ORIGINAL ARTICLE

Does the migration programme constrain dispersal and range sizes of migratory birds?

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ABSTRACT

Aim It is generally believed that the migration programme constrains the dispersal and hence range sizes of migratory bird species. This conclusion is based on analyses of breeding ranges of migratory versus non-migratory (resident) terrestrial bird species, and rests on the assumption that there are no ecological or evolutionary constraints on extending the non-breeding range. To investigate this assumption, the abilities of migrant and resident terrestrial species to colonize new wintering areas were compared.

Location Three major wintering regions of long-distance migrants: South America, sub-Saharan Africa and the Indian Subcontinent.

Methods It was determined whether the relative numbers of residents and short- and long-distance migrants were the same in those species that have dispersed to a novel wintering region as in the source species pools.

Results At the species level, long-distance migratory species are more likely to have non-breeding ranges that include more than one of the above regions than resident species. This indicates that the dispersal of migratory species is less constrained than that of resident species. The pattern holds irrespective of the inclusion or exclusion of species associated with coastal, freshwater and wetland habitats, and also holds for ecological groups such as aerial feeders. The pattern is most pronounced between the regions separated by the strongest dispersal barriers (South America and sub-Saharan Africa).

Main conclusions It is unlikely that the migration programme *per se* constrains dispersal, but rather that difficulties in establishing new non-breeding areas prevent range expansions in migrant species.

Keywords

Birds, constraints, dispersal, migratory orientation programme, range size, wintering areas.

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INTRODUCTION

Much research has been devoted to investigating the determinants of species ranges and patterns of species richness (e.g. Gaston & Blackburn, 2000; Whittaker *et al.*, 2001). Evolutionary and ecological processes over a wide range of spatial and temporal scales are involved in shaping present biogeographical patterns (Rosenzweig, 1995; Willig *et al.*, 2003). Central in understanding these processes are the interactions between organisms and their environment (Brown, 1995).

The capability of flight makes birds one of the most mobile terrestrial organisms, enabling a few bird species to travel more

than 20,000 km annually. Many migrating birds travel thousands of kilometres each year from their breeding to wintering areas and back, crossing deserts, mountains and seas. Even though the ranges of individual bird species cover vast expanses in this way, well-differentiated bird faunas exist on the major land masses, indicating that constraints are still acting on dispersal.

The range size of a species may be limited by ecological factors, for example when a species is unable to sustain itself in a given habitat, and by evolutionary factors, for example when a species is constrained from evolving specific adaptations (Kirkpatrick & Barton, 1997). Several studies indicate that the

migration programme of birds constrains the ability of avian taxa to disperse: a smaller proportion of migratory than resident species are distributed in both Europe and North America (Böhning-Gaese et al., 1998). Palaearctic migratory species are less likely than non-migratory (resident) species to have a range including both Scandinavia and Eastern Siberia (Bensch, 1999). Price et al. (1997) suggested habitat tracking of areas rendered inhospitable during the Pleistocene as a factor determining colonization success, and further suggested a role of geographic barriers and biotic interactions in preventing some taxa from spreading from small southern ranges. Furthermore, Henningsson & Alerstam (2005) found that the diversity of possible flyways affects species richness, and linked this to possible intrinsic constraints on the evolution of migration programmes. Bensch (1999) concluded that 'the relatively low colonization success of migratory species into new breeding areas may be because these new areas require novel migratory programmes (migratory distance, direction and timing) for the birds to reach suitable wintering grounds'.

These findings may seem surprising, since evolution of migratory behaviour can occur very rapidly, as demonstrated in several cases by observations of changes in the propensity to migrate, changes in migration period and distance, and novel migration directions and winter quarters (Berthold, 1996). A novel migratory direction and winter quarter has been suggested for the apparently increased wintering population of blackcaps Sylvia atricapilla in Britain. Orientation tests of birds in cages show the genetic basis of this change and suggest that it is based on microevolutionary processes (Berthold et al., 1992; Helbig et al., 1994).

Studies investigating the constraints on long-distance dispersal have considered large areas of relatively homogenous habitat in the Northern Hemisphere. Birds may be considered to range more freely in the non-breeding period, since they are not restricted by the need to find mates. However, the differences between the wintering regions for long-distance migrants, mainly South America, Africa and Asia, in habitat and interactions (e.g. competition, predators, diseases and parasites), and the strong barriers for dispersal between the regions have not been taken into account. Thus, regarding the role of the migration programme, these studies implicitly assume that these factors do not constrain expansion of the wintering range. In view of the likely evolutionary origin of most species with long-distance migration near or in the wintering area (e.g. Rappole, 1995; Helbig, 2003; Outlaw et al., 2003) it seems reasonable to bring the wintering distribution into focus.

The aim of this study is to test whether migrant species are less likely than non-migrant ones to have wintering ranges covering more than one region; that is, to show a lower propensity to colonize new regions. Data on the bird species occurring in South America, sub-Saharan Africa and the Indian Subcontinent in the non-breeding season are used, thus including both migratory species from more northerly areas and residents. Species occurring in more than one of these regions are then assumed to be evidence of dispersal from one

major wintering area to another (although the direction cannot be determined). If dispersal is equally likely in migratory and resident species, the same proportion of the various migratory categories (long- and short-distance migrant species and residents) should be expected in the species that disperse, i.e. occurring in more than one region, as in the presumed source species pool. To determine whether migratory behaviour constrains dispersal, I thus compare the proportions of long- and short-distance migrant species and residents in each major wintering region with the proportions in the shared species pools. The focus is on the species level, since migratory traits are highly labile (Helbig, 2003), and phylogenetic effects on migratory status were found to be insignificant and to explain less than 1% of interspecies variation in this trait (Böhning-Gaese & Oberrath, 1999).

MATERIALS AND METHODS

The species lists on regional avifaunas included all bird species from South America (Remsen et al., 2004), sub-Saharan Africa (Burgess et al., 1998) and the Indian Subcontinent (Grimmett et al., 1998). These lists also included information on species status, for example breeding, wintering or vagrant. To ensure the best overall consistency in comparisons, the taxonomy by Sibley & Monroe (1990) was used for all regions.

I only included species occurring regularly in the non-breeding season and frequenting non-pelagic habitat during this season (i.e. procellariiformes, some pelicaniformes, and some charadiiformes were excluded; Sibley & Monroe, 1990). Vagrants and species occurring on passage only were excluded. Thus, I included both non-migratory species that have established breeding populations in one or more of the regions and migratory species for which individuals regularly spend the non-breeding (wintering) season in at least one region. I refer to the non-migratory species as residents and to the migratory species as migrants.

Since barriers may be conceived differently by species associated with aquatic environments and their ecological requirements are distinctly different, Böhning-Gaese et al. (1998) and Bensch (1999) performed their analysis primarily on terrestrial taxa. To ease comparisons between this study and their studies, I performed an additional analysis on a data set for which families primarily associated with marine, freshwater or wetland habitats (geese, ducks, cranes, finfoots, waders, terns, gulls, rails, grebes, cormorants, pelicans, storks) were excluded. To control for the effect of including large and diverse groups with different dispersal capabilities and ecological requirements, I also performed the analyses on the groups that had the largest number of species in common between regions (strictly aerial feeders: swallows, swifts and nightjars).

The migratory status of each species was assigned to one of three categories: (1) long-distance migrants, (2) short-distance migrants, or (3) residents. Using breeding distributions according to Sibley & Monroe (1990), Poole (1992–2002), Flint et al. (1984) and Cramp (1977–94) species were defined as long-distance migrants when individuals from a major part

of the breeding distribution cross or circumfly (e.g. along a land bridge) a significant barrier, such as the Gulf of Mexico, the Mediterranean and the Sahara, the semi-deserts of Turkestan or the Himalaya and the Tibetan Plateau, to reach one of the wintering regions considered (Fig. 1). In short-distance migrants, there was no major part of the breeding distribution from where individuals cross or circumfly such barriers. In residents, no major addition of individuals in the year-round resident non-breeding population occurred. If for one species the category differed between regions, the species was assigned to the longest distance category.

In order to test whether the relative numbers in the various migratory categories in a shared species pool was different from the relative numbers in the potential source species pool, simple chi-square tests were used.

RESULTS

In total, 5662 non-pelagic species, including 266 long-distance and 194 short-distance migrant species, occurred regularly in the non-breeding season in the three regions. The relative number of species occurring in the different migratory categories was not equal ($P < 0.001$) in the different regions (Table 1, Fig. 2). The highest proportion of migratory species occurred on the Indian Subcontinent, there was a smaller proportion in Africa, and South America had the smallest proportion. For the shared species pools between South America and Africa and between Africa and India, a larger number of migrant species occurred than expected from their respective source species pools in the neighbouring major wintering area ($P < 0.001$ for all four pairwise comparisons between shared and source species pools). Thirty-six species

Table 1 Long- and short-distance migrant and resident species (as defined in the text) spending the non-breeding season in each major region (South America, sub-Saharan Africa and the Indian Subcontinent) including those occurring in more than one region. 'South America & Africa': species occurring in both regions. 'Africa & India': species occurring in both of the regions.

	South America	South America & Africa	Africa	Africa & India	India
Full data set					
Long-distance	91	19	145	91	140
Short-distance	43	7	56	47	152
Resident	2742	10	1688	50	832
Data set exclusive of marine, freshwater and wetland species					
Long-distance	54	3	85	35	73
Short-distance	22	2	27	21	102
Resident	2558	1	1564	31	765
Swallows only					
Long-distance	5	2	4	4	4
Short-distance	2	0	1	1	1
Resident	15	0	39	3	9

were shared between South America and Africa, and 188 species were shared between Africa and India (Table 1). Among species classified as long-distance migrants, 18 species, namely the northern shoveler, *Anas clypeata*; northern pintail, *Anas acuta*; common snipe, *Gallinago gallinago*; red knot, *Calidris canutus*; sanderling, *Calidris alba*; whimbrel, *Numenius phaeopus*; ruddy turnstone, *Arenaria interpres*; grey plover, *Pluvialis squatarola*; gull-billed tern, *Sterna nilotica*; Caspian
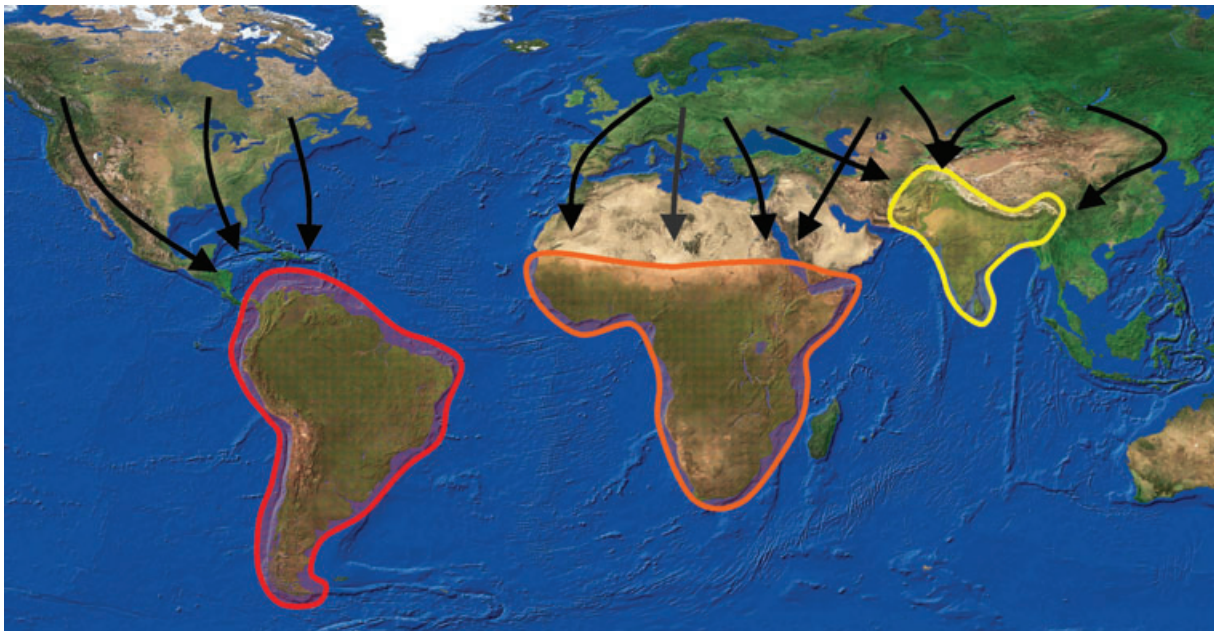

Figure 1 The three major wintering areas considered (South America, sub-Saharan Africa and the Indian Subcontinent), geographical barriers (sea, desert and mountain), and the major flyways (arrows) followed by migratory birds to reach these wintering areas.
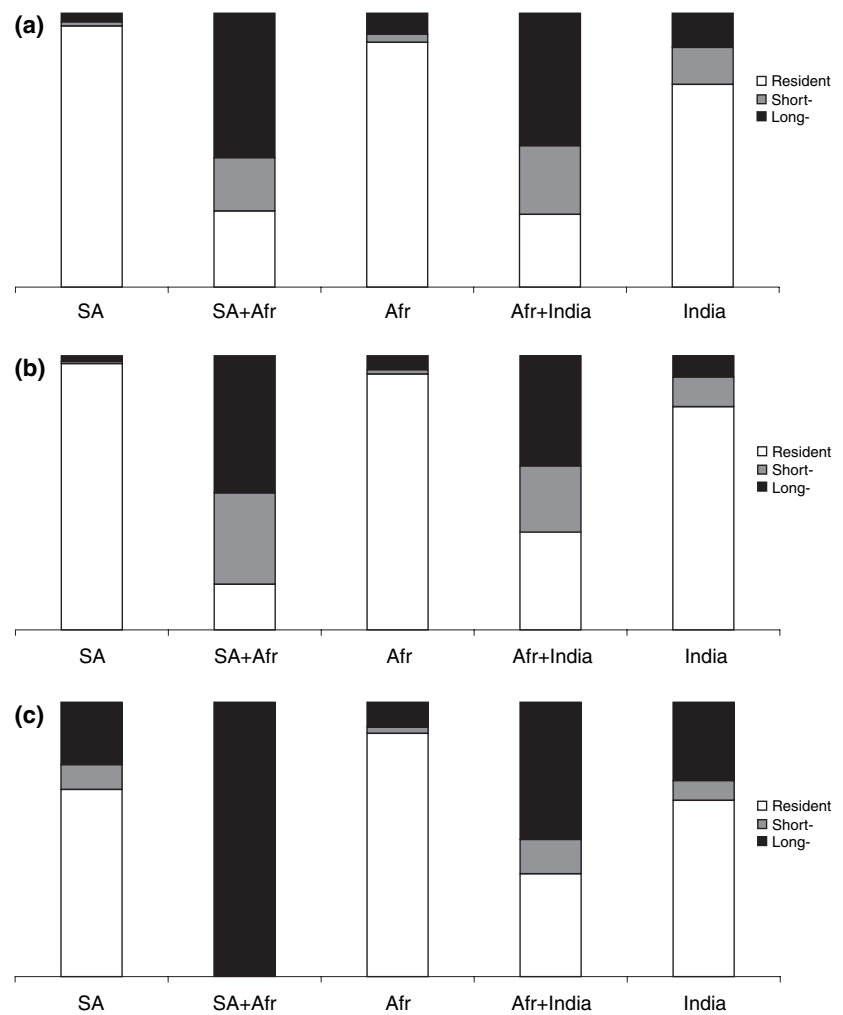
Figure 2 The proportions of the wintering bird community consisting of resident, short- and long-distance migrants for the three continents, South America (SA), sub-Saharan Africa (Afr) and the Indian Subcontinent (India). (a) All species, (b) excluding bird families that primarily use marine, coastal, freshwater and wetland habitats, and (c) swallows only. SA + Afr: species occurring in both SA and Afr; Afr + India: species occurring in both Afr and India. In (a) and (b), the level of probability that the observed proportions of long- and short-distance migrants and residents in a shared group (SA + Afr or Afr + India) are the same as those in any of the two neighbouring major species pools is less than 0.001 (chi-square test).

tern, *Sterna caspia*; sandwich tern, *Sterna sandvicensis*; common tern, *Sterna hirundo*; roseate tern, *Sterna dougallii*; osprey, *Pandion haliaetus*; black-crowned night-heron, *Nycticorax nycticorax*; glossy ibis, *Plegadis falcinellus*; barn swallow, *Hirundo rustica*; and sand martin, *Riparia riparia*, occurred in all three regions. Five short-distance migrants, namely the short-eared owl, *Asio flameus*; Kentish plover, *Charadrius alexandrinus*; peregrine falcon, *Falco peregrinus*; great egret, *Casmerodius albus*, and greater flamingo, *Phoenicopterus ruber*, also occurred in the three regions. Furthermore, six resident species, namely the fulvous whistling-duck, *Dendrocygna bicolour*; comb duck, *Sarkidiornis melanotos*; barn owl, *Tyto alba*; common moorhen, *Gallinula chloropus*; cattle egret, *Bubulcus ibis*; and striated heron, *Butorides striatus*, occurred in all three regions. One additional resident species, the rock pigeon, *Columba livia*, also occurred in all three regions, but its occurrence in South America stems from escaped feral birds.

Very similar results were obtained when only terrestrial species were included (Fig. 2b). The proportion of migrants was a little lower for all species pools, but the difference between the shared species pools and the source species pools even larger ($P < 0.001$ for all four pairwise comparisons). The same patterns were found for strictly aerial feeders, with a larger proportion of migrants than residents found in two wintering regions (Fig. 2c for swallows only).

DISCUSSION

The results indicate that migrants have a higher propensity to colonize new wintering areas than residents. The number of colonizations, as seen by shared wintering grounds, is relatively small, however, and it could indicate that the colonization of new non-breeding areas is nevertheless a major constraint on the breeding-range sizes of birds from the tropics and the subtropics.

The opposite pattern is seen in the breeding areas of the Northern Hemisphere, where migrants have a lower propensity to colonize new breeding grounds than residents (Böhning-Gaese *et al.*, 1998; Bensch, 1999). There are pronounced differences in the conditions affecting dispersal for species from the tropics and the subtropics compared with those in the more northerly breeding areas, and these differences may explain a large part of the differences in observed patterns. Large areas of continuous habitat are found at high latitudes (Breckle, 2002), and the land-bridge between North America and Eurasia is relatively recent compared with the long

isolation between the wintering regions considered (Brown & Gibson, 1983). Thus, there are limited barriers for dispersal at high latitudes. In contrast, strong barriers exist between the wintering regions considered and between these regions and associated breeding grounds for migrants. Breeding ranges of birds originating in the tropics and the subtropics may be limited by a combination of feasible migration distances, lack of habitat and possible competition. Furthermore, the need to find mates may restrict dispersal to new breeding areas, as, for example, vagrants will not often be able to reproduce successfully. Overall, however, the higher propensity in migrants to colonize new non-breeding ranges across strong barriers makes it unlikely that the migratory programme *per se* constrains dispersal.

Major shifts in location and plant composition have occurred in the possible breeding habitat of birds in the Northern Hemisphere. Migrating species are supposed to have tracked these changes (Williams & Webb, 1996; Price *et al.*, 1997). Furthermore, Böhning-Gaese *et al.* (1998) showed that more migrant species than residents had north–south distributions. This points to a likely scenario for dispersal from the tropical and subtropical breeding regions, where migrants are presumed to originate from (e.g. Rappole, 1995; Helbig, 2003; Outlaw *et al.*, 2003). Dispersal to new breeding areas is facilitated when the non-breeding and breeding habitats are the same. However, when migratory behaviour is developed, the probability of finding new non-breeding areas increases, although probably mostly for species that are more or less nomadic in the non-breeding season, a behaviour that may in itself be a precursor for the development of migratory behaviour (e.g. Berthold, 1996).

Relatively more open country/aerial feeding species occur in more than one wintering region compared with the total sample of terrestrial species. These species are typically day migrants with presumably often nomadic lifestyles (e.g. swallows, wagtails, raptors, swifts), and they are probably less dependent on local community interactions. Since migratory behaviour may facilitate gene flow (e.g. Helbig, 2003), restricting local adaptations and thus preventing dispersal to new areas (Kirkpatrick & Barton, 1997), it may be important for migratory species to be less specialized to local factors in order to facilitate dispersal to new regions. However, migratory species with presumably more specialized requirements, such as cuckoos, are also found in more than one wintering region. Interestingly, most of the examples of species groups in which more residents than long-distance migrants occur in more than one region (e.g. owls) are phylogenetically old groups (Sibley & Ahlquist, 1990). For some of these species the occurrence in more regions could be the result of vicariance events, in some cases possibly involving overlooked cryptic species.

For many resident species, difficulties in reaching new areas may limit ranges. Resident species typically have less intraspecific gene flow than migrant species (Helbig, 2003), which will facilitate the local adaptations necessary for dispersing to new

areas (Kirkpatrick & Barton, 1997). However, this will presumably also make them more prone to evolve into new species when spreading between continents, a process that could potentially confound the interpretation of the observed pattern.

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