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1 **Bird migration on Helgoland: The yield of 100 years of research**

2

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4

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11

12

13 **Abstract**

14 The island of Helgoland (North Sea) was the very first place on earth with systematic studies  
15 on bird migration (since the mid 19<sup>th</sup> century). The “Vogelwarte Helgoland” was founded in  
16 1910 and since 1909 more than 800,000 birds were ringed. Most are nocturnally migrating  
17 songbirds crossing the German Bight in broad-front on the way to or from their Scandinavian  
18 breeding grounds. Under good weather conditions (tail winds, clear sky) the majority of the  
19 migrants does not contact Helgoland, while deteriorating weather strongly increases the  
20 addiction to land. Wind can drift more rare birds to Helgoland, such as raptors and continental  
21 landbirds blown offshore or pelagic seabirds blown into the German Bight. Migrants stay for  
22 hours to weeks, depending on species, age, sex, body condition, season, weather, food  
23 availability, intra- and interspecific competition and predation pressure. The departure  
24 direction seems to be influenced by body and weather conditions, too. The reported  
25 circumstances of the almost 7,000 recoveries changed substantially throughout the last 100  
26 years and show definite regional differences. Indices from constant effort trapping revealed  
27 decreases in long distance migrants, while short/medium distance migrants did not change  
28 much. In all “true migrants” an advancement of mean spring passage time was observed since  
29 1960 (up to 18 days). Whereas changes in autumn were less uniform, the time between both  
30 periods increased in most species. Earliness in spring is best explained by local temperatures  
31 in short/medium distance migrants and by the winter-NAO-index in long distance migrants.

32

33 **Keywords** Bird migration • Island • Ringing • Weather • Climate change • History

34

35 **Introduction**

36 Remote islands at migration flyways often attract and concentrate large numbers of birds  
37 looking for stopover sites but also ornithologists interested in bird migration and lots of  
38 birders (e.g. Clarke 1912; Moore et al. 1990; Pyle et al. 1993; Berthold 1996; Newton 2008;  
39 Archer et al. 2010). This also holds for the tiny island of Helgoland, or Heligoland, in the  
40 south-eastern North Sea (Gätke 1895; Vauk 1972; Dierschke et al. 2010). Actually, Helgoland  
41 was the very first place on earth with systematic studies on bird migration (Newton 2008;  
42 Vaughan 2009; Archer et al. 2010; Møller et al. 2010), long before the “Vogelwarte  
43 Helgoland” was founded on Helgoland in 1910. However, with regard to the centenary of the  
44 Institute of Avian Research, as the “Vogelwarte Helgoland” is called since its change to the  
45 mainland in Wilhelmshaven after the Second World War (Bairlein and Becker 2010), we will

46 focus here mainly on the results of studies carried out on the island by the institute since 1910.  
47 Special emphasis will be placed on the 50 years long-term year-round trapping routine under  
48 standardized conditions.

49

## 50 **The location**

51 The island of Helgoland (54° 11' N, 07° 53' E) is a Triassic red sandstone rock on top of a  
52 pillow of Permian salt masses (Spaeth 1990), 61 m high and some 45 km away from the next  
53 island or coast, respectively. Between 1890, when the formerly British island became  
54 German, and the Second World War it was altered by intensive fortification and harbor  
55 building including considerable hydraulic sand filling. By this the size of the island increased  
56 from only 0.3 km<sup>2</sup> to 1 km<sup>2</sup>. From 1944 to 1947 the surface of the unpopulated plateau  
57 changed from a plane to a cratered appearance due to bombing. Today, almost 30% of the  
58 island is built-up and inhabited by about 1.300 people. Trees and shrubs are restricted to the  
59 residential areas and to few sites with shelter from storms, including the trapping garden of  
60 the Institute of Avian Research. The rest of the island is covered with pastures and meadows  
61 (Dierschke et al. 2010).

62 Just one kilometer to the east lies a second, with 0.7 km<sup>2</sup> even smaller island, the “Dune”. It is  
63 based on the remnants of Triassic and Cretaceous limestone and other sediments that formed a  
64 second cliff of similar size as that of the main island. Since limestone and gypsum are rare in  
65 the glacial landscape of northern Germany this second cliff was used as a quarry and finally  
66 disappeared in a storm tide in 1711 (Spaeth 1990). Considerable hydraulic sand filling in the  
67 1930ies also enlarged the remains of this islet which probably otherwise would have vanished  
68 meanwhile. Today its landscape is characterized by dunes. It also houses a small airfield and  
69 infrastructure for tourism (Dierschke et al. 2010).

70

## 71 **The beginning of ornithology on Helgoland**

72 The first written notes on “incredible swarms of birds” on the small island go back the  
73 16<sup>th</sup> century. For its inhabitants the huge numbers of birds were a welcome supplementation  
74 to their poor menu. Bird collectors became aware of the diversity of the island’s birdlife not  
75 before the beginning of the 19<sup>th</sup> century when a local cobbler started to sell bird skins to the  
76 first tourists visiting the recently founded seaside resort and to museums in Bremen and, later,  
77 in Berlin. From the 1830ies onwards, with increasing numbers of tourists also the first

78 ornithologists visited the island, not least because there where no restrictions on shooting and  
79 trapping of birds on the island (Stresemann 1967; Bairlein and Becker 2010). Among them  
80 was Johann Friedrich Naumann, author of the famous twelve volumes on the natural history  
81 of German birds (Naumann 1820-1844). In the foreword of the 11<sup>th</sup> volume he wrote: “The  
82 island of Helgoland is of such a high interest to German ornithology that it had to be  
83 mentioned very often in this opus.” In 1846 he published an article on bird migration in which  
84 he already highlighted that Helgoland is an excellent place for the study of bird migration  
85 (Naumann 1846). Naumann already recognized that geography, changing temperatures but  
86 also wind and “weather” may cause “enormous deviations” from the general direction of the  
87 migrants.

88 In 1837, the painter Heinrich Gätke came to the island where he lived for six decades until his  
89 death in 1897. Inspired by the hunters of the island he gained interest in collecting and  
90 observing birds and started to write an ornithological diary in 1847. His famous book “Die  
91 Vogelwarte Helgoland” published in 1891 was an epoch-making opus including detailed  
92 information on all birds observed on the island and summarizing a remarkable knowledge  
93 about bird migration, namely on relations between migration and weather. An English version  
94 “Heligoland as a bird observatory” (Gätke 1895), and – post hum – a second German edition  
95 (1900) followed (Bairlein and Hüppop 1997; Vaughan 2009). The ornithological diary  
96 established by Gätke is continued up to now, except for gaps due to the two World Wars.

97 Around 1880 the word “Vogelwarte” developed. Presumably it was based on the older  
98 “Sternwarte”, i.e. an astronomical observatory, and should emphasize Gätke’s enthusiastic  
99 efforts in bird watching (Ringleben 1958). Later, Gätke used this term for the title of his book,  
100 and in 1901 it became officially introduced with the founding of the “Vogelwarte Rossitten”  
101 by the German Ornithologists’ Society on the Courish Spit in the former East Prussia (today  
102 part of Russia) in 1901 (Fiedler 2001).

103

#### 104 **1909 to 2010: more than 800.000 marked birds**

105 With the knowledge of Gätke’s publications and observations a young enthusiastic man,  
106 Hugo Weigold, came to the island, employed as a fish biologist at the “Königliche  
107 Biologische Anstalt Helgoland” in 1909 (Bairlein and Becker 2010). However, seemingly he  
108 felt himself more as a successor of Gätke and started his own ornithological diary right from  
109 the day of his arrival on Helgoland. After the introduction of systematic bird ringing by the  
110 Danish teacher H.C.C. Mortensen in 1899 (Berthold 2001; Bønløkke et al. 2006) more and

111 more ringing schemes where established in Europe: Birds were ringed since 1903 in  
112 Rossitten, since 1908 in Hungary and since 1909 on the British Isles and on Helgoland (Drost  
113 1929). Together with August Thienemann from the “Vogelwarte Rossitten” (see above),  
114 Weigold ringed the first birds on Helgoland in October 1909 (Hüppop and Hüppop 2009;  
115 Bairlein and Becker 2010). He used rings from Rossitten first, own rings labelled “Helgoland  
116 Germania” existed from 1911 onwards. Numbers of birds ringed on Helgoland (Fig. 1)  
117 increased considerably from 1920 onwards, when Weigold intended and introduced the use of  
118 the Helgoland funnel trap or “Helgoländer Trichterreuse” (Weigold 1922). His successor  
119 Rudolf Drost who worked on Helgoland from 1924 to 1944 further improved this trap which  
120 is nowadays in worldwide use at numerous bird observatories (e.g. Newton 2008; Archer et  
121 al. 2010). Drost also increased the numbers of ringings by catching birds at the Helgoland  
122 lighthouse which attracted them in some foggy and misty nights in huge numbers (Drost  
123 1925, 1928, 1960).

124 After an initially tentative start of trapping and ringing of birds in the first quarter of the  
125 century, an average of about 6,400 birds could be ringed per year in the following 20 years  
126 (Fig. 1). Song Thrush *Turdus philomelos*, Blackbird *Turdus merula* and Redstart *Phoenicurus*  
127 *phoenicurus* were the most frequently trapped species in this period (Table 1). Then the  
128 ringing activity was interrupted for eight years due to the evacuation of the island at the end  
129 of the Second World War, but readopted with already about 1,500 trapped birds in the year  
130 1953. A maximum of trapping numbers was reached in 1976 with more than  
131 26,000 individuals, and Song Thrush, Blackbird and Garden Warbler *Sylvia borin* were the  
132 most frequently trapped species in the second period (Table 1). In total more than 800,000  
133 birds have been ringed on Helgoland from 1909 to 2010.

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

141 Although the conditions in the trapping garden with three funnel traps and standardized  
142 trapping effort were almost constant since the early to mid 1960ties, the ringing numbers  
143 varied to a high degree within the last 50 years. Reasons are a ringing ban for some species in

144 the 1960s, weather-related seasonal and annual fluctuations, and especially the substantial  
145 vegetation change of the island since it has been almost totally naked after the Second World  
146 War: compared to the year 2000, where 91% of the vegetation on the main island was spread  
147 outside the trapping garden, in 1960 it was still almost restricted (98%) to the trapping garden  
148 (Hüppop and Hüppop 2007).

149 Ringing at the Helgoland lighthouse, namely between the wars, resulted in high numbers of  
150 up to 1,558 birds in a single night (Drost 1928), while daily ringings in the trapping garden  
151 only exceptionally exceeded 500. Seabirds in the breeding colonies (Common Guillemot *Uria*  
152 *aalge*, Kittiwake *Rissa tridactyla*, Herring Gull and Lesser Black-backed Gull *Larus*  
153 *argentatus* and *fuscus*), but also migrants during their stopover at the island (gulls, waders,  
154 Northern Wheatears *Oenanthe oenanthe*) and breeding landbirds were trapped and ringed  
155 outside the trapping garden for special studies with further methods (e.g. Drost 1933; Vauk  
156 and Gräfe 1972; Prüter 1984; Bub 1985; Dierschke 1998; Dierschke and Delingat 2001;  
157 Sacher et al. 2006; Förschler et al. 2010).

158 In contrast to many other ringing stations the trapping garden on the island of Helgoland is  
159 characterized by several specialities. 1) The island is the only stopover site for landbirds  
160 within a radius of almost 50 km and accordingly high numbers of resting migrant birds  
161 concentrate here. 2) Since very few land-birds breed on Helgoland and almost no  
162 postbreeding dispersal reach this isolated island, reliable statements about the actual migration  
163 of Scandinavian breeding birds, mainly presenting the species spectrum, can be made. 3)  
164 Methods were sufficiently standardized and effort was constant and year-round throughout  
165 the last 50 years. Thus, the full extension of the migration periods as well as winter  
166 movements can be determined (Hüppop & Hüppop 2004). All these circumstances result in  
167 the most substantial long-term constant-effort bird migration dataset in Europe.

168

### 169 **Where do the birds come from, where do they go to?**

170 The main objective of bird ringing in its first decades was to learn more about migration  
171 routes, origins and destinations of migrants (Schüz and Weigold 1931). Today, a total of  
172 about 7,000 recoveries of birds ringed on Helgoland (Fig. 2) derive from 108 species (Hüppop  
173 and Hüppop 2009). Blackbird and Song Thrush were the most frequent, with more than 1,000  
174 individuals each, followed by Guillemot with more than 500 recoveries (Table 1; for maps for  
175 all species see Dierschke et al. 2010). About 18% of all recoveries originate from the period  
176 between 1909 and the end of the Second World War. Between 1959 and 1985, the average

177 number of recoveries reached 134 per year. Thereafter, numbers declined to an average of  
178 82 recoveries per year.

179 More than 1,500 birds of 96 species ringed abroad were recovered on Helgoland between  
180 1909 and 2008 (Fig. 2). Again Blackbird (275 recoveries) was most frequent, followed by  
181 Herring Gull (197 recoveries) and Great Black-backed Gull *Larus marinus* (86 recoveries).  
182 Before 1960, the number of occasional recoveries from abroad was insignificant; thereafter  
183 recoveries averaged around 28 per year (Hüppop and Hüppop 2009).

184 Most birds passing Helgoland breed in Denmark, Norway and Sweden and follow a  
185 southwestern route to Germany, the Netherlands, Belgium, France, the British Isles, the  
186 Iberian peninsula and Africa (Hüppop and Hüppop 2009; Dierschke et al. 2010). They  
187 confirm the favourable location of Helgoland within the spatial course of the west- and north-  
188 European migration event. Very few species with southern (e.g. Icterine Warbler *Hippolais*  
189 *icterina*) or southeastern migration routes (e.g. Marsh Warbler *Acrocephalus palustris* and  
190 Red-backed Shrike *Lanius collurio*) reach Helgoland, as revealed by the small number of  
191 recoveries from SE-Europe and Asia. Few recoveries stemmed from South Germany, only  
192 one from Switzerland and none from Austria (Hüppop and Hüppop 2009). Birds ringed on  
193 Helgoland seem to avoid the Alps.

194 Morphometrics of Northern Wheatears suggest high proportions of birds from Iceland and  
195 Greenland. The presumed Greenlandic origin is supported by stable isotopes analysis  
196 (Delingat et al. 2010). For several other (sub)species, an origin from North America or Siberia  
197 is likely although no recoveries of ringed birds exist (Dierschke et al. 2010).

198

### 199 **Weather effects on bird migration at Helgoland**

200 Heinrich Gätke already realized that weather was an important factor affecting migration  
201 intensity on Helgoland. He devoted a whole chapter of his book on “Meteorological  
202 conditions which influence migration” (Gätke 1895). Besides season and energetic constraints  
203 on distance, the number of birds that occur at a stopover site is influenced by the weather  
204 conditions at the previous stopover site, en route and at the current site. Further, bad weather  
205 during the preceding days might inhibit migration and hence cause “Zugstau” (the  
206 interruption of migration due to bad weather, leading to local accumulations of migrants ready  
207 for take-off). The arrival of birds is thus influenced by both, “direct” weather conditions close  
208 to the island that make the birds decide to land or to continue their flight, and “large-scale”

209 weather conditions that affect the volume of migrants aloft (e.g. Pyle et al. 1993; Saino et al.  
210 2010).

211 The concurrent and often not independent effects of different factors make statistical analyses,  
212 models and forecasts of bird migration extremely difficult (Alerstam 1978; van Belle et al.  
213 2007). Despite many recent technical innovations it is still valid what Gätke noticed more  
214 than 100 years earlier. “The meteorological influences which affect the migrations of birds are  
215 at the present time still very imperfectly understood” and that “such portions of the migration  
216 phenomenon as become apparent during its periodical recurrences are brought within the  
217 range of our observing faculties almost exclusively by meteorological conditions which are  
218 exercising a disturbing influence upon the normal progress of the migratory movement”  
219 (Gätke 1895). However, some “general rules” emerged.

220 Most species trapped on Helgoland are nocturnally migrating songbirds that cross the German  
221 Bight of the North Sea in broad-front migration on their way to or from their Scandinavian  
222 breeding grounds, namely along an northeast-southwest axis coming from Denmark and  
223 Sweden and heading for the coasts of Lower Saxony or The Netherlands (or in the reverse  
224 direction). Under certain circumstances, there is also considerable north-south (to/from  
225 Norway) or east-west (to/from SE-England) migration (Jellmann and Vauk 1978; Hüppop et  
226 al. 2004). Overall migration intensity is mainly dependent on wind conditions with strongest  
227 migration under tailwind conditions (Gätke 1895; Hilgerloh 1977; Hüppop et al. 2004, 2006).  
228 In some species correlations could be found between the amount of nocturnal counts and the  
229 number of trappings the next day (Dierschke 1989). However, neither call intensity nor  
230 trappings do necessarily reflect the real migration intensity. Adverse factors might force a  
231 high proportion of the migrants aloft to land, whereas under good conditions the majority of  
232 the birds will continue their flight to the mainland (which is within their range of vision)  
233 without landing or at least being heard on Helgoland (Jellmann and Vauk 1978; Dierschke  
234 1989). Mass “fallouts” always occur when initially optimal conditions (tail winds and clear  
235 sky) deteriorate, namely with the onset of fog or drizzle in the second half of the night. Then  
236 birds get disorientated and are attracted by the lighthouse or by the lights of the village (Drost  
237 1960; Dierschke et al. 2010).

238 Wind also causes drift in a number of species that normally do not occur on Helgoland, such  
239 as raptors, namely species with soaring migration, and continental landbirds blown offshore  
240 (Dierschke 2001; Dierschke et al. 2010) as well as pelagic seabirds blown into the German  
241 Bight (Krüger and Dierschke 2006; Dierschke et al. 2010). Simultaneous visual observations

242 of diurnal migration showed that migration intensity is lower at the island of Helgoland than  
243 at coastal islands and that diurnally migrating passerines often avoid to cross the open North  
244 Sea but rather follow the coastline both, in spring and autumn migration (Hüppop et al. 2010).

245 At Helgoland, numbers of spring trappings and sightings of the few species with a northwest-  
246 southeast migration direction generally outnumber those in autumn (Moritz 1983; Hüppop K  
247 et al. 2004; Busche and Dierschke 2007; Dierschke et al. 2010). This is assessed as  
248 “overshooting” the breeding ranges in spring under favourable migration conditions (warm  
249 weather and southeasterly winds). A similar prolonged migration can be observed in winter  
250 when species that normally winter north to east of Helgoland continue their migration under  
251 especially harsh weather conditions, such as (sudden) extreme cold spells coinciding with  
252 snow and ice (Dierschke et al. 2010).

253 Helgoland is also famous for its long list of rarities. The reasons for their occurrence are quite  
254 variable and still not understood (Newton 2008). The occurrence of vagrants on Helgoland  
255 can, depending on the species, be explained by dispersal, wind drift, overshooting, mirror-  
256 image and reversed-direction migration (for details see Dierschke et al. 2010).

257

### 258 **Stopover behaviour and ecology**

259 Migrants landing on Helgoland stay for hours to weeks, rarely even for months (e.g. Raiss  
260 1979), depending on species, age, sex, body condition, season, weather, food availability,  
261 intra- and interspecific competition and predation pressure. Even within closely related  
262 species, considerable differences in e.g. weather effects and in the frequency and duration of  
263 the stays are obvious with young birds being more vulnerable to harsh weather conditions  
264 than adults (Raiss 1979). However, mass mortality due to starvation during the migration  
265 times is very rare and mainly caused by enduring adverse storms and drops in temperature  
266 (Drost 1940; Antoniazza et al. 1974).

267 Compared to the Mediterranean Sea or to the Sahara, the North Sea is a small ecological  
268 barrier for birds resting on Helgoland (< 150 km if the migrants follow a northeast-southwest  
269 axis, c. 50 km if they use the shortest route). Accordingly, birds landing there carry only small  
270 or moderate fat deposits, while high fuel loads are rarely observed in trapped birds. Body  
271 condition is not a factor forcing birds to land on the island (Dierschke and Bindrich 2001;  
272 Dierschke 2006), stopovers on Helgoland rather seem to occur randomly. In favourable  
273 conditions, migrants will take the opportunity to refuel. Accordingly, in the funnel traps,  
274 recapture rates are much higher for lean birds than for birds with larger amounts of visible fat

275 stores (Dierschke 2006). Many frugivorous species stay longer on autumn migration during  
276 the period of high availability of ripe Elderberries *Sambucus nigra* than before or after this  
277 period (Ottich and Dierschke 2003). The density of passerines may affect departures due to  
278 crowding and interference (Dierschke 2006).

279 The Northern Wheatears, mainly trapped outside the trapping garden, e.g. prolonged their  
280 stopovers and defended territories whenever rich food patches occurred. Predation risk due to  
281 high numbers of raptors present on the island does not influence the departure decision of  
282 Northern Wheatears directly. However, it negatively affects the fuel deposition rate and thus  
283 indirectly the stopover decision (Schmaljohann and Dierschke 2006).

284 The decision to continue the migratory flight is also influenced by migration target and by  
285 weather, namely wind condition and cloud cover (Dierschke 2006). During spring migration,  
286 birds of the nominate subspecies of the Northern Wheatear breeding in Scandinavia have only  
287 a short flight to the next stopover needing hardly much fat and leave the island regardless of  
288 weather conditions in their seasonally appropriate direction. In contrast, those of the  
289 subspecies *O. o. leucorhoa*, which breed in Iceland and Greenland, face a long nonstop flight  
290 and stayed on much longer when wind and overcast are combined to adverse conditions  
291 (Dierschke and Delingat 2001; Dierschke 2006). Birds with high fuel loads show their  
292 seasonally appropriate migratory direction irrespective of the ecological barrier ahead,  
293 whereas lean birds avoid this direction and rather return to the mainland (Schmaljohann et al.  
294 2010).

295

### 296 **Circumstances of recovery of birds ringed on Helgoland**

297 Recoveries resulting from 100 years of bird ringing also render e.g. insight into the causes of  
298 mortality and changes of their relative importance. Recovery causes have changed  
299 considerably both, spatially and temporally. Generally a decrease in the proportion of birds  
300 killed by human persecution and an increase in the proportion due to pollution and due to  
301 anthropogenic structures (windows, vehicles, fisheries etc.) was observed (Hüppop and  
302 Hüppop 2002).

303 Recoveries of Guillemots bred on Helgoland are a good example for changing threats for  
304 seabirds (Hüppop and Hüppop 2009). Most of them have been reported as shot (mainly in  
305 Norway), were found oiled (predominantly along the shipping routes of the southern North  
306 Sea) or were retrieved through fishing activity (mainly in Sweden and Denmark). Throughout  
307 the 20<sup>th</sup> century the different threats for the Guillemot changed considerably (Fig. 3). Hunting

308 as a cause of death decreased since the end of the 1960s due to a change of hunting acts. The  
309 proportion of oiled birds increased up to a maximum of 21% in the 1980s. Besides hunting  
310 and oiling fishing activity became obvious as a substantial threat for seabirds in the 1980s  
311 (Hüppop 1996; Žydelis et al. 2009). In this decade the proportion of recovered birds killed  
312 due to fishing was 49%. Since the increase of fuel costs in the 1970s the use of the less  
313 expensive gillnet fishery, which is much more dangerous for diving seabirds and mammals,  
314 increased. It is even seen responsible for population decreases of Guillemots (Žydelis et al.  
315 2009). The subsequent decrease in recoveries reported “killed by fishery” is likely due to  
316 decreasing reporting in order to avoid a negative image (Mead 1993; Hüppop 1996; Hüppop  
317 and Hüppop 2009).

318 The recoveries of Song Thrushes give insight into the temporal and spatial development of  
319 songbird hunting throughout the last hundred years. Song Thrushes ringed on Helgoland  
320 breed in Fennoscandia and northwestern Russia and winter mainly in western Europe  
321 (Milwright 2006; Dierschke et al. 2010). With 56% to 72% of all recoveries hunting always  
322 played an important role in this species (Fig. 4). Most hunted Song Thrushes are reported  
323 from SW-European countries (cf. McCulloch et al. 1992; Payevsky and Vysotsky 2003;  
324 Milwright 2006) where the percentage even rose throughout the last hundred years (Fig. 5).  
325 This can be explained by an improved protection of other species which obviously resulted in  
326 a ‘compensatory’ increase in hunting of legitimate quarry species (McCulloch et al. 1992). In  
327 the British Isles, central and northern Europe the percentage of recoveries reported as hunted  
328 dropped to zero from the 1990ies onwards. In the three decades after the Second World War  
329 the survival rate of Song Thrushes ringed on Helgoland was significantly higher than in the  
330 years before 1945 and in the years since 1980. Presumably, this can be explained by a higher  
331 hunting pressure in whole Europe before the Second World War and increased losses due to  
332 anthropogenic structures and traffic in the last decades (Hüppop and Hüppop 2002).

333

### 334 **1960 to 2010: fifty years of constant effort trapping**

335 Birds are well known as indicators of environmental change (Furness and Greenwood 1993;  
336 Bauer and Berthold 1997; Gregory et al. 2009). Long-term constant effort trapping provides  
337 an excellent data set to reveal population dynamics (Berthold and Schlenker 1975; Dunn et al.  
338 2004), phenology (Jenni 1984; Berthold 2001; Newton 2008), annual rhythms (Gwinner  
339 1996) and the correlations between bird migration and environmental variables such as food  
340 offer, weather or climate throughout the annual cycle of birds (e.g. Berthold 1996, 2001;

341 Bairlein and Hüppop 2004; Newton 2011). Moreover, comparative analysis of standardized  
342 long-term datasets of different ringing can help to unravel large-scale migration processes  
343 (Bairlein and Schaub 2009).

344 The data on Helgoland have been collected with constant effort and methods since the early  
345 1960ies (three funnel traps, year-round trapping routine up to seven times per day during  
346 daylight; for details see Moritz 1982). Especially the year-round trapping routine allows the  
347 calculation of mean species-specific seasonal passage times as arithmetic means (or other  
348 measures) of the daily trapping totals (Hüppop & Hüppop 2004). Means have a much higher  
349 value than first arrival dates since the latter often differ dramatically from changes in the  
350 mean arrival date of the migration cohort as a whole (Mason 1995; Sparks et al. 2001; Miller-  
351 Rushing et al. 2006; Lehikoinen and Sparks 2010).

352

### 353 **Changes in numbers**

354 In contrast to the constant conditions within the trapping garden, the amount of vegetation  
355 outside the garden has increased substantially throughout the whole island after it had been  
356 erased almost totally at the end of the Second World War (see above). In order to be able to  
357 conduct trend analyses, we recalculated the ringing data using a correction factor for the  
358 substantially increasing island vegetation (corrected ringing number indices = CRNI; Hüppop  
359 and Hüppop 2007). From 1960 to 2004, the CRNI decreased in 49 of the 66 considered  
360 species (significantly in 40 of them). It increased in ten species (seven significantly) and in  
361 seven species it did not change. For all species taken together, CRNI decreased significantly  
362 by 42% (by 39% in the SMD-migrants and 55% in the LD-migrants). This striking decrease  
363 especially in LD-migrants is in accordance with very similar results from other Central and  
364 Eastern European as well as Scandinavian ringing stations (Hüppop and Hüppop 2007). CRNI  
365 divided in different ecological guilds show decreases by 33% in forest birds, 58% in farmland  
366 birds, 74% in waterside birds) and 46% in other categories.

367 The recent strong decrease of LD-migrants (Berthold et al. 1998; Sanderson et al. 2006;  
368 Heldbjerg and Fox 2008; Robinson et al. 2009; Both et al. 2010) is reflected also in the  
369 change of their proportion of all birds ringed in the trapping garden from 1968 to 2008  
370 (Fig. 6). Whereas the LD-migrants made 25.5% and the SMD-migrants correspondingly  
371 74.5% in 1968, the relation was 15.5% to 84.5% in 2008. Especially in the very last years  
372 extremely low proportions of LD-migrants are obvious (trapping number indices of SMD-  
373 migrants remained constant from c. 1980 onwards; Hüppop and Hüppop 2007).

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

383

### 384 **Phenology**

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

393

### 394 **Climate change related alterations in phenology**

395 By now there is no doubt that extensive global climate change has proceeded within the last  
396 decades which can be attributed to human activities (e.g. IPCC 2007; Solomon et al. 2009).  
397 Impacts on ecosystems, populations and species have become obvious and generally known  
398 (e.g. Walther et al. 2002; Root et al. 2003; Parmesan 2007; Loarie et al. 2009). For migrant  
399 bird species e.g. earlier arrival date in spring, earlier start of breeding, changes of several  
400 other breeding parameters or range extensions northwards have been shown, but also changes  
401 in autumn migration and in wintering behaviour are obvious (e.g. Burton 1995; Thomas and  
402 Lennon 1999; Bairlein and Winkel 2001; Cotton 2003; Hüppop and Hüppop 2003; Jenni and  
403 Kéry 2003; Møller et al. 2004, 2010; Sparks and Mason 2004; Jonzén et al. 2007; Rubolini et  
404 al. 2007).

405 For 24 species trapped in the trapping garden on Helgoland with sufficient sample size the  
406 calculation of yearly mean spring passage times (= msp-times; Hüppop and Hüppop 2003)  
407 was possible for the years 1960 to 2008. In this period 22 of them advanced their msp-time.  
408 This earliness was significant in 11 of 12 SMD-migrants, in all 10 LD-migrants and in  
409 Blackcap and Chiffchaff *Phylloscopus collybita* (which on Helgoland can be expected to  
410 belong to both groups; Zink 1973). The changes of msp-times ranged from a delay in  
411 Brambling *Fringilla montifringilla* by 2.5 days to an earliness of up to 17.4 days in Blackcap  
412 and 16.8 days in Chiffchaff within the past 48 years (Fig. 8). Although the LD-migrants pass  
413 Helgoland about six weeks later than the SMD-migrants, the extent of earliness (on average  
414 10 and 8.5 days in LD- and SMD-migrants, respectively) was not significantly different  
415 (Mann-Whitney-U-Test,  $U = 85.0$ ,  $p = 0.107$ ; Fig. 9). This is in contrast to many other  
416 studies, where LD-migrants did not advance their arrival times as much as SMD-migrants  
417 (Lehikoinen et al. 2004; Lehikoinen and Sparks 2010). However, this might be an artefact  
418 since first arrivals, as used in many calculations, did change differently from mean arrivals  
419 e.g. if population sizes decrease (Miller-Rushing et al. 2006) which actually is the case in  
420 many LD-migrants (see above). In many cases, first arrivals might be regarded as the outliers  
421 of the whole cohort.

422 Due to higher variability of the weather in early spring the msp-time is more variable in those  
423 species which arrive earlier, i.e. in SMD-migrants. In SMD-migrants the trend towards  
424 earliness is significantly stronger in the earlier migrating species than in the later ones. A  
425 similar relationship is found in LD-migrants, though not significant (Fig. 9; see also  
426 Lehikoinen et al. 2004; Lehikoinen and Sparks 2010).

427 In autumn the picture is quite different and not all uniform: From 26 species with sufficient  
428 sample size 11 species showed a trend towards delay and seven species a trend towards  
429 earliness in mean autumn migration time (map-time) from 1960 to 2008. Most species did not  
430 change their map-time significantly, only two species advanced and three species delayed  
431 significantly (Fig. 10). Maximal delays could be observed in Chiffchaff (10.0 days) and in  
432 Whinchat *Saxicola rubetra* (9.8 days), maximal earliness in Brambling (18.3 days) and in  
433 Sparrowhawk (12.4 days). No significant difference in the trend of map-time within the  
434 48 years could be observed between the two migration categories (Mann-Whitney-U-Test,  
435  $U = 66.0$ ,  $p = 0.928$ ). This contradicts other findings where LD-migrants had a tendency to  
436 advance their autumn migration times, whereas SMD-migrants rather had a tendency to  
437 migrate later (Jenni and Kéry 2003; Tøttrup et al. 2006; Filippi-Codaccioni et al. 2010;

438 Lehtikoinen and Sparks 2010). The reasons for that difference are still unknown and need  
439 further analyses.

440 In 20 species, sample sizes were sufficient to calculate both, msp- as well as map-times. From  
441 1960 to 2008 the difference between the two migration times increased in all but one of these  
442 species (in 10 SMD-migrants, 7 LD-migrants and in Blackcap and Chiffchaff) by up to  
443 26.5 days in Chiffchaff and 17.3 days in Chaffinch *Fringilla coelebs* (Fig. 11). Only the  
444 Brambling differed from this scheme and showed a significant decrease of the difference by  
445 19 days within the 48 years. The increase of the difference did not differ significantly between  
446 the two migration categories (Mann-Whitney-U-Test,  $U = 47.0$ ,  $p = 0.479$ ). Since it is largely  
447 a result of the earlier msp-time, this increase reflects a prolongation of the time spent at the  
448 Scandinavian breeding grounds with the opportunity to increase breeding success (Hüppop  
449 and Hüppop 2008).

450 Generally, the msp-times are in all species except Brambling negatively related to the local  
451 temperatures within the species-specific migration times (msp-temperatures) from 1960 to  
452 2008, significantly in 11 SMD- and seven LD-migrants, respectively, and in Blackcap and  
453 Chiffchaff ( $p_{(1)} < 0.05$ ; examples in Fig. 12). However, msp-temperatures explain on average  
454 a three times higher proportion of the variance in msp-time in SMD-migrants than in LD-  
455 migrants (Fig. 13; Mann-Whitney-U-Test,  $U = 106.5$ ,  $p = 0.0024$ ). We attribute this to the  
456 different migration and wintering strategies of the two groups: SMD-migrants winter much  
457 closer to Helgoland than LD-migrants (maps in Dierschke et al. 2010). This means that the  
458 sites of their last departures are closer to Helgoland and temperatures there are accordingly  
459 closer correlated with those in the Helgoland area. In contrast, LD-migrants coming from sites  
460 further away might experience “climatic barriers” en route with e.g. low temperatures (Ahola  
461 et al. 2004; Hüppop & Winkel 2006). This lowers the  $R^2$  of the correlations between msp-  
462 times and temperatures at Helgoland. Further, responses of birds and other organisms to  
463 climate change are much more than simply a reaction to instantaneous temperatures  
464 (Harrington et al. 1999; Day et al. 2010; Saino et al. 2011). While temperatures in winter and  
465 early spring are crucial for the time of budburst, insect winter survival and speed of insect  
466 development, they have comparatively smaller effects later in the season. E.g., the threshold  
467 for aphid development is as low as roughly  $4^{\circ}\text{C}$  (Hullé et al. 2010) and aphid population  
468 growth rate is positively correlated with the accumulated time with temperatures above this  
469 threshold before budburst and negatively correlated with the number of periods of five  
470 consecutive chill days during winter (Day et al. 2010). Hence, the occurrence of food

471 organisms during the spring passage of LD-migrants is decisively influenced by the weather  
472 long before the LD-migrants pass Helgoland.

473 The msp-times of the LD-migrants are better explained by the large scale climatic  
474 phenomenon of the North Atlantic Oscillation (NAO). The NAO influences, besides many  
475 other things, the strength of the winter and early spring throughout the whole passage area of  
476 the LD-migrants within western and northern Europe. The winter-NAO-index describes the  
477 situation in winter and early spring (December to March), with positive indices going along  
478 with stronger winds from the west and associated higher temperatures and higher levels of  
479 precipitation from the Atlantic Ocean namely to central and northwest Europe (Hurrell et al.  
480 2001; Visbeck et al 2001). In 23 of our 24 species on Helgoland msp-times are negatively  
481 correlated with the winter-NAO-index (significantly in nine SMD-migrants, nine  
482 LD-migrants and in the Chiffchaff;  $p_{(1)} < 0.05$ ; examples in Fig. 12), i.e. birds arrive earlier  
483 after mild winters. Although their mean migration times differ by about six weeks, the  
484 influence of the NAO-index does not differ between the two migration categories (Fig. 13,  
485 Mann-Whitney-U-Test,  $U = 45.0$ ,  $p = 0.339$ ). Thus, their msp-time is influenced by the NAO  
486 in winter that is by the “preparation of the spring”, to the same degree. Mild winters  
487 associated with a positive NAO-index cause e.g. the spring migration of the green spruce  
488 aphid (*Elatobium abietinum*, a pest species of spruce trees) in England to start earlier, to  
489 continue for longer and to contain more aphids, but not to end earlier (Westgarth-Smith et al.  
490 2007). As expected, the msp-temperatures explains on average a higher proportion of the  
491 variance than the winter-NAO-index in the SMD-migrants while the opposite is true in the  
492 LD-migrants (Fig. 13).

493 Climate variables measured during breeding and autumn migration times have changed less  
494 consistently throughout the last five decades than in winter and spring. Accordingly, we were  
495 not yet able to explain the few observed changes in map-time by climate variables (Hüppop  
496 and Hüppop 2005).

497

## 498 **Conclusions**

499 More than 160 years of ornithological research on the small island of Helgoland, including a  
500 century by the Institute of Avian Research “Vogelwarte Helgoland”, resulted in a list of more  
501 than 1,200 publications (Dierschke et al. 2010). It includes hundreds of short notes on field  
502 ornithology as well as several books and many papers published in scientific journals  
503 covering a broad spectrum of topics. Reviewing all of them would have been far beyond the

504 scope of this article, e.g. articles on seabird ecology and studies on impacts of oil, chemical  
505 and garbage pollution, of human disturbances, of fisheries and of windfarms on birds had to  
506 be largely neglected here (but see Bairlein and Becker 2010 and Dierschke et al. 2010 for  
507 further details).

508 Presumably the biggest treasures of the station on Helgoland are the long-term dataset won by  
509 constant effort bird catching in the trapping garden and the immediate access to birds and bird  
510 migration. Modern technology, progress in biochemical methods, computer facilities and the  
511 feasibility of experimental approaches keep the field wide open for many still unanswered  
512 questions and further exciting research.

513

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519

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772 **Figure captions and table**

773

774 Fig. 1: Annual sums of ringings on total Helgoland from 1909 to 2009 (n = 795,604)

775

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

779

780 Fig. 3: Circumstances of recovery of Guillemots *Uria aalge* ringed on Helgoland in six  
781 periods from 1909 to 2008 (n = 653; after Hüppop and Hüppop 2009)

782

783 Fig. 4: Circumstances of recovery of Song Thrushes *Turdus philomelos* ringed on Helgoland  
784 in six periods from 1909 to 2008 (n = 1,091)

785

786 Fig. 5: Recoveries of Song Thrushes *Turdus philomelos* ringed on Helgoland reported as  
787 hunted in six periods from 1909 to 2008 in northern European (top, n = 236) and southern  
788 European countries (bottom, n = 859)

789

790 Fig. 6: Trend in the proportion of SMD-migrants (black) and LD-migrants (grey) ringed in the  
791 trapping garden on Helgoland from 1968 to 2008 (after Hüppop and Hüppop 2007,  
792 supplemented)

793

794 Fig. 7: Annual phenology of the SMD-migrants (black columns) and the LD-migrants (grey  
795 columns) in the trapping garden on Helgoland from 1960 to 2008 (after Hüppop and Hüppop  
796 2004, supplemented)

797

798 Fig. 8: Shift in msp-time in 24 species on Helgoland from 1960 to 2008 trapped with constant  
799 effort (asterisks indicate significant changes according to linear regression,  $p_{(2)} < 0.05$ )

800

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

805

806 Fig. 10: Shift in map-time in 26 species on Helgoland from 1960 to 2008 trapped with  
807 constant effort (asterisks indicate significant changes according to linear regression,  $p_{(2)} <$   
808  $0.05$ )

809

810 Fig. 11: Mean shift in the difference between msp- and map-time in 20 species on Helgoland  
811 from 1960 to 2008 trapped with constant effort (asterisks indicate significant changes  
812 according to linear regressions,  $p_{(2)} < 0.05$ )

813

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

822

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

830

831 Table 1: The ten most frequently on Helgoland ringed species before and after the Second  
 832 World War and the ten most frequently recovered species

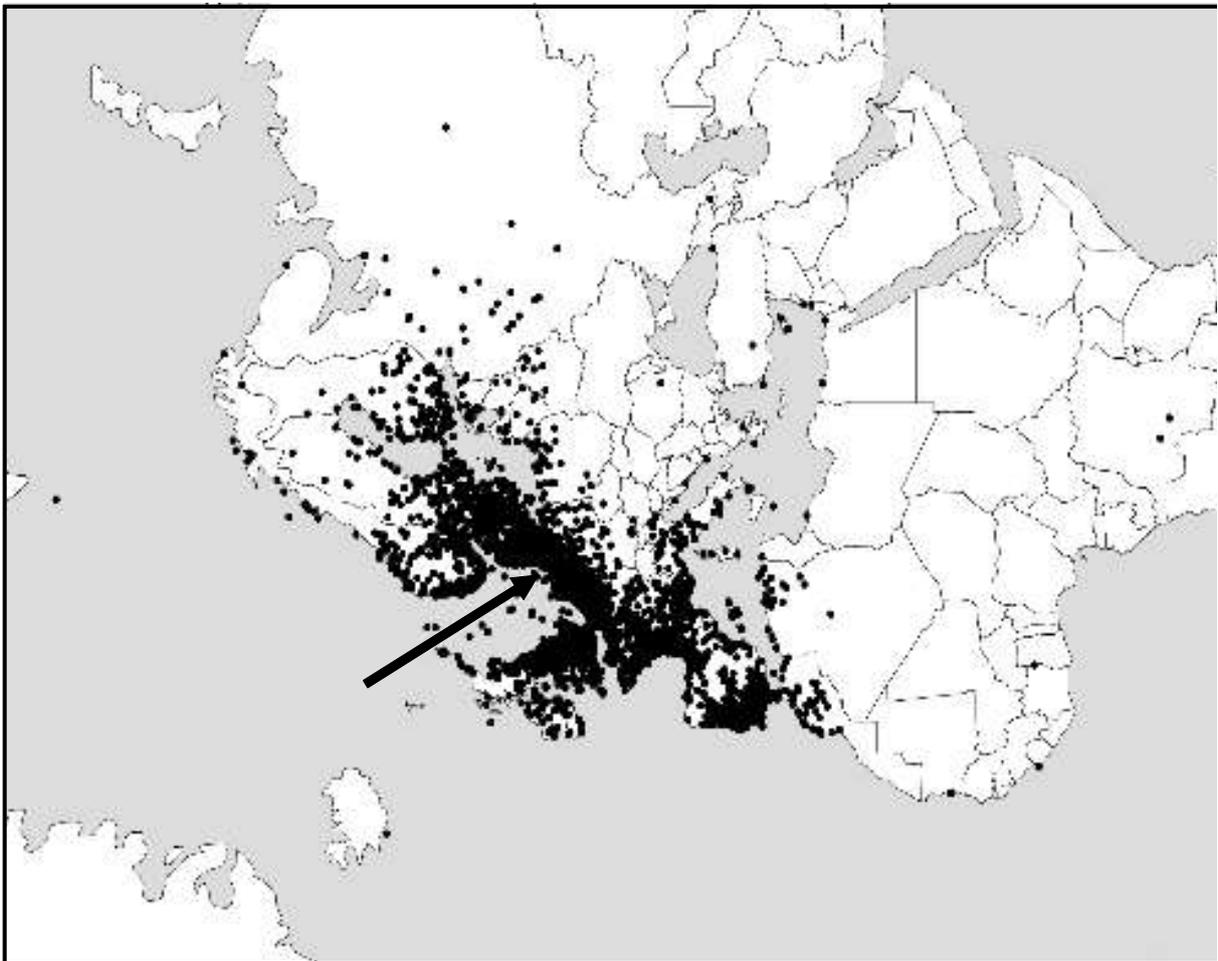
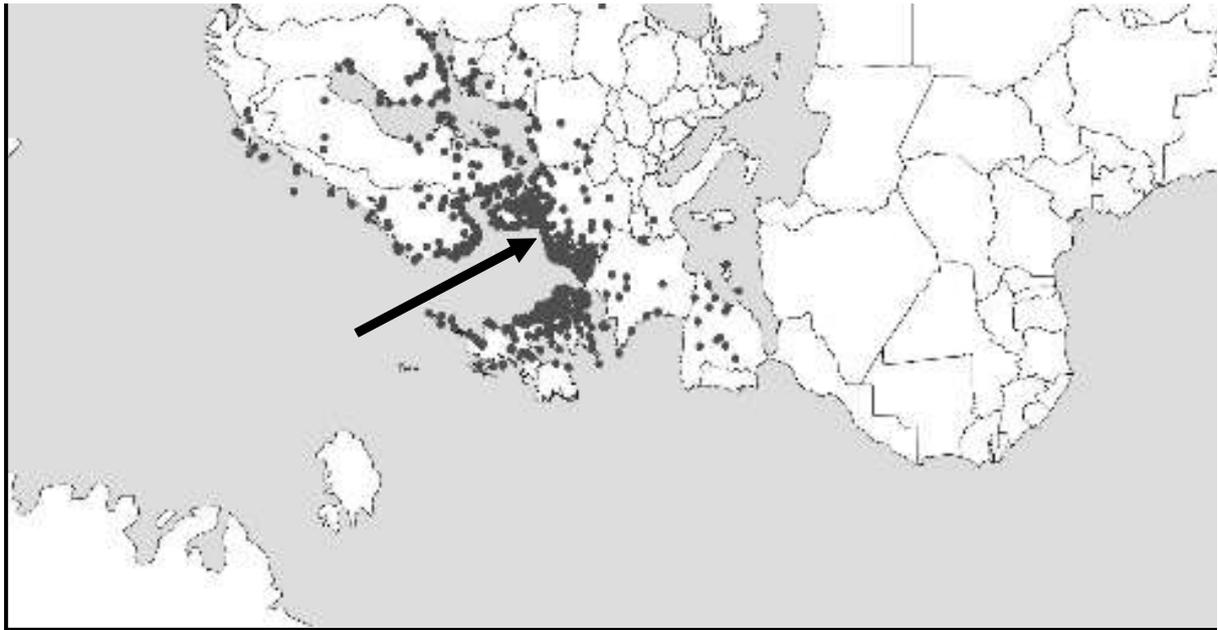
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Ringings from 1909 to 1945			Ringings from 1953 to 2009			Recoveries from 1909 to 2008		
Species	n	%	Species	n	%	Species	n	%
Song Thrush	21,458	15.9	Song Thrush	119,801	18.1	Blackbird	1,378	19.9
<i>Turdus philomelos</i>			<i>Turdus philomelos</i>	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

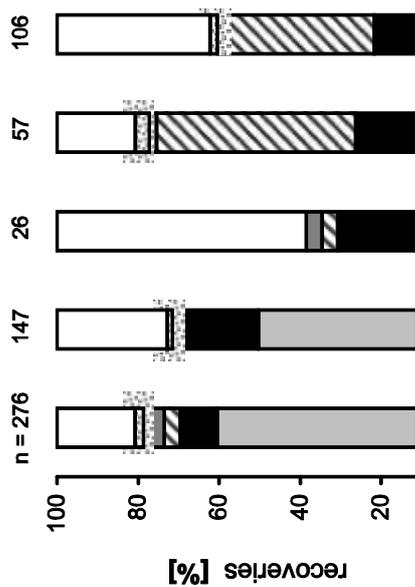
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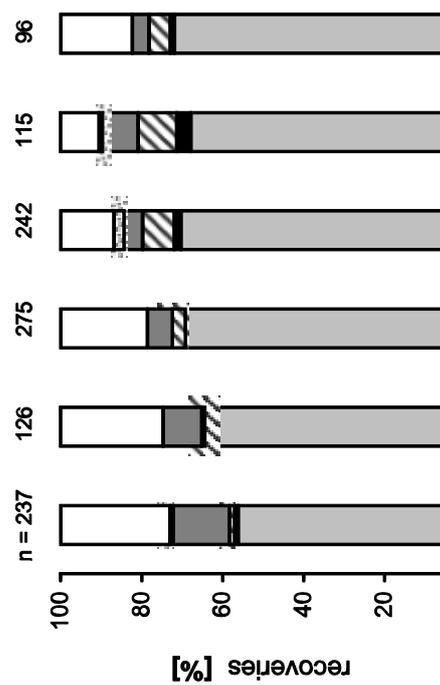
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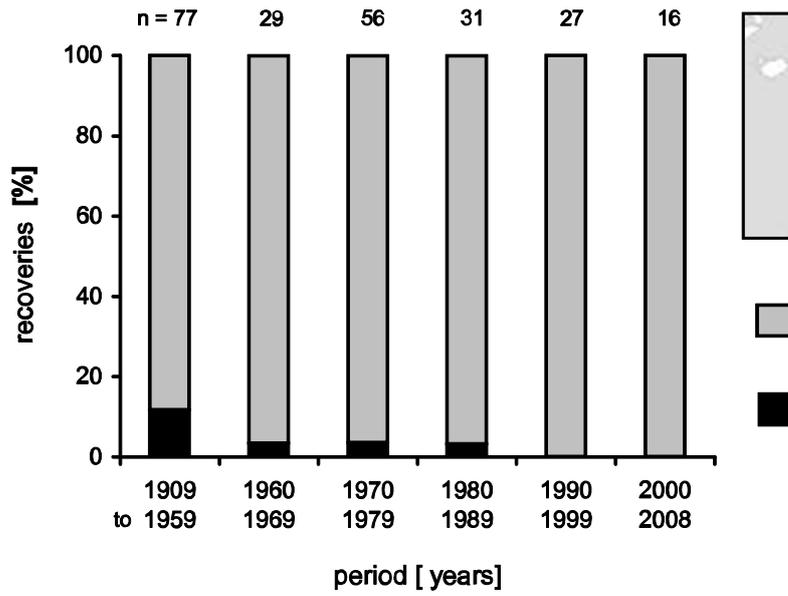
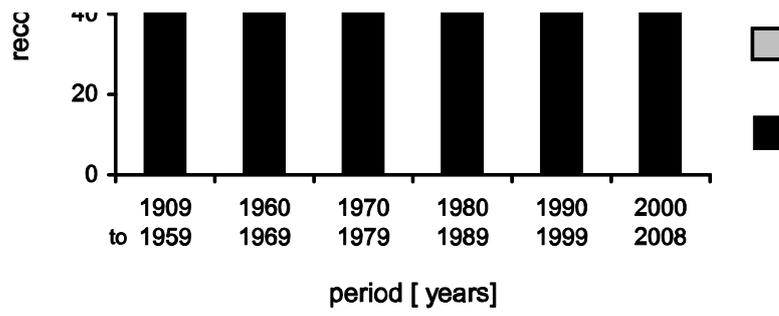
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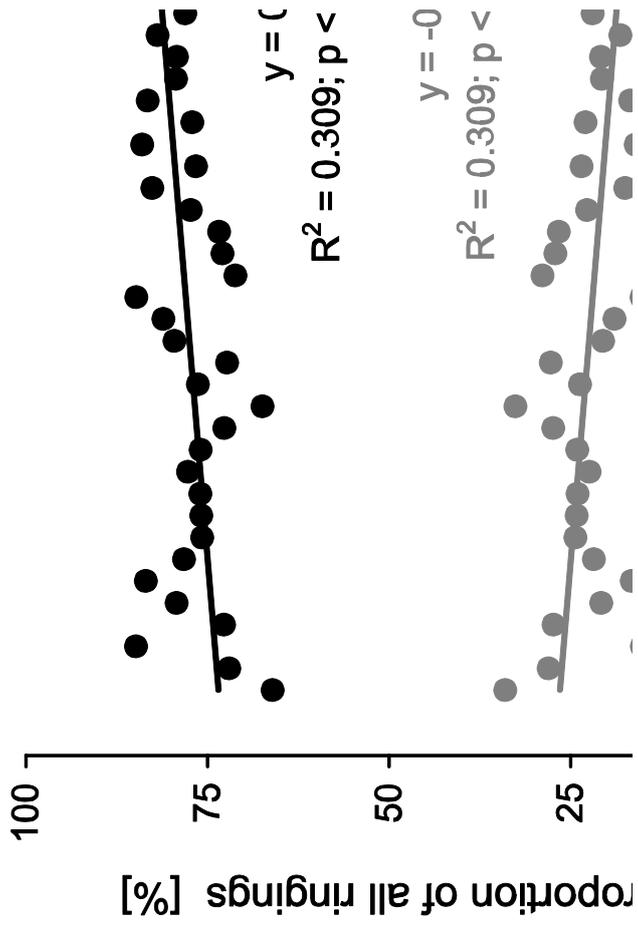


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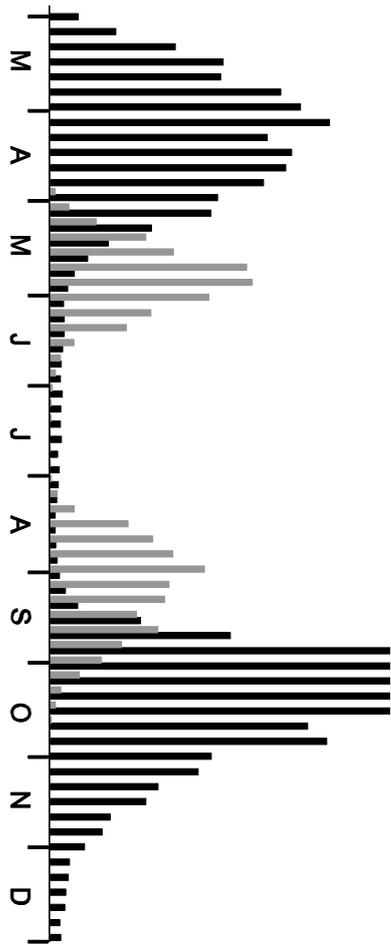


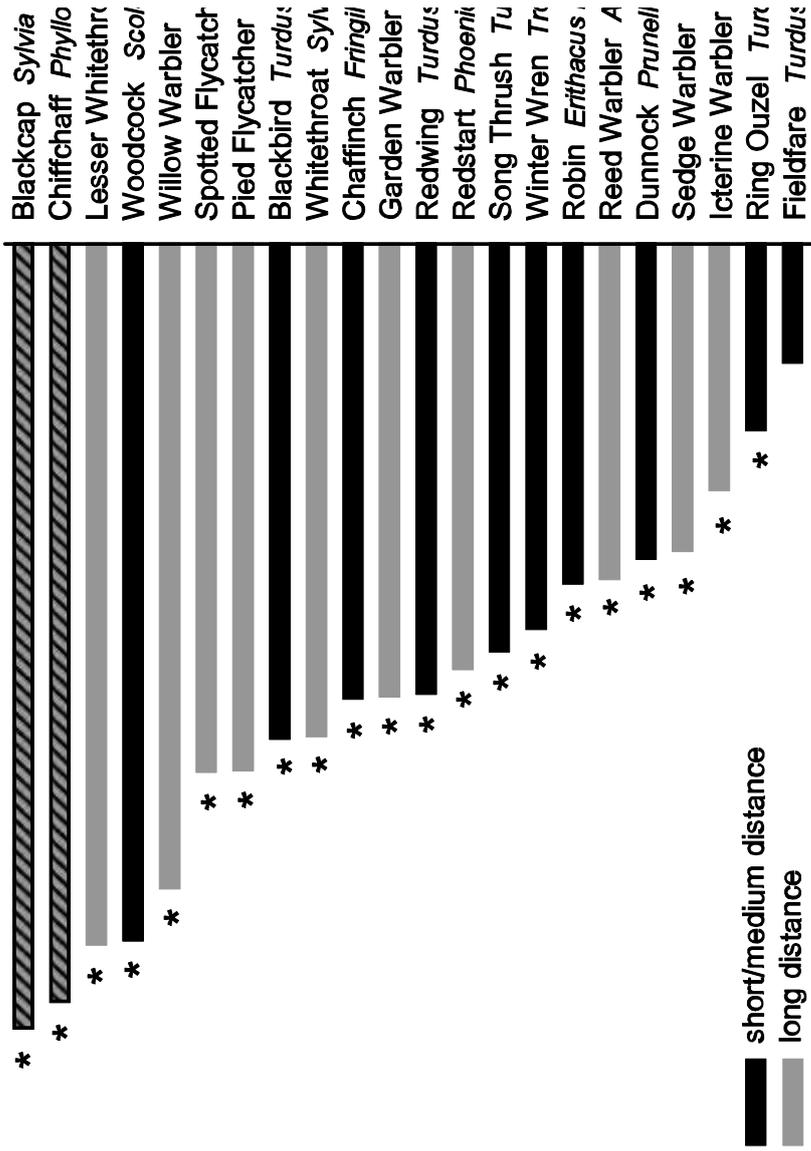
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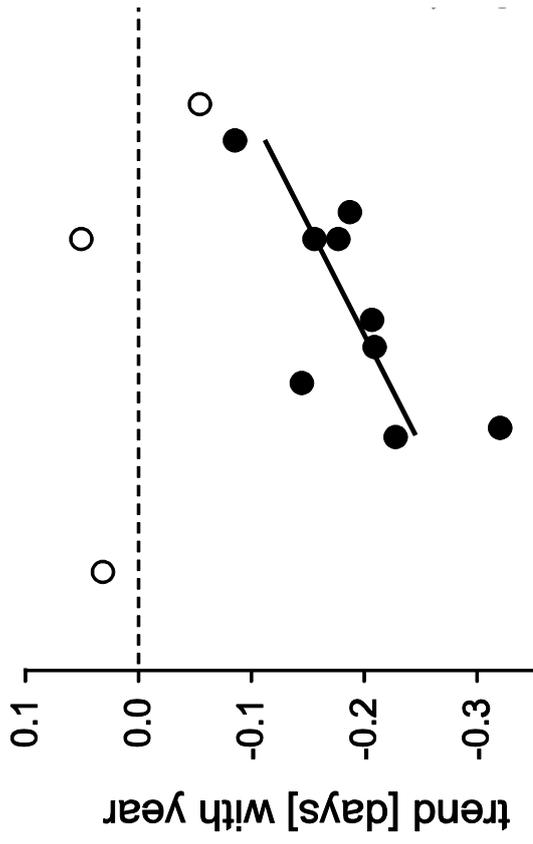




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