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Post-breeding dispersal, breeding site fidelity and migration/wintering areas of migratory populations of Song Thrush *Turdus philomelos* in the Western Palearctic

R. D. P. MILWRIGHT
17 Forehill, Ely, Cambridgeshire CB7 4AA, UK

Song Thrush *Turdus philomelos* ring recovery data gathered over 90 years in central, north and east Europe were analysed in their breeding zones and in 14 migration/wintering areas in Europe, North Africa and the Near East. Few post-breeding movements were over 20 km before the end of September. Subsequent-year breeding site fidelity was high in May to August. Migratory *T p philomelos* moved southwest in autumn on a broad front. Scandinavian and northwest Russian birds moved down the northwest coast of continental Europe arriving in large numbers in southwest France in October; many adults then moved on to winter in west Iberia. Those ringed in central Europe, from Switzerland to Belarus, tended to follow the Rhine–Rhône route to the French Mediterranean before dispersing to winter in east Iberia, the Balearics and Algeria. Southeast European birds moved to north and west Italy in the autumn/early winter, many adults moving on to Corsica or Sardinia. Birds breeding in the Netherlands and northwest Germany appear to have two migration patterns. A short-distance group dispersed through Belgium to northwest France in autumn/early winter, moving on to England and Wales in late winter. A long-distance group migrated to southeast Biscay in October, many then moving on in midwinter to west Iberia. Recoveries of birds ringed in the Netherlands and northwest Germany showed a change to a more sedentary population after 1989, raising the possibility that the less migratory *T p clarkei* has increased in abundance relative to *T p philomelos* in this area. Subspecific identification would be useful to assess future changes in range boundaries of *philomelos* and *clarkei* within northern Europe.

Song Thrushes *Turdus philomelos* are medium-sized thrushes breeding over a vast range from Ireland to Lake Baikal, and southern Spain and Iran to Lapland and Arctic Russia (Hagemeijer & Blair 1997). The breeding range has expanded from 60°N to 70°N in Scandinavia during the 20th century (Melde & Melde 1991). Three Western Palearctic subspecies are recognised. The Scottish Western Isles contain the resident *hebridensis.* The largely resident *clarkei* occurs in Britain & Ireland, northwest France, Belgium and the Netherlands (Lack 1986, Cramp 1988). The rest of continental Europe holds the nominate *philomelos* whose populations vary from non-migratory in the west to highly migratory in central, northern and eastern Europe (Hagemeijer & Blair 1997). Migratory Song Thrushes winter in west Europe, around the Mediterranean Basin, the Transcaucasus, around the northern end of the Persian Gulf (Dementiev & Gladkov 1954, Cramp 1988), and in Eritrea (Moreau 1972). Previous analyses of the species' movements have concentrated on birds moving to or from particular countries (Ashmole 1962, Wernham *et al* 2002) or have used old data sets, which can now be updated (Zink 1981).

This paper reports an analysis of 17 long-term data sets with late summer, autumn, winter and subsequent breeding season recoveries of Song Thrushes ringed in the breeding season from the Maas/Rhine valleys (Netherlands–Switzerland) eastwards to Lake Baikal. Post-breeding dispersal, between-season breeding site fidelity and migration/wintering patterns are examined. Combined data for many years are analysed and long-term temporal changes investigated. The results describe an average picture of migratory Song Thrush movements, which may hide year-to-year variations.

METHODS

Ringing and recovery data (15,742 recoveries) were obtained from ringing schemes (Table 1). Breeding populations were assumed to be migratory if fewer than

Email: digby.milwright@ntlworld.com

Table 1. Data sets analysed.

Country of ringing	Period
Austria	1951–2002
Czech Republic	1935–2003
Denmark	1933–2002
Finland	1930–2002
Germany Helgoland	1909–1999
Germany Radolfzell	1948–2002
Greece	1986–2000
Hungary	1929–2005
Lithuania	1956–2001
Netherlands	1913–2004
Norway	1922–2003
Poland	1933–2004
Slovakia	1938–2002
Sweden	1922–2002
Switzerland	1913–2003
USSR/Russia (inc. Belarus, Estonia, Latvia, Ukraine and Siberia)	1929–2000
Yugoslavia (all former Yugoslav states)	1951–1999

10% of December–February recoveries were in their 'Home' area (movements less than 20 km).

Breeding zones and breeding seasons

The breeding area follows Cramp (1988). Areas where migrating Song Thrushes have been ringed in the breeding season were divided into four ringing zones and seven sub-zones (Fig 1) by grouping adjacent national ringing areas with similar recovery patterns (Milwright 1994, 2002). Germany and Russia were further divided – northwest Russia with Finland and the Baltic Republics forms zone A2, and northwest Germany with Netherlands forms zone D, (selected to include the eastern boundary of *clarkei* breeding range). For convenience, short names, which were not intended as a complete geographical description of each area, were given to each zone.

The basic unit for analysis in this paper was 'the Song Thrush recovery of known breeding origin'. Long-distance recoveries occurred in any month but such movements were at a minimum in May–July. This was considered the 'core' breeding season for the post-breeding dispersal analysis of same-season August–November recoveries (below). The breeding site fidelity analysis, of birds recovered in any subsequent April–September period (below), included birds ringed in the period May–August.

Over much of their range Song Thrushes start breeding in April, when many from the migratory

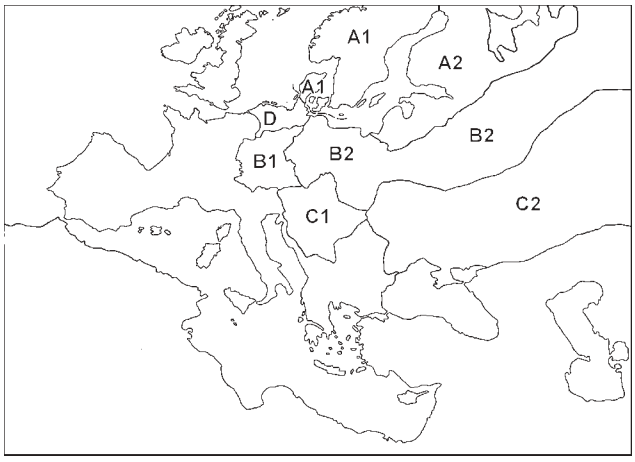

Figure 1. Ringing (breeding) zones where migratory Song Thrushes have been ringed in the breeding season. Short names are in brackets. A1, W Scandinavia. A2, Baltics/Finland/NW Russia (E Baltic). B1, W Central Europe (WC Europe). B2, E Central Europe (EC Europe). C1, SE Europe. C2, S&E Russia/Ukraine/Siberia (S&E Russia). D, Netherlands/NW Germany.

populations are still on return migration. Assessment of breeding origin of April-ringed birds is confused by these passage birds, particularly in the western breeding zones. In zones further to the north and east this becomes less of a problem since those birds present in April can be considered to have arrived at their breeding site. Therefore, for analysis of migration/winter movements, records of April-ringed birds were included only (a) when ringed anywhere as nestlings or newly fledged juveniles, or (b) when ringed in the north and east breeding zones.

Post-breeding dispersal analysis and breeding site fidelity analysis both showed that most September recoveries were under 20 km from their breeding sites, although a few had already moved long distances 'downstream' to migration/winter areas. For the migration/winter analysis, September-ringed birds were included when ringed in the north and east breeding areas. The small east Russian/Siberian sample was enlarged by including all birds ringed east of 40°E.

Migration/winter season and areas

Autumn and spring migration periods were both included within the 'migration/winter' period of September–April. All Home recoveries (0–20 km) during December–February were also included in the analysis, but Home recoveries in September–November and March/April were not considered to have shown either an intention to remain in the Home area for the winter or to migrate, and were rejected.

The migration/winter recovery areas were defined mainly by boundaries between large water catchments.

These follow Milwright (2002), with some changes and renaming, and are placed in five groups, North (N1–3), West (W1–3), South (S1–4), Southeast (SE1–3) and East (E1) (Fig 2). For convenience, short names are given to some zones. These names are not intended to represent a complete geographical description of each area.

Age determination

Song Thrushes ringed as nestlings or newly fledged juveniles and recovered in their first winter were designated 'juvenile' (not 'first-winter' to avoid confusion with adults recovered in their first winter after ringing). Those ringed as adults (one year or older), and those ringed at any age and recovered more than one winter later were 'adults'. Birds not aged at ringing and recovered in the first subsequent winter remain 'unaged'. Where juvenile:adult ratios were shown, unaged birds were excluded.

Hunting index

Song Thrush hunting indices were calculated for each migration/winter area (McCulloch *et al* 1992). Indices were generally high but there were variations between areas. Iberian, southern French, Italian and Greek indices were high (range 90–94%). Belgian, north French and Algerian ranges were medium (70–76%), and England/Wales, Netherlands and north Germany were low (2–8%). Taking means of these three groups, a 5% index increases the chance of recovery (over 'background, no hunting') by just over 5% (5/95 x 100), a 73% index by just over 270% (73/27 x 100), and a 92% index by just over 1,150% (92/8 x 100). This method gave a long-term index. Many other factors also affect chance of recovery, notably the catching of already-ringed birds by bird ringers – particularly active in the three low index areas. However, considering the hunting effect alone, a very rough correction to recovery rates was made by multiplying low-index area recovery numbers by 10 and medium area numbers by three.

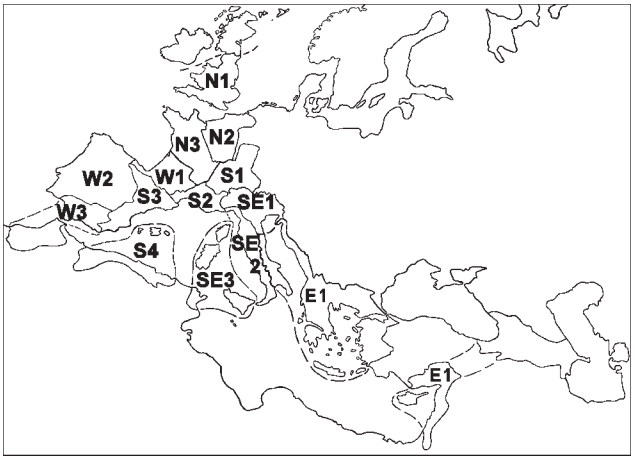

Figure 2. Winter recovery areas of migratory Song Thrushes. Short names are in brackets. North: N1, England/Wales; N2, Belgium/NE France; N3, NW France. West: W1, SE Biscay; W2, W Iberia; W3, S Iberia/Morocco. South: S1, S Rhine-N Rhône; S2, French Mediterranean; S3, E Iberia; S4, Balearics/Algeria. Southeast: SE1, N Italy; SE2, W Italy; SE3, Corsica/Sardinia/Tunisia/Sicily (Corsica/Tunisia). East: E1, S Adriatic/Aegean/Levant/Transcaucasus (Aegean/Levant).

Statistics and histograms

Significance levels for each cell in Tables 2–6 were derived from individual-cell χ^2 values adjusted for the relevant degrees of freedom (*eg* 21 df in Table 5). Using data from all zones of origin and all recovery areas, three 7x14 tables were constructed of juvenile, adult and all recoveries. Percentages of recoveries in each cell were calculated in columns (zone of origin) but compared in rows (recovery areas). These were used to construct histograms for each recovery area (Fig 3). Thus, the percentage of all recoveries from each zone of origin that were recovered in a given recovery area were compared within that area directly with those from all other zones. This method produced an individual histogram representing the distribution of ringing origins for each recovery area. A similar procedure, using month of recovery instead of zone of origin, was used to construct temporal histograms (Figs 4–5).

For clarity, scales for the histograms (Figs 3–5) were selected so that the largest histogram bar in each histogram is at a similar height in all cases. The absolute percentage values on y-axes varied from one histogram to another due to variations in recovery circumstances/rates between different recovery areas. Comparison of the frequency distributions between histograms allows differences in recovery circumstances/rates between recovery areas to be eliminated from the analysis, since all recoveries in each recovery area, whatever their zone of origin, were subjected to the same hunting pressures or recovery circumstances. Standard errors calculated for each histogram bar are not shown in Figs 3–5 because of the large number of bars, and the consequent loss of clarity.

RESULTS

Post-breeding dispersal (August–November)

A total of 391 Song Thrushes (351 juvenile, 40 adult) were ringed in May to July and recovered in the first

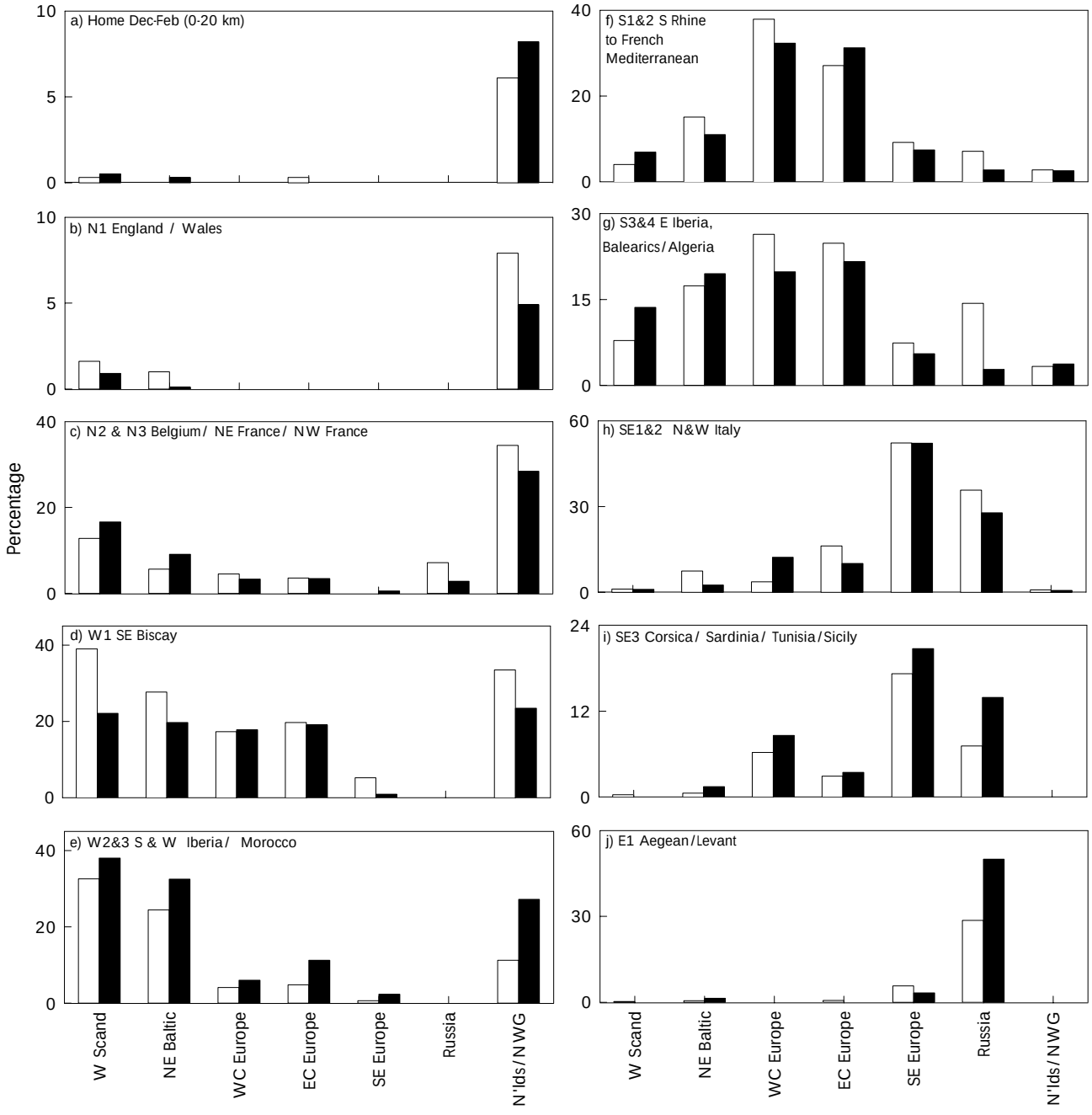

Figure 3. Percentages of juvenile (open bars) and adult (filled bars) recoveries from each ringing zone recovered in each recovery area. Relative frequency distributions should be compared, but absolute percentages should not (see Methods).

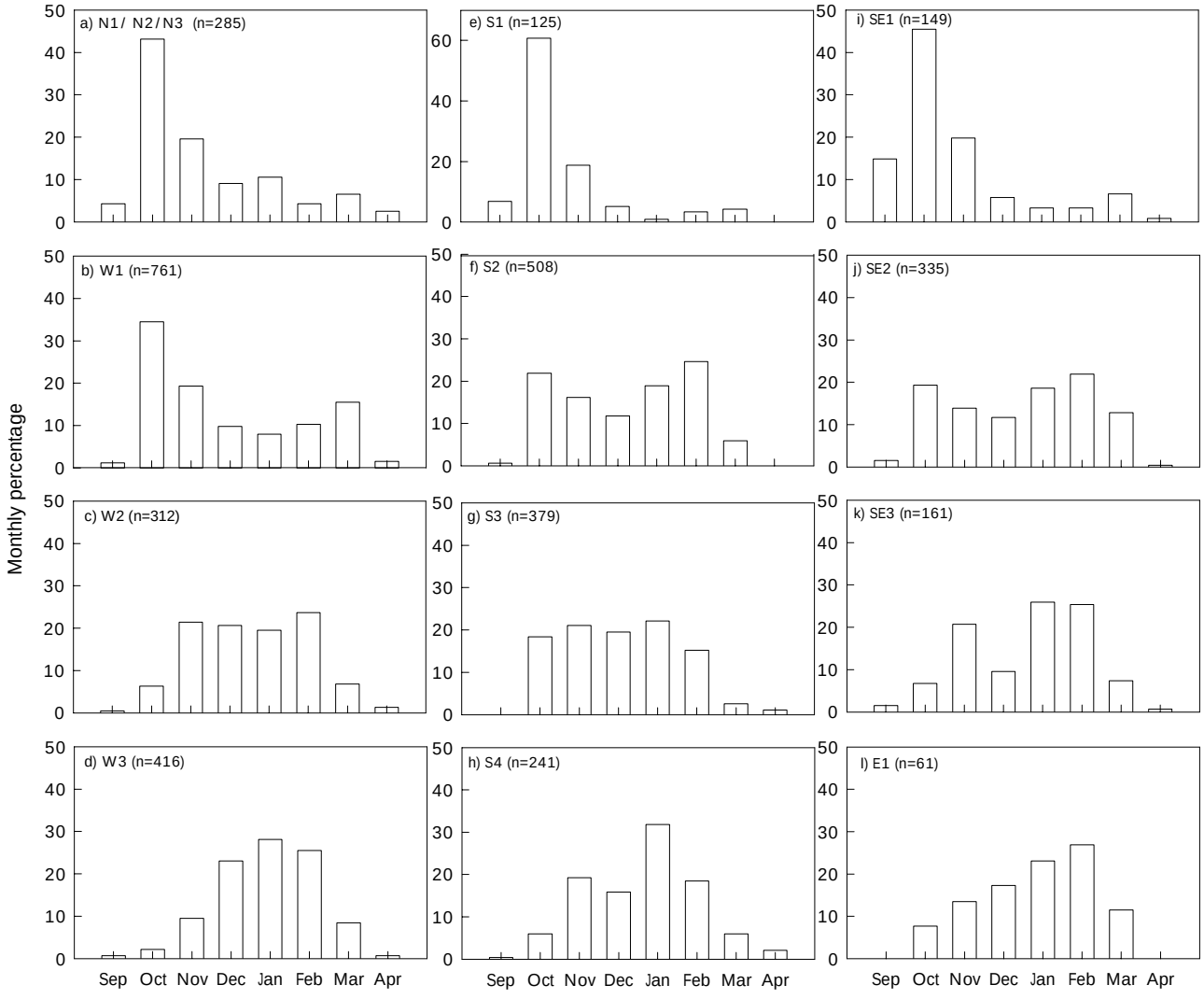

Figure 4. Monthly percentages of Song Thrushes ringed in zones A, B and C that were recovered in each recovery area. Relative frequency distributions should be compared, but absolute percentages should not (see Methods).

August/September after ringing. Of the August recoveries (148 juvenile, 23 adult), 96% showed movements of less than 20 km (Table 2). Three with movements over 100 km were one juvenile 125 km from its ringing site but still within its zone of origin, one Czech juvenile (an early migrant in N Italy), and one adult ringed in Sweden in late May which was recovered east of Leningrad (either a relocation during the breeding season or an early reverse migratory movement).

Of September recoveries (203 juvenile, 17 adult), 75% were within 20 km of the ringing site. The 39 September movements over 100 km included three between 144 and 332 km but still within their zone of origin, and 36 'downstream' in the migration/wintering areas: the longest movement was a juvenile moving 3,100 km from Sweden to Spain.

There were 1,838 birds that were recovered in their first October/November after ringing, but the overall Home (0–20 km) recovery rate in these months was low (8%). Most (90%) had already arrived in the migration/winter areas.

However, zone D birds (Netherlands/NW Germany) differed from the rest. They had a higher October/November Home recovery rate throughout, and since 1990 a startling rise in that rate (Table 3). The difference in rates before (10%) and after (87%) January 1990 within zone D was highly significant ($\chi^2 = 198.19$, $P < 0.001$). No such temporal change was found in data from other ringing zones. The difference

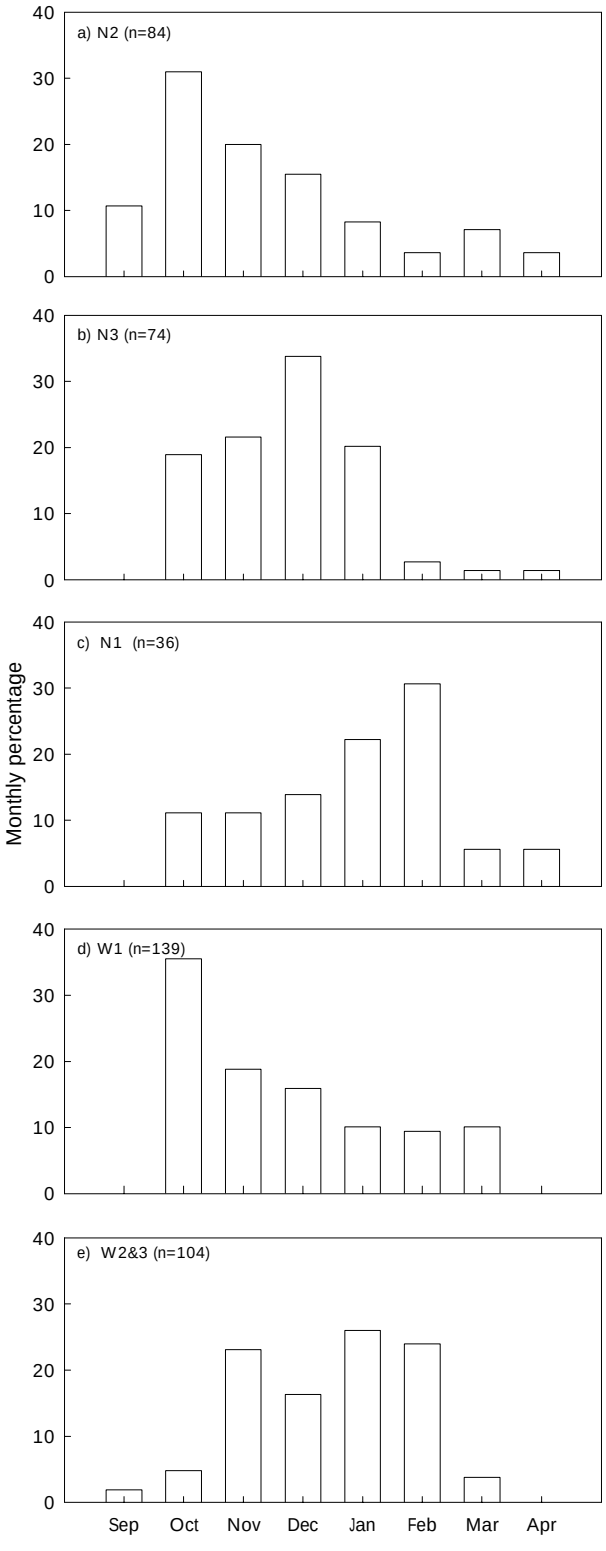

Figure 5. Monthly percentages of Song Thrushes ringed in zone D (Netherlands/NW Germany) that were recovered in each North and West recovery area. Compare relative frequency distributions.

between the pre-1990 rate for zone D birds (10%) and those from all other ringing zones (2%) was also highly significant ($\chi^2 = 35.86$, $P < 0.001$).

Breeding site fidelity between years

In total, 632 Song Thrushes ringed in May–August were recovered in subsequent years in April–September (Table 4). Of the 460 recovered in a subsequent May–August period, 90% had returned to within 20 km of their ringing site, but less than 3% (12) had moved to distant breeding sites. Seven distant recoveries, ringed in May on the island of Helgoland, were probably late migrants rather than local breeders. Late migrants or late reports probably also account for 25 subsequent April recoveries which were still in migration/winter areas, but if these are excluded then 85% (118/138) of April recoveries were also within 20 km of their ringing site. Half of subsequent-year September recoveries were already in the migration/winter areas. Excluding these, 87% (34/39) had moved less than 20 km.

Of all 0–20 km subsequent-year May–August recoveries, 61% were ringed in zone D (Netherlands/NW Germany), but there was a remarkable temporal change at or about 1990. Before 1990 the percentage of zone D Home recoveries was 85% (77/91). From 1990 this rose significantly to 99% (176/177) ($\chi^2 = 22.29$, $P < 0.001$). No similar changes were found in the data from the other ringing zones.

Migration/winter recoveries

Ringing in the breeding season in the breeding zones produced 4,310 September–April recoveries outside the zone of origin. Of these, 101 (2%) were outside the expected migration/winter recovery areas. Most of these were in other breeding areas in September–November but, nonetheless, downstream of their own breeding site (*eg* a Finnish bird in south Sweden) and apparently moving toward the expected migration/wintering areas; these were rejected from the analysis. Those recovered in December–February within 20 km of the ringing site (46 birds) were included as winter Home recoveries, making 4,255 recoveries for analysis (Table 5).

Winter Home recoveries from each ringing zone were 8% in zone D (Netherlands/NW Germany), but less than 0.5% for all the other ringing zones: this compares with 74% breeding-to-winter movements of less than 20 km for *clarkei* in Britain & Ireland (Wernham *et al* 2002).

Birds ringed in zones A, B and C

All Song Thrushes breeding in these zones are of the migratory group of nominate *philomelos.* Outside these breeding zones only a few of this group (*c* 7% of the total) breed in zone D. Table 6 shows that Song Thrushes

Table 2. Numbers and dispersal distances of August/September recoveries of migratory Song Thrushes ringed in the same season May–July (minimum ringing–recovery interval 31 days).

Month of recovery	Dispersal distance (km) 0–20		21–100		over 100		Total
	n	%	n	%	n	%	
August	164	95.9	4	2.3	3	1.7	171
September	165	75.0	16	7.3	39	17.7	220

Table 3. Numbers and dispersal distances of October/November recoveries of birds ringed in May–August.

Ringing zone	Dispersal 0–20 km		Any winter area		Total
	n	%	n	%	
Zone D (pre-1990)	27	9.7	250	90.3	277
Zone D (post-Jan 1990)	83	86.5	13	13.5	96
All other ringing zones	34	2.3	1,431	97.7	1,465

ringed in these zones were much more likely to be recovered in the high hunting index areas (south France, Iberia, Italy, Greece/Aegean and Levant), than either Fieldfares or nominate Redwings ($\chi^2 = 57.8$, $P < 0.001$).

The patterns of breeding origin of recoveries in Home areas (movements of less than 20 km), and areas N1 (England/Wales), N2 (Belgium/NE France) and N3 (NW France) (Fig 3a–c), showed obvious similarities. The few zone A, B or C birds that were recovered in these areas peaked in October (Fig 4a) – an autumn passage mainly from zones A1 (W Scandinavia) and A2 (Baltics/Finland/NW Russia). Much greater numbers of birds from these zones were recovered on passage in October in area W1 (SE Biscay).

Recoveries in areas W1, W2 (W Iberia) and W3 (S Iberia/Morocco) (Fig 3d, e) were dominated by birds ringed in zones A1, A2 and D, with highest percentages from A1. From all of these ringing zones there were higher proportions of juveniles in area W1, but adults dominate in W2 and W3. Of the recoveries in W3, 6% (21) were in western Morocco. Relatively high proportions of both age groups from zones B1 (W Central Europe) and B2 (E Central Europe) were also found in W1.

Monthly recoveries (Fig 4b–d) in area W1 peaked in October with a smaller return passage peak in March. In W2 recoveries were spread evenly from November to February, while in area W3 there was a peak in January. Areas W2 and W3 both showed a sharp fall in March, coinciding with the March rise in W1.

The principal origin of recoveries in areas S1–2 (S Rhine to French Mediterranean) was zones B1 (WC Europe) and B2 (EC Europe) (Fig 3f). These origins also contributed the highest percentages in areas S3 (E Iberia) and S4 (Balearics/Algeria), although many adults from zone A2 were also recovered in these southern areas (Fig 3g). There was no consistent pattern of juvenile:adult ratio here. In B4, 136 of the recoveries were in the Balearic Islands and 105 were in Algeria.

Few recoveries occurred in area S1 (Rhine–Rhône). These peaked sharply in October (Fig 4e). An October peak in area S2 (French Mediterranean) was followed by a midwinter dip and a larger peak in February (Fig 4f). Further south in S3 (E Iberia) there was an even spread from October to February (Fig 4g), while in S4 (Balearics/Algeria) recoveries peaked in January and then declined (Fig 4h).

The principal zones of origin of recoveries in SE1–2 (N Italy & W Italy) were C1 (SE Europe) and C2 (S&E Russia) (Fig 3h). These zones were also the origin of the highest percentages of recoveries in SE3 (Corsica/Tunisia) (Fig 3i), where 64% were adults. Recoveries in SE1 (N Italy) peaked sharply in October (Fig 4i), and few occurred here after November. In SE2 (W Italy) there was a midwinter dip in December and peaks in October and February (Fig 4j). Few birds appeared in SE3 (Corsica/Tunisia) until November and numbers peaked in January/February (Fig 4k). Of the SE3 recoveries, 129 were found in Sardinia or Corsica, and 7 in Tunisia, but only one on the largest Mediterranean island, Sicily.

Table 4. Subsequent-year April–September recoveries of migratory Song Thrushes ringed in May–August.

Month of recovery	Dispersal distance 0–20 km		21–100 km		distant breeding site (>100 km)		'downstream'migration/ winter area		Total
	n	%	n	%	n	%	n	%	
April	118	72.4	8	4.9	12	7.4	25	15.3	163
May–August	414	90.0	21	4.6	12	2.6	13	2.8	460
September	34	43.6	2	2.6	3	3.8	39	50.0	78

Table 5. Winter (September–April) recoveries of Song Thrushes ringed in the breeding season in migratory population breeding zones. Percentages are calculated in columns to be compared across rows. Levels of statistical significance (sig) for more recoveries than expected (+) or fewer recoveries than expected (–) are indicated by: + or –, $P < 0.05$, $\chi^2 = 32.67$ to 38.93; ++ or – –, $P < 0.01$, $\chi^2 = 38.93$ to 157.20; +++ or – – –, $P < 0.001$, $\chi^2 > 157.21$ (degrees of freedom 21).

		Ringing zones				
		A1–2	B1–2	C1–2	D	
Recovery areas		W Scandinavia/ & E Baltic	Central Europe	SE Europe/ S&E Russia	Netherlands/ NW Germany	Total
Home	n	5	1	0	40	46
(0–20 km,	%	0.3	0.1	0.0	7.8	
Dec–Feb)	sig				+++	
N1–2	n	108	17	0	120	245
England/Wales	%	5.4	1.3	0.0	23.3	
Belgium/NE France	sig		– –	–	+++	
N3	n	127	31	2	73	233
NW France	%	6.4	2.4	0.2	14.1	
	sig		–		++	
W1	n	804	252	17	207	1,280
SE Biscay	%	40.2	19.8	3.6	40.1	
	sig	+++	– –	– – –		
W2–3	n	346	66	4	36	452
W&S Iberia	%	17.3	5.2	0.9	7.0	
Morocco	sig	+++	– –	– –		
S1–4	n	496	694	63	34	1,287
S Rhine to	%	24.8	54.6	13.6	6.6	
Algeria	sig	– –	+++	– –	—	
SE1–3	n	100	211	334	6	651
N&W Italy	%	5.5	16.5	71.6	1.2	
Corsica/Tunisia	sig	– – –		+++	– –	
E1	n	14	2	45	0	61
Aegean/	%	0.7	0.2	9.6	0.0	
Levant	sig			+++		
Total		2,000	1,270	469	516	4,255

Few recoveries were found in the vast area E1 (Aegean/Levant). A few zone C1 (SE Europe) juveniles have been recovered there, but the only important area of origin was zone C2 (S&E Russia) (Fig 3j). Only 1% of all recoveries were ringed in C2, but they contributed 46% of the recoveries here. Four of these were recovered in SE Italy, 18 in Greece/Aegean, and 6 in Levant/Transcaucasus. Recoveries built steadily to a February peak followed by a sharp fall to nil by April (Fig 4l).

Birds ringed in zone D

Migratory movements of zone D (Netherlands/NW Germany) birds differed in several respects (see above: post-breeding dispersal and breeding site fidelity) from those ringed in other zones, and are dealt with

Table 6. Fieldfare *T pilaris*, nominate Redwing *T i iliacus* and nominate Song Thrush recoveries in high hunting index recovery areas (south France, Iberia, Italy and Aegean/Levant) and other migration/winter areas.

Hunting index of recovery areas	Fieldfare		Redwing		Song Thrush		Total
	n	%	n	%	n	%	
Low and medium	823	41	409	24	417	11	1,649
High	1,182	59	1,300	76	3,322	89	6,162
Total	2,005	100	1,709	100	3,739	100	8,111

separately here. Zone D ringed birds were only 12% of all recoveries, but 45% of all recoveries in any Home area, area N1 (England/Wales), N2 (Belgium/NE France) and N3 (NW France) (Table 5, Fig 3a–c). There were more adults in the Home area and juveniles in the other three areas. From all other ringing zones these recovery areas attracted only 8%, a highly significant difference ($\chi^2 = 4498.9$, $P < 0.001$). By contrast, only 8% of zone D birds were recovered in areas W3, S1–4, SE1–3 (and none in E1), compared to 47% of birds from all other zones. In area N1 (England/Wales), the resident subspecies is *clarkei*. Of area N1 recoveries from all ringing zones 71% were ringed in zone D, which also contains the eastern limit of *clarkei* breeding range.

The zone D Home winter recoveries showed a temporal change from about the start of the 1990s. Up to 1990 the Home December–February recovery percentage was 6% (30/471), but subsequently this rose significantly to 22% (10/45) ($\chi^2 = 12.40$, $P < 0.001$). No similar temporal changes were found in data from other ringing zones.

Monthly recoveries (Fig 5a–e) showed zone D birds dispersing in early autumn into adjacent N2 (Belgium/NE France) then to N3 (NW France) during the early winter. Recoveries in N1 (England/Wales) built to a sharp February peak (area N1 shown in Fig 5c to illustrate sequence). Some October recoveries showed a longer migration to W1 (SE Biscay) then a move to spend November to February in W2 (W Iberia). The late winter peak in N1 could be partly an artefact due to differing methods of recovery. Hunted birds were more likely to have an early-season recovery date, whereas recoveries due to natural mortality may peak in the late winter as adverse weather and falling food reserves took their toll. Few zone D birds were recovered away from their ringing zone/Home area after February.

DISCUSSION

Data used for this analysis were heavily biased by uneven ringing effort (47% of recoveries were from birds ringed in Scandinavia/NW Russia *vs* 1% from the rest of Russia/Ukraine/Siberia). This imbalance will have a similar effect to that seen in Redwing *T iliacus* analyses (Milwright 2002, 2003). For example, high ringing effort combined with high hunting pressure resulted in many recoveries of Finnish-ringed Redwings in Italy; however, these were less representative than they appeared, since they were hunted alongside much larger numbers of unringed Redwings, probably from central/eastern Russia and Siberia. Spring/summer recoveries of Redwings ringed during autumn/winter in Italy included none at all in Finland but many in central Russia (Milwright 2002, 2003).

Bias from differing recovery rates in hunting and non-hunting areas was probably less important for Song Thrushes than for Fieldfares and Redwings, since lower percentages of Song Thrushes appeared outside the high hunting areas. Bias due to year-on-year increases or decreases in hunting rates within individual areas (Fiedler *et al* 2004) is unlikely to be visible in this study due to the very long data periods. However, timing bias within each autumn/winter period will be caused by hunted birds being killed early in the season (thus not available for later recovery), as against birds in non-hunting areas, which may survive to be recovered later in midwinter, when weather is worse and food stocks have become depleted.

Many recoveries resulted from Song Thrushes ringed in zones A1 (W Scandinavia) and A2 (E Baltic), because ringing schemes there were very active, and these birds migrated to some of the highest hunting index areas in Europe. Of all recoveries in SE Biscay and W Iberia, 66% (1150/1732) were from these zones. Most of these birds appeared to have passed down the northwest coast of continental Europe, arriving in very large numbers in SE Biscay in October (a 'leap-frog' migration over most zone D birds). Numbers in SE Biscay then declined as the winter advanced. In W and S Iberia the numbers of recoveries rose over the winter, to a February peak. Return migration started in March as indicated by a sharp fall of recoveries within W Iberia while the number of recoveries within SE Biscay rose again. Recoveries of juvenile birds predominated in SE Biscay, and adults in W Iberia, so

it was likely that the early-winter move to W Iberia contained many more adults.

Although birds from zones B1 (WC Europe) and B2 (EC Europe) were only 30% of the whole data set, they made up 54% (696/1287) of all recoveries in the Rhine–Rhône, French Mediterranean, E Iberia and Balearics/Algeria recovery areas. Birds migrating over the Rhine–Rhône col caused a sharp peak of recoveries there in October but few stayed for the winter. Recoveries in the French Mediterranean peaked in October, suggesting that the area was a migration reception area, and also in February when birds were gathering for the return migration. There was a more even spread of recoveries from October to February in E Iberia. In the Balearics and Algeria, few had arrived by October and numbers peaked in January, then declined sharply. Moderate numbers of both age classes of birds from these breeding areas wintered in SE Biscay, probably dispersing into this area from the French Mediterranean via the Carcassonne gap. In contrast to the October peak of northern European breeders (zones A1 and A2), birds from zones B1 and B2 which reached SE Biscay peaked there in January.

Birds ringed in zone C1 (SE Europe) were only 10% of the whole data set but they provided 53% of recoveries in N Italy, W Italy and Corsica/Tunisia. Recoveries in N Italy suggest that this was almost entirely an October reception area. Birds then moved over the Apennines to W Italy in early winter and later in the winter to Corsica/Tunisia. Only 1% of all recoveries were ringed in zone C2, (S&E Russia/Ukraine/W Siberia). However, 79% of recoveries in Albania, Greece/Aegean and Levant/Transcaucasus came from this breeding area.

Migratory *philomelos* were much more likely to cross the west Mediterranean Sea than either Redwings or Fieldfares (Milwright 1994, 2002). Recovery totals in northwest Africa and the Mediterranean islands were: W Morocco 22, N Algeria 108, Balearics 138, Sardinia/Corsica 155 and Tunisia 7. However, only a single bird was recovered on the biggest island, Sicily, two on Crete, four on Cyprus and none on the coasts of Egypt or Libya. The paucity of recoveries around the eastern Mediterranean could reflect low numbers of wintering Song Thrushes in these high hunting index areas. However, it is as likely that the reason for the low recovery numbers in this area is that only a low proportion of migrants from S&E Russia would be ringed.

It is clear that Song Thrushes have a different migration/winter distribution pattern from Redwings and Fieldfares. There were much smaller numbers of Song Thrushes recovered in the intermediate areas of Belgium, north France and south Germany, suggesting a greater proportion made a single flight to the autumn reception areas – N and W Italy, French Mediterranean, and SE Biscay. In winter, compared to Redwings and Fieldfares, much larger proportions of Song Thrushes were recovered in Iberia (especially E Iberia), the Balearics and Algeria. However, the reasons for these differences remain obscure. Recoveries of all three species are very largely the result of hunting in these areas, but different species preferences by the hunters in different areas seems an unlikely cause for the differences in recovery patterns between Song Thrushes and the other two species.

It was apparent that birds breeding in zone D (Netherlands/NW Germany) differed substantially from all others considered here. Radar studies have shown that many thrushes, sometimes including large groups of Song Thrushes, cross the North Sea from Norway to Britain (Lack 1963, Myres 1964). However the ringing evidence strongly suggests that these movements are unusual.

When hunting index correction (x10) was applied, these recovery areas were seen to be important wintering areas for zone D birds (although not for other populations), and recovery rates here became much higher than for zone D birds recovered in the high index areas of southwest Europe. Similarly, recoveries in Belgium/NE France and NW France when corrected (x3) showed these areas also held large numbers of wintering zone D birds. Thus, many zone D birds either did not migrate, or had relatively short migrations (200–600 km) to areas already occupied by resident *clarkei*, and where very few migratory *philomelos* from this or other breeding zones go.

Three changes were found in zone D recoveries from 1990 onwards: (a) a sharp rise in October/November same-season Home recoveries; (b) fewer changes of breeding site between breeding seasons; and (c) more Home recoveries in the winter (December–February). It is tempting to link these changes to global warming, as birds with less need to move in the winter stayed closer to their breeding sites, but more work is necessary to establish this point. Zone D includes the eastern boundary of the range of *clarkei*, in whose core breeding areas, England, Wales, Ireland, Belgium and northern France, the birds are very sedentary (Wernham *et al* 2002). Zone D birds had much higher recovery rates within the *clarkei* range than Song Thrushes from any other zones, and they are also becoming more sedentary since 1990. However, if zone D *clarkei* are responsible for the well-established pre-1990 migrations to Belgium/NE France, NW France and England/Wales, they were displaying behaviour that differed from that of the core area (resident) *clarkei* by migrating at all, and also that

of migratory *philomelos* from close-by breeding sites in Denmark, east Germany and southern Sweden, by migrating to Belgium, north France and England/Wales.

Clarkei appears to be increasing within zone D. This could be at the expense of migratory *philomelos,* which may be being pushed further east within zone D, and later possibly out of it. This hypothesis remains to be tested as little recent racial identification has been done in the Netherlands or northwest Germany. During the period of these changes (since 1990) there have been high levels of ringing in the Netherlands, but recovery numbers suggest reduced ringing of Song Thrushes in the German section of this zone. If this is so there could be an increase in the proportion of *clarkei* ringed in the whole zone, simply because this race occurs predominantly in the Netherlands.

Zone D recoveries in SE Biscay peaked in October then declined, but in W Iberia they were high from November and February. This migration pattern was similar to that of *philomelos* ringed in W Scandinavia and E Baltic, and it seems likely that these zone D birds were also *philomelos* (most originate in the German section). There were few records of birds moving to SE Biscay or W Iberia from zone D after 1990. This could be due either to a reduced ringing of German Song Thrushes in zone D, or to *clarkei* spreading throughout zone D (at the same time becoming less migratory).

Adult Fieldfares *T pilaris* and adult nominate Redwings *T i iliacus* migrate to more distant destinations than juveniles (Milwright 1994, 2002). Similarly, at both the western (Iberian) and eastern (Italian and Greek) ends of their winter range, adult nominate *philomelos* Song Thrushes migrate further than juveniles. However, zone D Song Thrush Home recoveries were predominantly adult, while zone D recoveries in Belgium, north France and England/Wales were predominantly juvenile. Assuming these birds are *clarkei,* this race appears to reverse the usual pattern – a trait it appears to share with another thrush subspecies, the Icelandic Redwing *T i coburni* (Milwright 2002).

Five migration routes were shown by this study, the first four from within breeding areas of *philomelos* – (a) Scandinavia to W Iberia, (b) Central Europe to E Iberia/ Balearics/Algeria, (c) SE Europe to W Italy/Corsica/ Sardinia and (d) eastern Russia to Aegean/Levant. These were all more or less parallel to each other, suggesting a broad front of migration to the southwest by all the migratory populations of *philomelos*, along approximately the same great-circle direction.

The fifth migration route was the short loop migration – Netherlands/NW Germany to Belgium to NW France to England/Wales and back to Netherlands/NW Germany. Since this route originates in a zone which contains breeding *clarkei*, and the route is entirely within the *clarkei* range, it seems likely that these migrants were of this subspecies. No studies are known to have been carried out to demonstrate DNA differences between *philomelos* and *clarkei*, but recent work at a North Sea bird observatory (M Martin, unpublished data from 2005 in the Isle of May Special Notes Log, vol 4), confirmed two clearly different morphological forms closely agreeing with descriptions of *clarkei* and *philomelos* in Cramp (1988), and no intermediate forms. Further work is needed to ascertain the dynamics of the *philomelos* and *clarkei* populations, particularly at and near to the eastern *clarkei* range boundary. Ideally this should at least involve the allocation of a racial identity, using plumage differences, to all ringed Song Thrushes.

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REFERENCES

Ashmole, M.J. (1962) The migration of European thrushes: a comparative study based on ringing recoveries. *Ibis* **104**, 522-529.

Cramp, S. (ed) (1988) *The birds of the Western Palearctic. Vol V.* Oxford University Press, Oxford.

Dementiev, G.P., & Gladkov, N.A. (1954) *Ptitsy Sovietskogo,* Soyuza.

Fiedler, W., Bairlein, F. & Köppen, U. (2004) Using large-scale data from ringed birds for the investigation of effects of climate change on migrating birds: pitfalls and prospects. *Advances in Ecological Research* **35,** 48-67.

Hagemeijer, W.J.M., & Blair, M.J. (1997) *The EBCC Atlas of European Birds. Their Distribution and Abundance*. T. & A.D. Poyser, London.

Lack, D. (1963) Migration across the North Sea studied by Radar. Part 4, Autumn. *Ibis* **105**, 1-54.

Lack, P. (1986) *The Atlas of wintering birds in Britain and Ireland*. T. & A.D. Poyser, Calton.

McCulloch, M.N., Tucker, G.M. & Baillie, S.R. (1992) The hunting of migratory birds in Europe: a ringing recovery analysis. *Ibis* **134 suppl**, 55-65.

Melde, F. & Melde, M. (1991) *Die Singdrossel* Turdus philomelos. Ziemsen, Wittenburg.

Milwright, R.D.P. (1994) Fieldfare *Turdus pilaris* ringing recoveries during autumn, winter and spring, analysed in relation to river basins and watersheds in Europe, and the Near East. *Ringing & Migration* **15**, 128-189.

Milwright, R.D.P. (2002) Redwing *Turdus iliacus* migration and wintering areas shown by the recoveries of birds ringed in the breeding season in Fennoscandia, Poland, the Baltic Republics, Russia, Siberia and Iceland. *Ringing & Migration* **21**, 5-15.

Milwright, R.D.P. (2003) Migration routes, breeding areas and between-winter recurrence of nominate Redwings *Turdus iliacus iliacus* revealed by recoveries of winter ringed birds. *Ringing & Migration* **21**, 183-192.

Moreau, R.E. (1972) *The Palaearctic–African Bird Migration Systems*. Academic Press, London and New York.

Myres, M.T. (1964) Dawn ascent and re-orientation of Scandinavian thrushes (*Turdus sp*) migrating at night over the northeastern Atlantic in autumn. *Ibis* **106**, 7-51.

Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. (eds) (2002) *The Migration Atlas: movements of the birds of Britain and Ireland*. T. & A.D. Poyser, London.

Zink, G. (1981) *Der Zug Europäischer Singvögel. Bd. 3*. Vogelzug-Verlag, Möggingen.

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