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ORIGINAL ARTICLE

Bird migration on Helgoland: the yield from 100 years of research

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Abstract The island of Helgoland (or Heligoland; in the North Sea) was the very first place on Earth to be the focus of systematic studies on bird migration (since the mid-nineteenth century). The "Vogelwarte Helgoland" was founded in 1910, and since 1909 more than 800,000 birds have been ringed. Most of these are nocturnally migrating songbirds that cross the German Bight in a broad front on their way to or from their Scandinavian breeding grounds. In good weather conditions (tail winds, clear sky), the majority of the migrants does not land on Helgoland, but deteriorating weather strongly increases their attraction to this island. Wind can cause rare birds such as raptors and continental landbirds to be blown offshore or pelagic seabirds to be blown into the German Bight, where they can drift to Helgoland. Migrants stay for hours to weeks, depending on species, age, sex, body condition, season, weather, food availability, intra- and interspecific competition, and predation pressure. The direction of departure also appears to be influenced by body and weather conditions. The reported circumstances for the almost 7,000 recoveries have changed substantially over the last 100 years, and show definite regional differences. Indices from constant-effort trapping reveal decreased numbers of long-distance migrants, while numbers of short/medium-distance migrants have not changed much. In all "true migrants," the mean spring passage time has become earlier since 1960 (by up to 18 days). Whereas changes in autumn are less uniform, the time between both periods has increased in most species. This earliness in spring is best explained by local temperatures in short/medium-distance migrants, and by the winter NAO index in long-distance migrants.

Keywords Bird migration · Island · Ringing · Weather · Climate change · History

Introduction

Remote islands along migration flyways often attract and concentrate large numbers of birds that are looking for stopover sites, but also ornithologists who are interested in bird migration, as well as lots of birders (e.g., Clarke 1912; Moore et al. 1990; Pyle et al. 1993; Berthold 1996; Newton 2008; Archer et al. 2010). This also holds for the tiny island of Helgoland (or Heligoland) in the south-eastern North Sea (Gätke 1895; Vauk 1972; Dierschke et al. 2011). Actually, Helgoland was the very first place on Earth to be the subject of systematic studies on bird migration (Newton 2008; Vaughan 2009; Archer et al. 2010; Møller et al. 2010), long before the "Vogelwarte Helgoland" was founded on Helgoland in 1910. However, considering that 2010 was the centenary of the Institute of Avian Research, as the "Vogelwarte Helgoland" has been called since its move to the mainland in Wilhelmshaven after the Second World War (Bairlein and Becker 2010), we will focus here mainly on the results of studies carried out on the island by the institute since 1910. Special emphasis will be placed on the long-term, year-round trapping routine that has been performed under standardized conditions for the last 50 years.

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The location

The island of Helgoland (54° 11′N, 07° 53′E) is a Triassic red sandstone rock on top of a pillow of Permian salt masses (Spaeth 1990). It is 61 m high and some 45 km away from the next island or coast, respectively. Between 1890, when the formerly British island became German, and the Second World War it was altered by intensive fortification and harbor building, including considerable hydraulic sand filling. This caused the size of the island to increase from only 0.3 to 1 km^2. From 1944 to 1947, the surface of the unpopulated plateau changed from a planar to a cratered appearance due to bombing. Today, almost 30% of the island is built-up and inhabited by about 1,300 people. Trees and shrubs are restricted to the residential areas and to a few sites that are sheltered from storms, including the trapping garden of the Institute of Avian Research. The rest of the island is covered with pastures and meadows (Dierschke et al. 2011).

Just 1 km to the east lies a second, even smaller (0.7 km^2), island: the "Dune." It is based on the remnants of Triassic and Cretaceous limestone and other sediments that formed a second cliff of a similar size to that of the main island. Since limestone and gypsum are rare in the glacial landscape of northern Germany, this second cliff was used as a quarry and finally disappeared in a storm tide in 1711 (Spaeth 1990). Considerable hydraulic sand filling in the 1930s also enlarged the remains of this islet, which would probably have vanished otherwise. Today its landscape is characterized by dunes. It also houses a small airfield and infrastructure for tourism (Dierschke et al. 2011).

The beginning of ornithology on Helgoland

The first written notes on "incredible swarms of birds" on the small island go back the sixteenth century. For its inhabitants, the huge numbers of birds were a welcome supplement to their poor diets. Bird collectors became aware of the diversity of the island's birdlife sometime after the beginning of the nineteenth century, when a local cobbler started to sell bird skins to the first tourists to visit the recently founded seaside resort as well as to museums in Bremen and later Berlin. From the 1830s onwards, with increasing numbers of tourists came the first ornithologists to visit the island, not least because there where no restrictions on the shooting and trapping of birds there (Stresemann 1967; Bairlein and Becker 2010). Among them was Johann Friedrich Naumann, author of twelve famous volumes on the natural history of German birds (Naumann 1820–1844). In the foreword of the eleventh volume he wrote: "The island of Helgoland is of such great interest to German ornithology that it had to be mentioned very often in this opus." In 1846 he published an article on bird migration in which he highlighted that Helgoland is an excellent place for studying bird migration (Naumann 1846). Naumann already recognized that geography, changing temperatures, as well as wind and "weather" can cause "enormous deviations" in the directions of migrants from their usual paths.

In 1837, the painter Heinrich Gätke came to the island, and lived there for six decades until his death in 1897. Inspired by the hunters of the island, he became interested in collecting and observing birds, and started to write an ornithological diary in 1847. His famous book *Die Vogelwarte Helgoland*, published in 1891, was an groundbreaking opus that included detailed information on all birds observed on the island and summarized a great deal of knowledge on bird migration (namely on relations between migration and weather). An English version, *Heligoland as a Bird Observatory* (Gätke 1895), and a second (posthumous) German edition (1900) followed (Bairlein and Hüppop 1997; Vaughan 2009). The ornithological diary established by Gätke is continued to this day, although there are gaps in the diary due to the two World Wars.

Around 1880, the word "Vogelwarte" was created. It was presumably based on the older "Sternwarte" (an astronomical observatory), and thus emphasizes Gätke's enthusiastic bird-watching efforts (Ringleben 1958). Later, Gätke used this term for the title of his book, and in 1901 it was officially introduced with the founding of the "Vogelwarte Rossitten" by the German Ornithologists' Society on the Courish Spit in the former East Prussia (today part of Russia) in 1901 (Fiedler 2001).

1909 to 2010: more than 800,000 marked birds

A young and enthusiastic man named Hugo Weigold came to the island in 1909, where he was employed as a fish biologist at the "Königliche Biologische Anstalt Helgoland" (Bairlein and Becker 2010). However, he knew of Gätke's publications and observations, and seemingly considered himself to be more of a successor to Gätke, as he started his own ornithological diary right from the day of his arrival on Helgoland. After the introduction of systematic bird ringing by the Danish teacher H.C.C. Mortensen in 1899 (Berthold 2001; Bønløkke et al. 2006), more and more ringing schemes were established in Europe: birds were first ringed in 1903 in Rossitten, in 1908 in Hungary, and in 1909 on the British Isles and on Helgoland (Drost 1929). Together with August Thienemann from the "Vogelwarte Rossitten" (see above), Weigold performed the first bird ringing on Helgoland in October 1909 (Hüppop and Hüppop 2009; Bairlein and Becker 2010). He

used rings from Rossitten first, but used his own rings labeled "Helgoland Germania" from 1911 onwards. The number of birds ringed on Helgoland (Fig. 1) increased considerably from 1920 onwards, when Weigold introduced the use of the Helgoland funnel trap or "Helgoländer Trichterreuse" (Weigold 1922). His successor, Rudolf Drost (who worked on Helgoland from 1924 to 1944) further improved this trap, which is now used around the world at numerous bird observatories (e.g., Newton 2008; Archer et al. 2010). Drost also increased the number of ringed birds by catching them at the Helgoland lighthouse, which attracted huge number of them on foggy and misty nights (Drost 1925, 1928, 1960).

After an initially tentative start to the trapping and ringing of birds in the first quarter of the century, an average of about 6,400 birds were ringed per year in the following 20 years (Fig. 1). Song Thrush *Turdus philomelos*, Blackbird *Turdus merula*, and Redstart *Phoenicurus phoenicurus* were the most frequently trapped species in this period (Table 1). The ringing activity was then interrupted for 8 years due to the evacuation of the island at the end of the Second World War, but it was readopted in the year 1953 with about 1,500 birds that had already been trapped. A maximum in the number of trapped individuals was reached in 1976 (>26,000), and Song Thrush, Blackbird and Garden Warbler *Sylvia borin* were the species most frequently trapped during the second period (Table 1). In total, more than 800,000 birds were ringed on Helgoland from 1909 to 2010.

From the late 1930s onwards, most of the ringing took place in the trapping garden. Here, slightly more birds were trapped and ringed during autumn migration (56%) than throughout spring migration (43%), and less than 1% were trapped between the species-specific migration times (1960–2004, Hüppop and Hüppop 2007). 72% of all birds caught—mainly migrating songbirds that breed in Scandinavia (see below)—were short/medium-distance migrants (= SMD migrants), and 22% were long-distance migrants (= LD migrants). The vast majority of birds were forest birds (96%).

Although the conditions in the trapping garden with three funnel traps and standardized trapping effort have been almost constant from the early to mid 1960s, the ringing numbers have varied greatly over the last 50 years. The reasons for this are a ringing ban for some species in the 1960s, weather-related seasonal and annual fluctuations, and (in particular) substantial changes in the vegetation on the island since it was virtually free of vegetation after the Second World War: compared to the year 2000, when 91% of the vegetation on the main island was outside the trapping garden, in 1960 it was still almost completely restricted (98%) to the trapping garden (Hüppop and Hüppop 2007).

Ringing at the Helgoland lighthouse between the wars resulted in high numbers of ringed birds—up to 1,558 in asingle night (Drost 1928), while daily ringing in the trapping garden only exceptionally exceeded 500. Seabirds in the breeding colonies (Common Guillemot *Uria aalge*, Kittiwake *Rissa tridactyla*, Herring Gull and Lesser Black-backed Gull *Larus argentatus* and *fuscus*) as well as migrants that stop over at the island (gulls, waders, Northern Wheatears *Oenanthe oenanthe*) and breeding landbirds were trapped and ringed outside the trapping garden for special studies with other methods (e.g., Drost 1933; Vauk and Gräfe 1962; Prüter 1984; Bub 1985; Dierschke 1998; Dierschke and Delingat 2001; Sacher et al. 2006; Förschler et al. 2010).

In contrast to many other ringing stations, the trapping garden on the island of Helgoland is characterized by several special features. First, the island is the only stopover site for landbirds within a radius of almost 50 km, so high numbers of resting migrant birds concentrate here. Second, since very few land birds breed on Helgoland and almost no postbreeding dispersal reaches this isolated island, reliable statements about the actual migration of Scandinavian breeding birds—highlighting the species spectrum—can be made. Third, methods have been sufficiently standardized and effort has been constant and year-round throughout the last 50 years. Thus, the full extents of migration periods and winter movements can be

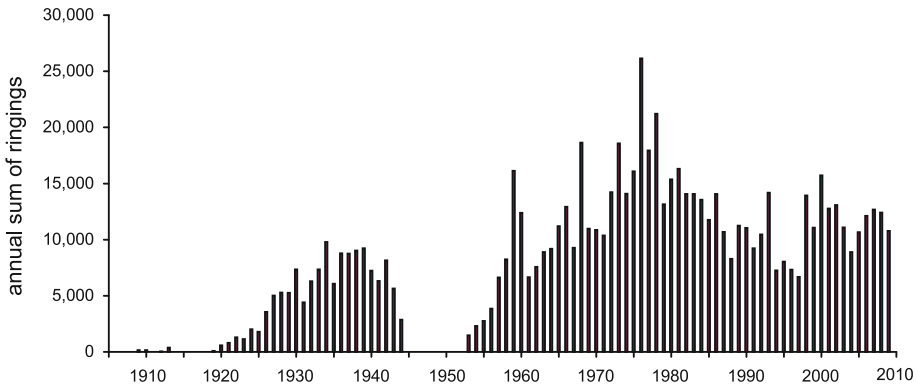

Fig. 1 Annual total numbers of ringed birds on Helgoland from 1909 to 2009 (n = 795,604)

Table 1 The ten bird species most frequently ringed on Helgoland before and after the Second World War, and the ten most frequently recovered species

Ringings from 1909 to 1945			Ringings from 1953 to 2009			Recoveries from 1909 to 2008		
Species	*n*	%	Species	*n*	%	Species	*n*	%
Song Thrush *Turdus philomelos*	21,458	15.9	Song Thrush *Turdus philomelos*	119,801	18.1	Blackbird *Turdus merula*	1,378	19.9
Blackbird *Turdus merula*	18,283	13.5	Blackbird *Turdus merula*	119,401	18.1	Song Thrush *Turdus philomelos*	1,091	15.8
Redstart *Phoenicurus phoenicurus*	16,050	11.9	Garden Warbler *Sylvia borin*	44,296	6.7	Guillemot *Uria aalge*	653	9.4
Starling *Sturnus vulgaris*	8,952	6.6	Robin *Erithacus rubecula*	40,663	6.2	Starling *Sturnus vulgaris*	375	5.4
Robin *Erithacus rubecula*	8,264	6.1	Chaffinch *Fringilla coelebs*	40,464	6.1	Chaffinch *Fringilla coelebs*	340	4.9
Chaffinch *Fringilla coelebs*	7,044	5.2	Willow Warbler *Phylloscopus trochilus*	27,213	4.1	Sparrowhawk *Accipiter nisus*	298	4.3
Willow Warbler *Phylloscopus trochilus*	5,526	4.1	Redstart *Phoenicurus phoen.*	27,208	4.1	Herring Gull *Larus argentatus*	269	3.9
Garden Warbler *Sylvia borin*	5,209	3.9	Redwing *Turdus iliacus*	26,925	4.1	Redwing *Turdus iliacus*	227	3.3
Whitethroat *Sylvia communis*	4,418	3.3	Blackcap *Sylvia atricapilla*	26,236	4.0	Woodcock *Scolopax rusticola*	169	2.4
Redwing *Turdus iliacus*	4,271	3.2	Dunnock *Prunella modularis*	22,810	3.5	Robin *Erithacus rubecula*	166	2.4
All species	134,935		All species	660,669		All species	6,914	

determined (Hüppop and Hüppop 2004). All of these circumstances result in the most substantial long-term constant-effort bird migration dataset in Europe.

Where do the birds come from, and where do they go to?

The main objective of bird ringing in its first few decades was to learn more about migration routes, the origins and the destinations of migrants (Schüz and Weigold 1931). Today, a total of about 7,000 recoveries of birds ringed on Helgoland (Fig. 2) cover 108 species (Hüppop and Hüppop 2009). Blackbird and Song Thrush have been the most frequent, with more than 1,000 individuals recovered for each species, followed by Guillemot, with more than 500 recoveries (Table 1; for maps of all species, see Dierschke et al. 2011). About 18% of all recoveries originate from the period between 1909 and the end of the Second World War. Between 1959 and 1985, the average number of recoveries reached 134 per year. Thereafter, numbers declined to an average of 82 recoveries per year.

More than 1,500 birds of 96 species ringed abroad were recovered on Helgoland between 1909 and 2008 (Fig. 2). Again, Blackbirds (275 recoveries) have been the most frequent, followed by Herring Gulls (197 recoveries) and Great Black-backed Gulls *Larus marinus* (86 recoveries). Before 1960, the number of occasional recoveries from abroad was insignificant; thereafter, recoveries averaged around 28 per year (Hüppop and Hüppop 2009).

Most birds passing through Helgoland breed in Denmark, Norway and Sweden and follow a southwestern route to Germany, the Netherlands, Belgium, France, the British Isles, the Iberian peninsula and Africa (Hüppop and Hüppop 2009; Dierschke et al. 2011). These confirm the favorable location of Helgoland within the spatial courses of west- and north-European migration events. Very few species with southern (e.g., Icterine Warbler *Hippolais icterina*) or southeastern migration routes (e.g., Marsh Warbler *Acrocephalus palustris* and Red-backed Shrike *Lanius collurio*) reach Helgoland, as revealed by the small number of recoveries from SE Europe and Asia. Few recoveries have stemmed from South Germany, only one has come from Switzerland, and none from Austria (Hüppop and Hüppop 2009). Birds ringed on Helgoland seem to avoid the Alps.

The morphometrics of Northern Wheatears suggest high proportions of birds from Iceland and Greenland. This

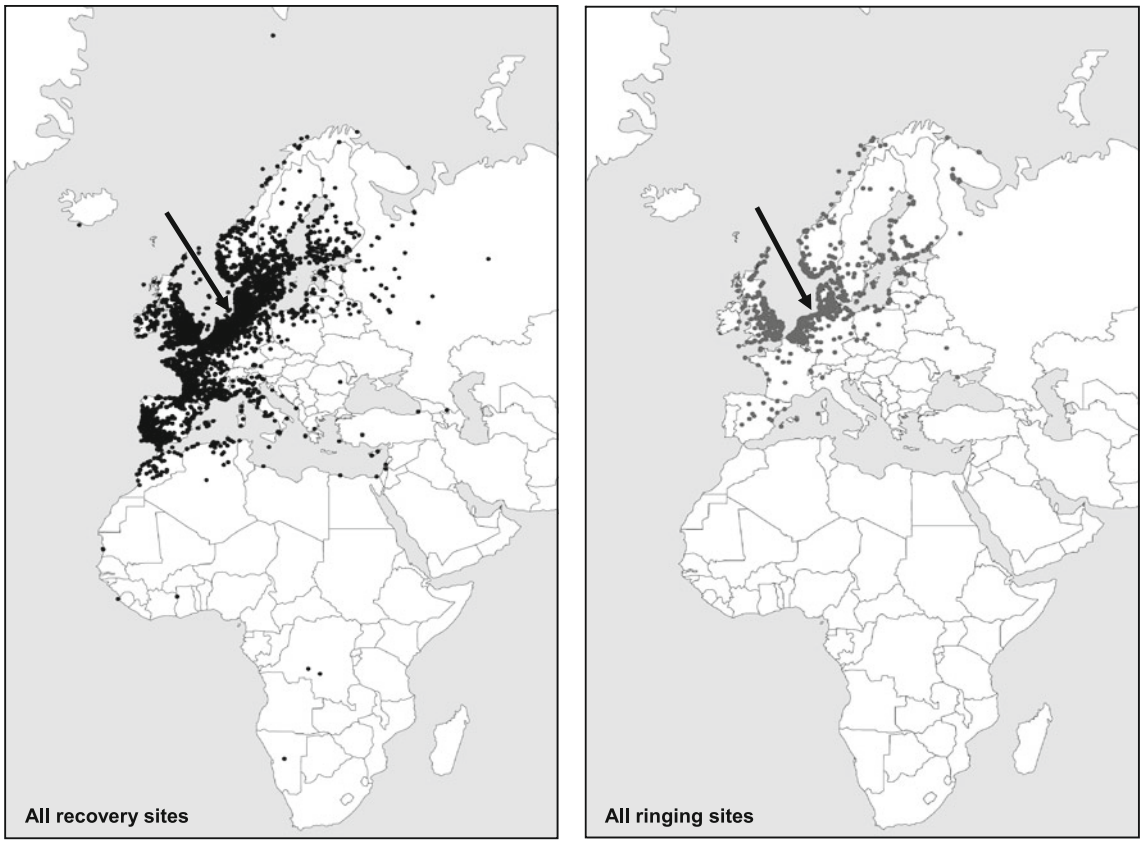

Fig. 2 All recovery sites of birds ringed on Helgoland ($n = 6{,}914$ recoveries, excluding those on Helgoland itself), and all ringing sites of birds recovered on Helgoland ($n = 1{,}516$ recoveries) from 1909 to 2008. *Arrows* denote Helgoland

presumed Greenlandic origin is supported by stable isotope analysis (Delingat et al. 2010). Several other (sub)species probably originate from North America or Siberia, although there have been no recoveries of ringed birds in such cases so far (Dierschke et al. 2011).

Weather effects on bird migration at Helgoland

Already Heinrich Gätke realized that weather was an important factor in migration intensity on Helgoland. He devoted a whole chapter of his book to the meteorological conditions that influence migration (Gätke 1895). Besides season and energetic constraints on distance, the number of birds that occur at a stopover site is influenced by the weather conditions at the previous stopover site, en route and at the current site. Further, bad weather during the preceding days can inhibit migration and hence cause "Zugstau" (the interruption of migration due to bad weather, leading to local accumulations of migrants that are ready for take-off). The arrival of birds is thus influenced by both the "direct" weather conditions close to the island, which influence whether the birds decide to land or to continue their flight, and the "large-scale" weather conditions, which affect the volume of migrants aloft (e.g., Pyle et al. 1993; Saino et al. 2010).

The concurrent—and often not independent—effects of different factors make statistical analyses, models and forecasts of bird migration extremely difficult (Alerstam 1978; van Belle et al. 2007). Despite many recent technical innovations, the comments made by Gätke over 100 years ago are still true: "the meteorological influences which affect the migrations of birds are at the present time still very imperfectly understood," and "such portions of the migration phenomenon as become apparent during its periodical recurrences are brought within the range of our observing faculties almost exclusively by meteorological conditions which are exercising a disturbing influence upon the normal progress of the migratory movement" (Gätke 1895). However, some "general rules" have emerged.

Most of the species trapped on Helgoland are nocturnally migrating songbirds that cross the German Bight of the North Sea in a broad front while on their way to or from their Scandinavian breeding grounds, namely along a northeast–southwest axis from Denmark and Sweden to the coasts of Lower Saxony or the Netherlands (or in the reverse direction). Under certain circumstances, there is also considerable north–south (to/from Norway) or

east–west (to/from SE England) migration (Jellmann and Vauk 1978; Hüppop et al. 2004). The overall migration intensity is mainly dependent on the wind conditions, with the strongest migration occurring under tailwind conditions (Gätke 1895; Hilgerloh 1977; Hüppop et al. 2004, 2006). In some species, there are correlations between the nocturnal counts and the number of trappings the next day (Dierschke 1989). However, call intensity and trappings do not necessarily reflect the real migration intensity. Adverse factors can force a high proportion of the migrants aloft to land, whereas under good conditions the majority of the birds will continue on their flights to the mainland (which is within their range of vision) without landing or at least being heard on Helgoland (Jellmann and Vauk 1978; Dierschke 1989). Mass "fall-outs" always occur when initially optimal conditions (tail winds and a clear sky) deteriorate; namely with the onset of fog or drizzle in the second half of the night. In such cases, the birds become disorientated and are attracted by the lighthouse or by the lights of the village (Drost 1960; Dierschke et al. 2011).

Wind also causes drift in a number of species that normally do not occur on Helgoland, such as raptors (species with soaring migration) and continental landbirds blown offshore (Dierschke 2001; Dierschke et al. 2011), as well as pelagic seabirds blown into the German Bight (Krüger and Dierschke 2006; Dierschke et al. 2011). Simultaneous visual observations of diurnal migration showed that the migration intensity is lower at the island of Helgoland than at coastal islands, and that diurnally migrating passerines often avoid crossing the North Sea, preferring to follow the coastline during both spring and autumn migrations (Hüppop et al. 2010).

At Helgoland, the number of spring trappings and the sightings of the few species with a northwest–southeast migration direction generally outnumber those in autumn (Moritz 1983; Hüppop et al. 2004; Busche and Dierschke 2007; Dierschke et al. 2011). This is considered to be due to the birds "overshooting" their breeding ranges in spring under favorable migration conditions (warm weather and southeasterly winds). Similar prolonged migrations can be observed in winter, when species that normally winter north to east of Helgoland continue their migrations under especially harsh weather conditions, such as (sudden) extreme cold spells coinciding with snow and ice (Dierschke et al. 2011).

Helgoland is also famous for its long list of rarities. The reasons for their occurrence are quite variable and are still not understood (Newton 2008). The occurrence of vagrants on Helgoland can, depending on the species, be explained by dispersal, wind drift, overshooting, or mirror-image and reversed-direction migration (for details see Dierschke et al. 2011).

Stopover behavior and ecology

Migrants landing on Helgoland stay for hours to weeks, or even (rarely) for months (e.g., Raiss 1979), depending on the species, age, sex, body condition, season, weather, food availability, intra- and interspecific competition and predation pressure. Even within closely related species, considerable differences in (for example) weather effects and in the frequency and duration of the stay are obvious, with young birds being more vulnerable to harsh weather conditions than adults (Raiss 1979). However, mass mortality due to starvation during the migration period is very rare, and is mainly caused enduring adverse storms and drops in temperature (Drost 1940; Antoniazza et al. 1974).

Compared to the Mediterranean Sea or the Sahara, the North Sea is a rather small ecological barrier to birds resting on Helgoland (<150 km if the migrants follow a northeast–southwest axis; ca. 50 km if they use the shortest route). Accordingly, birds landing there carry only small or moderate fat deposits, while high fuel loads are rarely observed in trapped birds. Body condition is not a factor that forces birds to land on the island (Dierschke and Bindrich 2001; Dierschke 2006); stopovers on Helgoland appear to occur rather randomly. Under favorable conditions, migrants will take the opportunity to refuel. Accordingly, in the funnel traps, recapture rates are much higher for lean birds than for birds with large amounts of visible fat stores (Dierschke 2006). Many frugivorous species stay longer during autumn migration in order to take advantage of the period when Elderberries *Sambucus nigra* ripen than before or after this period (Ottich and Dierschke 2003). The density of passerines may affect departures due to crowding and interference (Dierschke 2006).

Northern Wheatears, which are mainly trapped outside the trapping garden, prolong their stopovers and defend territories whenever rich food patches occur. Predation risk due to high numbers of raptors present on the island does not influence the departure decisions of Northern Wheatears directly. However, it does negatively affect the fuel deposition rate and thus (indirectly) the stopover decision (Schmaljohann and Dierschke 2005).

The decision to continue the migratory flight is also influenced by the target of migration and the weather; namely wind conditions and cloud cover (Dierschke 2006). During spring migration, birds of the nominate subspecies of the Northern Wheatear breeding in Scandinavia have only a short flight to the next stopover, so they need hardly any fat, and leave the island regardless of the weather conditions in the seasonally appropriate direction. In contrast, those of the subspecies *O. o. leucorhoa*, which breed in Iceland and Greenland, face a long nonstop flight, and stay on much longer when wind and overcast conditions

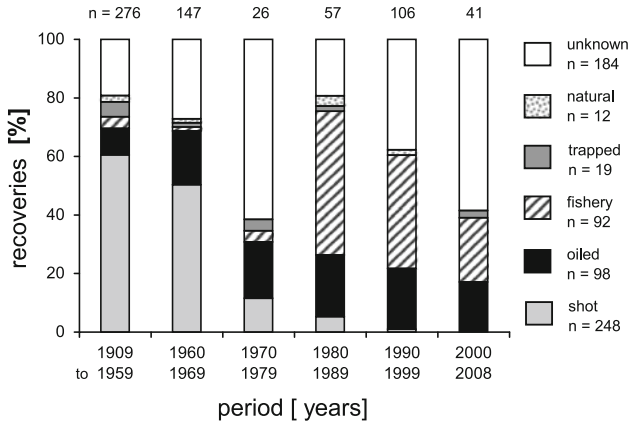

Fig. 3 Circumstances for the recoveries of Guillemots *Uria aalge* ringed on Helgoland in six periods from 1909 to 2008 ($n = 653$; after Hüppop and Hüppop 2009)

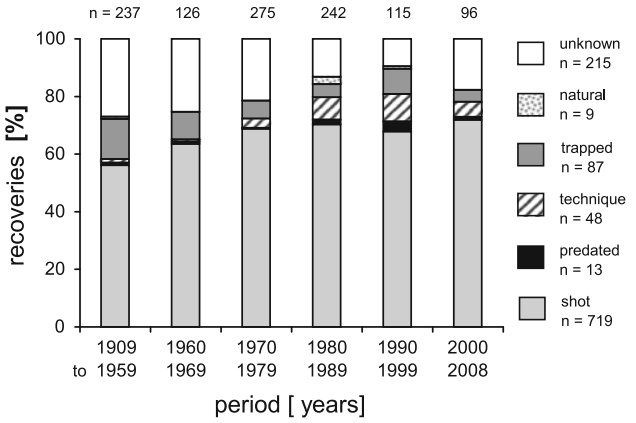

Fig. 4 Circumstances for the recoveries of Song Thrushes *Turdus philomelos* ringed on Helgoland in six periods from 1909 to 2008 ($n = 1{,}091$)

combine to give adverse flying conditions (Dierschke and Delingat 2001; Dierschke 2006). Birds with high fuel loads show their seasonally appropriate migratory direction irrespective of the ecological barrier ahead, whereas lean birds avoid this direction and instead return to the mainland (Schmaljohann et al. 2010).

Circumstances of the recoveries of birds ringed on Helgoland

Recoveries resulting from 100 years of bird ringing also yield insights into the causes of mortality and the changes in their relative importance over the years. The reasons for recovery have changed considerably, both spatially and temporally. Generally speaking, a decrease in the proportion of birds killed by human persecution and an increase in the proportion killed by pollution and anthropogenic structures (windows, vehicles, fisheries, etc.) have been observed (Hüppop and Hüppop 2002).

Recoveries of Guillemots bred on Helgoland are a good example of the changing threats to seabirds (Hüppop and Hüppop 2009). Most Guillemots were reported to have been shot (mainly in Norway), found oiled (predominantly along the shipping routes of the southern North Sea) or retrieved through fishing activity (mainly in Sweden and Denmark). Throughout the twentieth century, the threats to the Guillemot changed considerably (Fig. 3). Hunting as a cause of death has decreased since the end of the 1960s due to new hunting acts. The proportion of oiled birds increased up to a maximum of 21% in the 1980s. Besides hunting and oiling, fishing activity became increasingly important as a threat to seabirds in the 1980s (Hüppop 1996; Žydelis et al. 2009). In that decade, the proportion of recovered birds killed due to fishing was 49%. With the increase in fuel costs in the 1970s, the less expensive gillnet fishery—which is much more dangerous to diving seabirds and mammals—found increasing use. It was even seen to be responsible for a decline in some populations of Guillemots (Žydelis et al. 2009). While recoveries that are reported to be due to fishing have since decreased, this is probably because fewer such deaths are reported in order to avoid a negative image (Mead 1993; Hüppop 1996; Hüppop and Hüppop 2009).

The recoveries of Song Thrushes provide insight into the temporal and spatial development of songbird hunting over the last 100 years. Song Thrushes ringed on Helgoland breed in Fennoscandia and northwestern Russia, and winter mainly in western Europe (Milwright 2006; Dierschke et al. 2011). Given that it has accounted for 56–72% of all recoveries, hunting has always played an important role in this species (Fig. 4). Most hunted Song Thrushes have been reported from SW European countries (cf. McCulloch et al. 1992; Payevsky and Vysotsky 2003; Milwright 2006), where the percentage has actually risen over the last 100 years (Fig. 5). This can be explained by improvements in the protection of other species, which has obviously resulted in a "compensatory" increase in the hunting of legitimate quarry species (McCulloch et al. 1992). In the British Isles, central and northern Europe, the percentage of recoveries that were reported as being due to hunting dropped to zero from the 1990s onwards. In the three decades after the Second World War, the survival rate of Song Thrushes ringed on Helgoland was significantly higher than in the years before 1945 and in the years since 1980. This can presumably be explained by a higher hunting pressure across the whole of Europe before the Second World War, and increased losses due to anthropogenic structures and traffic over the last few decades (Hüppop and Hüppop 2002).

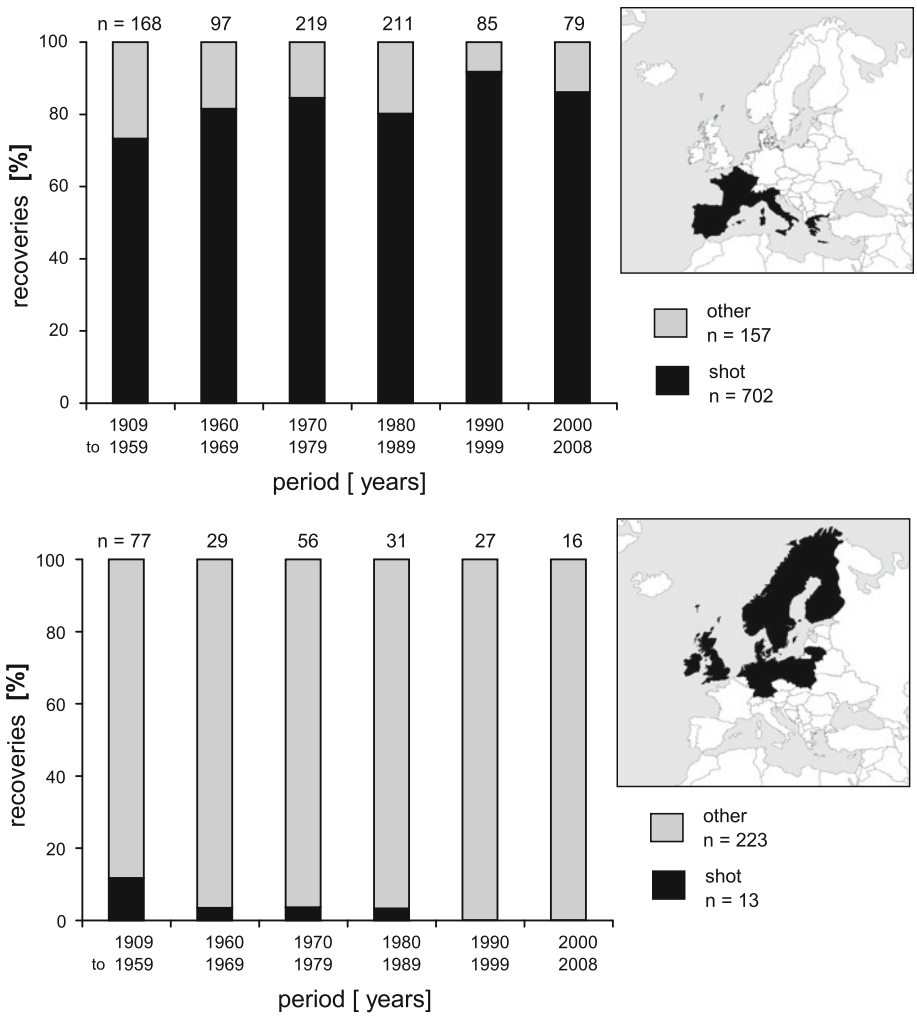

Fig. 5 Recoveries of Song Thrushes *Turdus philomelos* ringed on Helgoland that were reported to have been hunted in six periods from 1909 to 2008 in southern European (*top*, $n = 859$) and northern European countries (*bottom*, $n = 236$)

1960 to 2010: fifty years of constant-effort trapping

Birds are well known to be indicators of environmental change (Furness and Greenwood 1993; Bauer and Berthold 1997; Gregory et al. 2009). Long-term constant-effort trapping provides an excellent data set for revealing population dynamics (Berthold and Schlenker 1975; Dunn et al. 2004), phenology (Jenni 1984; Berthold 2001; Newton 2008), annual rhythms (Gwinner 1996), and the correlations between bird migration and environmental variables such as food offer, weather or climate throughout the annual cycles of birds (e.g., Berthold 1996, 2001; Bairlein and Hüppop 2004; Newton 2011). Moreover, a comparative analysis of standardized long-term ringing datasets can help to unravel large-scale migration processes (Bairlein and Schaub 2009).

Data on Helgoland have been collected with constant effort and methods since the early 1960s (three funnel traps, a year-round trapping routine of up to seven times per day during daylight; for details see Moritz 1982). In particular, the year-round trapping routine allows the calculation of mean species-specific seasonal passage times as arithmetic means (or other measures) of the daily trapping totals (Hüppop and Hüppop 2004). Means are far more valuable than first arrival dates, since the latter are often very different from changes in the mean arrival date of the migration cohort as a whole (Mason 1995; Sparks et al. 2001; Miller-Rushing et al. 2008; Lehikoinen and Sparks 2010).

Changes in numbers

In contrast to the constant conditions within the trapping garden, the amount of vegetation outside the garden has increased substantially throughout the whole island since it was erased almost completely at the end of the Second World War (see above). In order to be able to conduct trend analyses, we recalculated the ringing data using a correction factor for the substantially increasing island vegetation (corrected ringing number indices = CRNI; Hüppop and Hüppop 2007). From 1960 to 2004, the CRNI decreased in 49

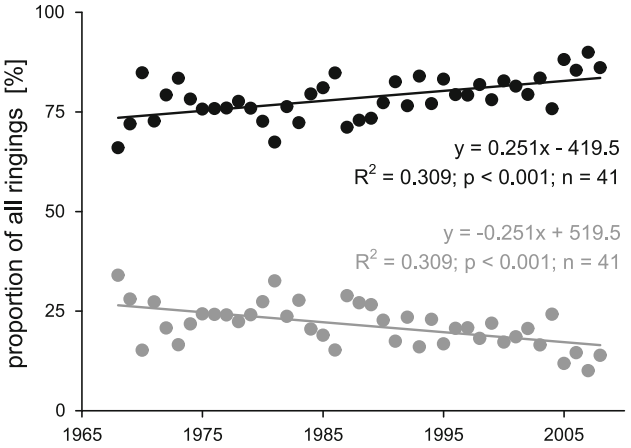

Fig. 6 Trend in the proportions of SMD migrants (*black*) and LD migrants (*gray*) ringed in the trapping garden on Helgoland from 1968 to 2008 (after Hüppop and Hüppop 2007, supplemented)

of the 66 considered species (significantly in 40 of them). It increased in ten species (seven significantly), and in seven species it did not change. For all species taken together, CRNI decreased significantly by 42% (by 39% in the SMD migrants and 55% in the LD migrants). This striking decrease, especially in LD migrants, is in accordance with very similar results from other Central and Eastern European as well as Scandinavian ringing stations (Hüppop and Hüppop 2007). CRNI divided into different ecological guilds show decreases of 33% in forest birds, 58% in farmland birds, 74% in waterside birds, and 46% in other categories.

The recent strong decrease in LD migrants (Berthold et al. 1998; Sanderson et al. 2006; Heldbjerg and Fox 2008; Robinson et al. 2009; Both et al. 2010) is also reflected in the change in the proportion of birds ringed in the trapping garden from 1968 to 2008 (Fig. 6). Whereas the LD migrants made up 25.5% and the SMD migrants correspondingly comprised 74.5% in 1968, the relation was 15.5 vs. 84.5% in 2008. Particularly in very recent years, extremely low proportions of LD migrants have been noted (trapping number indices of SMD migrants remained constant from c. 1980 onwards; Hüppop and Hüppop 2007).

The trends in the CRNI correlate significantly with the population trends in Sweden and Norway from 1970 to 1990, but not with population trends in Germany, Denmark and Finland (Hüppop and Hüppop 2007). In a year-by-year comparison of the CRNI at Helgoland with indices from summer counts in Sweden from 1975 to 2004, the two series are conspicuously parallel, not only for the many individual species, but also for all species in the two migration categories and in the ecological guilds, respectively. The close coherence between the CRNI from Helgoland and the breeding populations in Sweden indicates that the trapping data from Helgoland are well suited for use as an indicator of population changes in Sweden (Hüppop and Hüppop 2007).

Phenology

The year-round phenology of all birds together in the trapping garden shows distinct spring and autumn migration periods, with only a few birds caught in winter and summer (Fig. 7). Both seasons are characterized by two peaks that reflect the migration times of the SMD migrants and the LD migrants (for the phenology of individual species, see Hüppop and Hüppop 2004). The spring migration pattern of the SMD migrants has a maximum at the beginning of April, while that of the LD migrants peaks at the end of May. During the autumn migration, LD migrants peak at the end of August while the maximum for SMD migrants is in the middle of October.

Climate change related alterations in phenology

It is now clear that extensive global climate change has occurred over the last decades, and that this can be

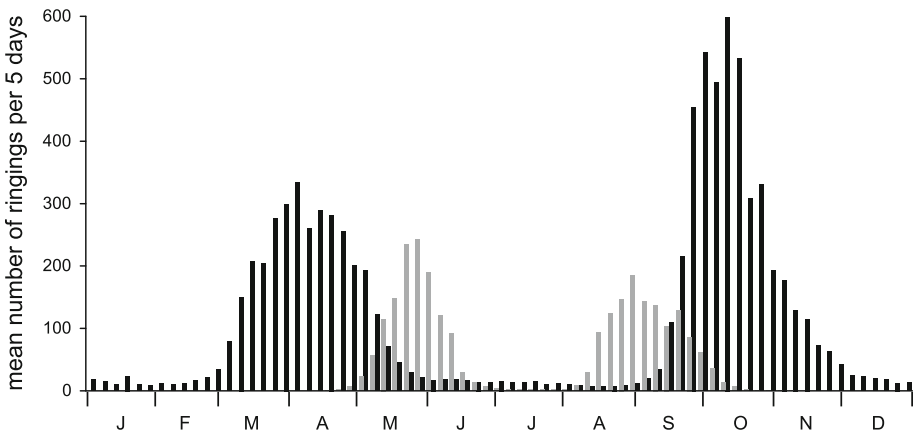

Fig. 7 Annual phenologies of the SMD migrants (*black columns*) and the LD migrants (*gray columns*) in the trapping garden on Helgoland from 1960 to 2008 (after Hüppop and Hüppop 2004, supplemented)

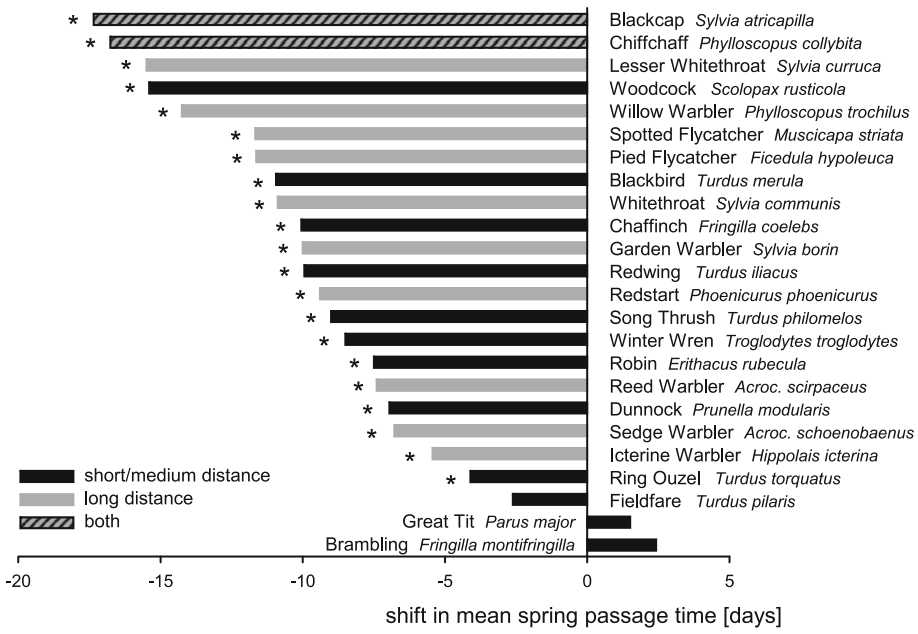

Fig. 8 Shift in msp time in 24 species on Helgoland from 1960 to 2008 that were trapped with constant effort (*asterisks* indicate significant changes according to linear regression, $P_{(2)} < 0.05$)

attributed to human activities (e.g., IPCC 2007; Solomon et al. 2009). Impacts on ecosystems, populations and species have become obvious and well known (e.g., Walther et al. 2002; Root et al. 2003; Parmesan 2007; Loarie et al. 2009). For migrant bird species, earlier arrival dates in spring, earlier starts to breeding, and changes in various other breeding parameters or range extensions northwards have been observed, as well as rather obvious changes in autumn migration and wintering behavior (e.g., Burton 1995; Thomas and Lennon 1999; Bairlein and Winkel 2001; Cotton 2003; Hüppop and Hüppop 2003; Jenni and Kéry 2003; Møller et al. 2004, 2010; Sparks and Mason 2004; Jonzén et al. 2007; Rubolini et al. 2007).

For 24 species trapped in the trapping garden on Helgoland, sample sizes were sufficient to calculate yearly mean spring passage times (= msp times; Hüppop and Hüppop 2003) for the years 1960–2008. In this period, 22 of them advanced their msp times. This earliness was significant in 11 of the 12 SMD migrants, in all 10 LD migrants, and in Blackcap and Chiffchaff *Phylloscopus collybita* (which, on Helgoland, can be expected to belong to both groups; Zink 1973). The changes in msp times ranged from a delay in Brambling *Fringilla montifringilla* of 2.5 days to an earliness of up to 17.4 days in Blackcap and 16.8 days in Chiffchaff within the past 48 years (Fig. 8). Although the LD migrants pass through Helgoland about 6 weeks later than the SMD migrants, the extent of the earliness (10 and 8.5 days on average in the LD and SMD migrants, respectively) was not significantly different (Mann–Whitney U test, $U = 85.0$, $P = 0.107$; Fig. 9). This result conflicts with those from many other studies, where LD migrants did not advance their arrival times as much as SMD migrants (Lehikoinen et al. 2004; Lehikoinen and Sparks 2010). However, this may be an artefact, since first arrivals (as used in many calculations) change differently from mean arrivals—for example, if population sizes decrease (Miller-Rushing et al. 2008), which actually is the case in many LD migrants (see above). In many cases, first arrivals might be regarded as outliers for the whole cohort.

Due to the higher variability of the weather in early spring, the msp time is more variable in species that arrive earlier (i.e., in SMD migrants). In SMD migrants, the trend towards earliness is significantly stronger in

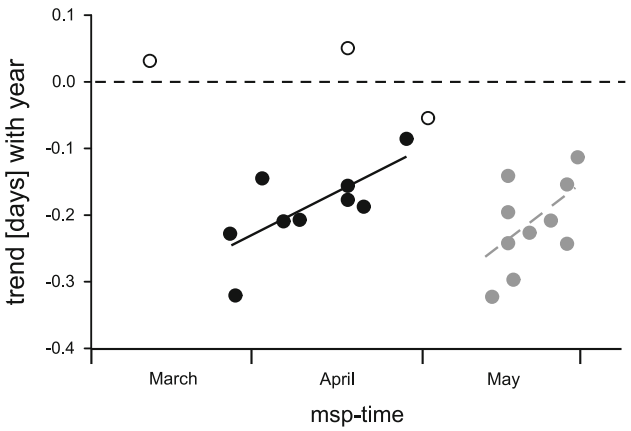

Fig. 9 Trend in mean spring passage time (msp time) with year in relation to mean msp time in SMD migrants (*black*; $y = 0.004x - 0.607$, $R^2 = 0.538$, $P_{(2)} < 0.025$, $n = 9$) and in LD migrants (*gray*; $y = 0.006x - 1.124$, $R^2 = 0.305$, $P_{(2)} < 0.1$, $n = 10$) in the trapping garden on Helgoland from 1960 to 2008 (*white* = SMD species without any significant trends in msp time)

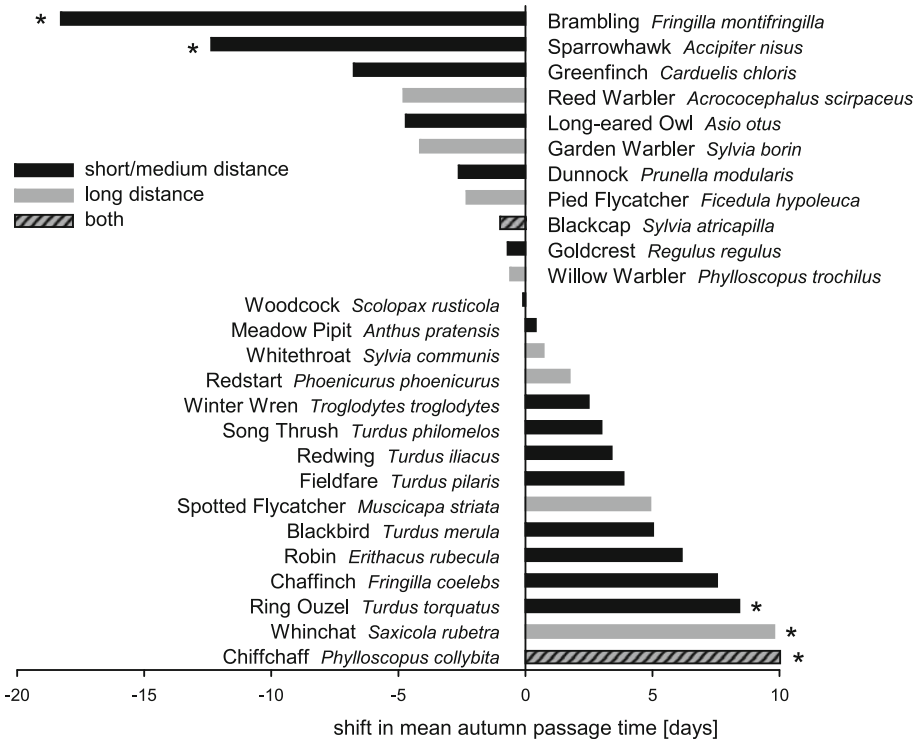

Fig. 10 Shifts in map time in 26 species on Helgoland from 1960 to 2008 that were trapped with constant effort (*asterisks* indicate significant changes according to linear regression, $P_{(2)} < 0.05$)

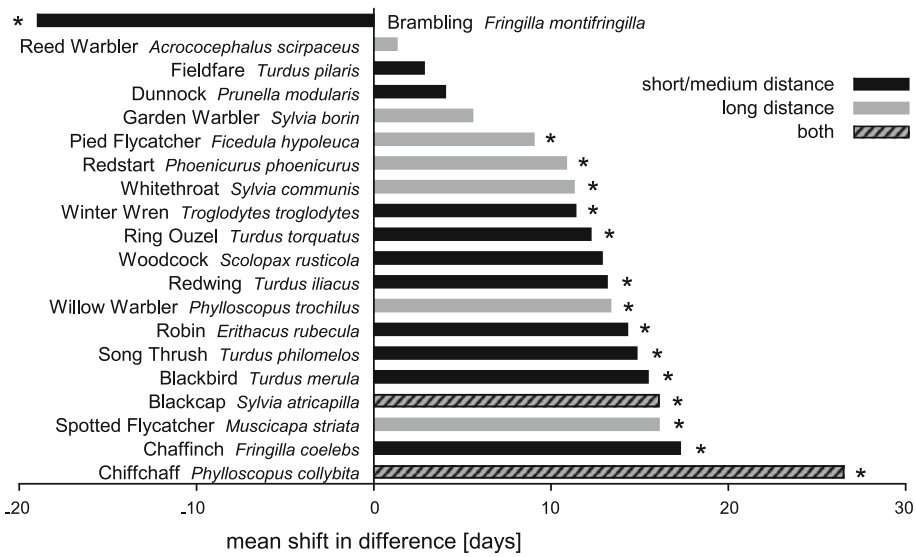

Fig. 11 Mean shifts in the difference between msp and map times for 20 species on Helgoland from 1960 to 2008 that were trapped with constant effort (*asterisks* indicate significant changes according to linear regressions, $P_{(2)} < 0.05$)

earlier-migrating species than in later-migrating ones. A similar relationship is found in LD migrants, though it is not significant (Fig. 9; see also Lehikoinen et al. 2004; Lehikoinen and Sparks 2010).

In autumn, the picture is quite different and not all uniform: among 26 species with sufficient sample sizes, eleven species showed a trend for a delay, and seven species showed a trend for earliness in mean autumn migration time (map time) from 1960 to 2008. Most species did not change their map times significantly; only two species advanced and three species delayed significantly (Fig. 10). The largest delays were observed in the Chiffchaff (10.0 days) and the Whinchat *Saxicola rubetra* (9.8 days), and the greatest advances were seen in the Brambling (18.3 days) and the Sparrowhawk (12.4 days). No significant difference in the map time trend over 48 years was observed between the two migration categories (Mann–Whitney U test, $U = 66.0$, $P = 0.928$). This contradicts other findings, where LD migrants had a tendency to advance their autumn migration times whereas SMD migrants had a tendency to migrate later (Jenni and Kéry 2003; Tøttrup et al. 2006; Filippi-Codaccioni et al. 2010;

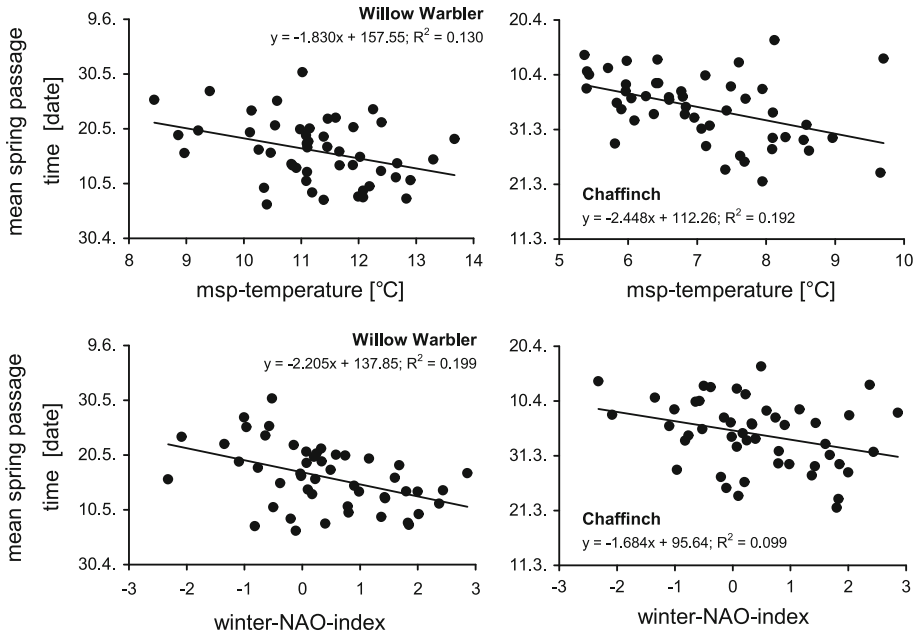

Fig. 12 Relations between the msp time (Julian Day is used in the regressions) of a LD migrant (Willow Warbler *Phylloscopus trochilus*) and a SMD migrant (Chaffinch *Fringilla coelebs*), based on constant-effort trapping on Helgoland, to the mean local spring passage temperature during the species-specific migration time (msp temperature), and to the winter NAO index from 1960 to 2008. NCEP/NCAR reanalysis temperatures were provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, CO, USA (http://www.cdc.noaa.gov/data). The winter NAO index data were derived from the Climatic Research Unit at the University of East Anglia, Norwich, UK (http://www.cru.uea.ac.uk/cru/data/nao.htm)

Lehikoinen and Sparks 2010). The reasons for this difference are still unknown, and require further analyses.

In 20 species, sample sizes were sufficient to calculate both msp and map times. From 1960 to 2008, the difference between the two migration times increased in all but one of these species (in ten SMD migrants, seven LD migrants, and in the Blackcap and Chiffchaff): by up to 26.5 days in Chiffchaff and 17.3 days in Chaffinch *Fringilla coelebs* (Fig. 11). Only the Brambling did not conform to this trend, and showed a significant decrease in the difference by 19 days over the 48 years. The increase in the difference did not differ significantly between the two migration categories (Mann–Whitney U test, $U = 47.0$, $P = 0.479$). Since it is largely a result of the earlier msp time, this increase reflects a prolongation of the time spent at the Scandinavian breeding grounds, with the opportunity to increase breeding success (Hüppop and Hüppop 2008).

Generally (in all species except Brambling), the msp time is negatively related to the local temperature within the species-specific migration time (msp temperatures) from 1960 to 2008. This relation is significant in eleven SMD and seven LD migrants, respectively, and in Blackcap and Chiffchaff ($P_{(1)} < 0.05$; see examples in Fig. 12). However, msp temperatures explain on average three times more of the variance in msp time in SMD migrants than in LD migrants (Fig. 13; Mann–Whitney U test, $U = 106.5$, $P = 0.0024$). We attribute this to the different migration and wintering strategies of the two groups: SMD migrants winter much closer to Helgoland than LD migrants (see the maps in Dierschke et al. 2011). This means that their final departure sites are closer to Helgoland, and temperatures there are accordingly more closely correlated with those in the Helgoland area. In contrast, LD migrants from sites further away may experience "climatic barriers" en route with, for example, low temperatures (Ahola et al. 2004; Hüppop and Winkel 2006). This lowers the R^2 of the correlations between msp times and temperatures at Helgoland. Further, responses of birds and other organisms to climate change are much more complex than a straightforward reaction to instantaneous temperatures (Harrington et al. 1999; Day et al. 2010; Saino et al. 2011). While temperatures in winter and early spring are crucial to the time of budburst, insect winter survival and the speed of insect development, they have comparatively smaller effects later in the season. For example, the threshold for aphid development is as low as roughly 4°C (Hullé et al. 2010), and the aphid population growth rate is positively correlated with the amount of time that the temperature is above this threshold before budburst, and negatively correlated with the number of periods of five consecutive chill days during winter (Day et al. 2010). Hence, the occurrence of food organisms during the spring passage of LD migrants is decisively influenced by the weather long before the LD migrants pass through Helgoland.

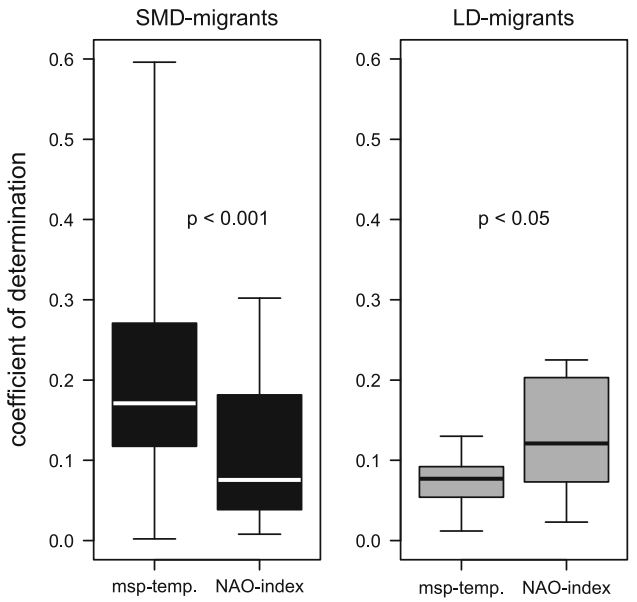

Fig. 13 *Boxplots* (median, quartiles and extremes) of coefficients of determination for linear regressions of mean spring passage time on msp temperature and on winter NAO index, based on constant-effort trappings on Helgoland from 1960 to 2008 for the two migration categories (*SMD* short/medium-distance migrants, $n = 12$ species; *LD* long-distance migrants, $n = 10$ species). Differences within migration categories were tested for significance by Wilcoxon paired-sample tests, and between categories with Mann–Whitney U tests (see text)

The msp times of the LD migrants are better explained by the large-scale climatic phenomenon of the North Atlantic Oscillation (NAO). The NAO influences, besides many other things, the strength of the winter and early spring throughout the whole area of passage of the LD migrants within western and northern Europe. The winter NAO index describes the situation in winter and early spring (December to March), with positive indices corresponding with stronger winds from the west and associated higher temperatures and higher levels of precipitation from the Atlantic Ocean, namely to central and northwest Europe (Hurrell et al. 2001; Visbeck et al. 2001). In 23 of our 24 species on Helgoland, msp times were negatively correlated with the winter NAO index (significantly in nine SMD migrants, nine LD migrants and the Chiffchaff; $P_{(1)} < 0.05$; see examples in Fig. 12); in other words, the birds arrive earlier after mild winters. Although their mean migration times differ by about 6 weeks, the influence of the NAO index does not differ between the two migration categories (Fig. 13, Mann–Whitney U test, $U = 45.0$, $P = 0.339$). Thus, their msp times are influenced by the NAO in winter; that is, by the "preparation for the spring," to the same degree. Mild winters associated with a positive NAO index cause, for example, the spring migration of the green spruce aphid (*Elatobium abietinum*, a pest to spruce trees) in England to start earlier, to continue for longer, and to contain more aphids, but not to end earlier (Westgarth-Smith et al. 2007). As expected, the msp temperature explains a higher proportion of the variance on average than the winter NAO index in the SMD migrants, while the opposite is true in the LD migrants (Fig. 13).

Climate variables measured during breeding and autumn migration times have changed less consistently over the last five decades than those in winter and spring. Accordingly, we are not yet able to explain the few observed changes in map times by climate variables (Hüppop and Hüppop 2005).

Conclusions

More than 160 years of ornithological research on the small island of Helgoland, including a century by the Institute of Avian Research "Vogelwarte Helgoland," resulted in more than 1,200 publications (Dierschke et al. 2011). This includes hundreds of short notes on field ornithology, as well as several books and many papers that have been published in scientific journals covering a broad spectrum of topics. Reviewing all of them would have been far beyond the scope of this article; for instance, we had to largely ignore articles on seabird ecology and studies of the impacts of oil, chemical and garbage pollution, human disturbances, fisheries and windfarms on birds here (but see Bairlein and Becker 2010 and Dierschke et al. 2011 for further details).

Presumably the biggest treasures provided by the station on Helgoland are the long-term dataset, which has been attained through constant-effort bird catching in the trapping garden, and the immediate access to birds and bird migration afforded by the station. Modern technology, progress in biochemical methods, computer facilities and the feasibility of experimental approaches offer many opportunities to answer open questions and bear the potential for new and exciting research.

Acknowledgments We are grateful to the thousands of people who have worked as staff or volunteers for the Vogelwarte Helgoland and the Institute of Avian Research, respectively, on the island of Helgoland. In particular, we take our hats off to those who ensured that ornithological studies on this small rock survived, even during the worst periods of the last century. We thank Franz Bairlein and Heiko Schmaljohann for useful comments on an earlier version of this paper.

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