.1600-0706.2003.12124.x.)
- Pielou, E. C. 1979 *Biogeography*. New York: Wiley.
- Piersma, T., Beintema, A. J., Davidson, N. C., Munster, O. A. G. M & Pienkowski, W. 1987 Wader migration systems in the East Atlantic. *Wader Study Group Bulletin* 49 Suppl. IWRB Special Publications 7, 35–56.
- Salomonsen, F. 1955 The evolutionary significance of bird-migration. *Dan. Biol. Medd.* **22**, 1–62.
- Summers, R. W., Underhill, L. G., Pearson, D. J. & Scott, D. A. 1987 Wader migration systems in southern and eastern Africa and western Asia. *Wader Study Group Bulletin* 49 Suppl. IWRB Special Publications. 7, 15–34.
- Sutherland, W. J. 1998 Evidence for flexibility and constraints in migration systems. *J. Avian Biol.* **29**, 441–446.
- Wetlands International RSDB 2001 The Ramsar site database on wetlands of international importance as listed on the convention of Ramsar 1971. (<http://www.wetlands.org/RSDB/>.)
- Williams, T. C. & Webb III, T. 1996 Neotropical bird migration during the ice age: orientation and ecology. *Auk* **113**, 105–118.
- Williams, T. C. & Williams, J. M. 1991 The orientation of transoceanic migrants. In *Bird migration: the physiology and ecophysiology* (ed. E. Gwinner), pp. 7–21. Berlin: Springer.

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