Autumn migration of thrushes over eastern Finland: a comparison of visible migration and ringing recovery patterns

MARKKU J. HUTTUNEN
Department of Biology, University of Joensuu, PO Box 111, FIN-80101 Joensuu, Finland

The migration of thrushes Turdus spp over eastern Finland was investigated using data from 4,482 foreign recoveries of five species ringed in Finland between 1913 and 2001, and records of visible migration of nearly 28,000 thrushes observed during diurnal autumn movements between 1996 and 2001. Ringing recoveries suggested that the main autumn direction of movement from eastern Finland is southwest for Redwings T iliacus, Fieldfares T pilaris and Song Thrushes T philomelos, west-southwest for Blackbirds T merula and south for Mistle Thrushes T viscivorus. Visible migration records for Mistle Thrushes seemed to correspond well with ringing recoveries, but the other thrush species showed different directions of movement, mainly towards the west-northwest or along a west-northwest to east-southeast axis, possibly due to the influence of lake districts as guidelines. The available wind data showed that the thrushes flew in an inappropriate west-northwest direction on most peak movement days regardless of wind direction, though some correspondence with moderately strong head or cross winds was evident. The majority of foreign recoveries of thrushes ringed in Finland were found between western and southern Europe but a small proportion of birds have also been recovered from southeast and northwest sectors. The rather irregular migratory behaviour of Redwings and Fieldfares is exemplified by the ringing recoveries of individual birds, or birds from the same brood, in entirely different areas during subsequent winters. This might be explained by drift during migration, movements during hard weather or intense nomadic behaviour.

The migratory movements of thrushes Turdus spp have been studied by a variety of methods including ringing (Ashmole 1962, Andreotti et al 1999, 2001, Main 2002, Milwright 2002), and visual and radar observation (Alerstam 1975, 1976, Åkesson 1993, Myres 1964). Ashmole (1962) was the first to describe European-scale movements of thrushes based on ringing recovery analyses, which were later complemented by more specific analyses by, for example, A ndreotti et al (1999, 2001) for Italy, Main (2002) for Fennoscandia and Milwright (2002) for a major part of known wintering areas. Although these analyses have identified the most important wintering areas in southwest Europe, some recoveries and observations suggest a minor southeast migration (Ashmole 1962, A lerstam 1975, 1981, Milwright 2002). The unexpected southeast to south-southeast migration of North European thrushes, mainly Redwings T iliacus and, possibly, Fieldfares T pilaris have been reported by several studies (Lee 1963, Myres 1964, A lerstam et al 1973, A lerstam 1975), and many of the birds were found to migrate during daytime.

Most diurnal migrants orientate using major topographical features, and migratory movements seem to be heavily influenced by leading lines both in coastal and inland areas (A ble 1980, Bergman & Donner 1964). Migrational drift with a following wind can displace night migrants from leading lines but, during daytime, birds using guidelines or landmarks are able to adjust for the wind effect (Richardson 1990). Wind direction may, therefore, be of paramount importance for migratory activity and orientation. A lerstam (1975, 1976) has pointed out that both day and night migrating thrushes do not fly on a fixed heading but adjust their heading direction in a way that compensates for wind drift. Some other studies on night-migrating thrushes have shown the use of headings which were not adjusted for wind drift, but instead used different strategies by selecting flight altitudes where drift was minimized (L indgren & Nilsson 1975, Cochran 1987, Cochran & Kjos 1985).

Recoveries of ringed thrushes have shown different degrees of fidelity to wintering areas (Ashmole 1962, A ndreotti et al 2001) but how widespread this behaviour might be still remains to be resolved. Some Redwings, Fieldfares and Blackbirds T merula may spend parts of the same, or successive, winters in widely different regions, while Song Thrushes T philomelos and Mistle Thrushes T viscivorus show different behaviour, perhaps
due to more limited habitat requirements. In this study, the general migratory movements of thrushes from eastern Finland were investigated using ringing recoveries and observations of visible migration, with a special emphasis on northwest- and southeast-oriented movements.

**METHODS**

**Ringing recoveries**

Ringing recovery data for five species of thrushes (Blackbird, Song Thrush, Mistle Thrush, Redwing and Fieldfare) were supplied by the Finnish Ringing Centre. Data were available for 4,482 foreign recoveries of those species ringed in Finland during the period 1913 to 2001. The selection of ringing recoveries was based on the following criteria: all foreign recoveries, ringed in Finland and recovered at least 50 km from the ringing site were included. For further analyses, some minimum intervals between ringing and recovery, and separation according to the recovery season, were used.

To analyse ringing recoveries, Finland was arbitrarily divided into six regions according to the place of ringing (Fig 1): 1) Southern Finland (below 61°N); 2) Western Finland (between 61°N and 64°N, and west of 24°E); 3) Central Finland (61°N to 64°N, and 24°E to 28°E); 4) Eastern Finland (61°N to 64°N, and east of 28°E); 5) 'Middle' Finland (64°N to 66 N) and 6) Northern Finland (66°N to 70°N). In addition, for evaluating the possible southeast- or northwest-oriented movements, Finland was arbitrarily divided into two longitudinal areas according to the place of ringing; west or east of 26°E. Individuals that were ringed as nestlings on the same day, and with consecutive ring numbers (62%) or within three ring numbers of each other (38%), were assumed to be siblings from the same brood. Juveniles were defined as full-grown birds in their first calendar year. Modes were used to show the most common months for Finnish ringings and foreign recoveries.

**Visible migration and wind directions**

Visible migration directions for nearly 28,000 thrushes, of five different species, were observed by ornithologists in eastern Finland from 1996 to 2001. Observations were generally made between 0600 hrs and 1500 hrs from 1 September to 31 October each year. Field observations of Redwings and unidentified small thrushes were pooled, as were observations of Fieldfares and unidentified large thrushes, since these are the most common thrush species seen in the area.

Data on the approximate surface wind direction and strength were obtained from the weather maps of the Finnish Meteorological Institute. Surface wind data were used and usually correlated with winds at higher altitudes (Richardson 1978). The data were generally collected before noon. Wind strength varied between 2 and 15 ms⁻¹.

**Data analysis and statistics**

Ringing recoveries and visible migration directions were subjected to vector calculation, yielding a mean heading for each species (Batschelet 1981). Mean vectors are relative to the radius (r) or diameter (r⁻) of the circle and are relative to 1.0, so that a vector of zero would mean a totally random circular distribution, 0.5 would suggest a more concentrated mean orientation, and 1.0 would mean that all the birds orientate in exactly the same direction. The Rayleigh test was used to show whether bearings differed significantly from a random
circular distribution (Batschelet 1981). To calculate a mean axis of orientation for bimodal data on visible migration, vector analysis was performed after first applying the doubling-of-angles procedure recommended by Batschelet (1981). A mean axis of orientation was used for Fieldfares and Blackbirds, as the mean vector length calculated from double angles ($r_2$) was greater than the mean unimodal vector ($r$).

Since there were no significant differences in ring recovery directions between age groups (in all cases $P > 0.05$), they were pooled for each species (Fig 2). Circular statistics were used to analyse whether the birds’ mean visible migration direction differed from the mean direction of ringing recoveries (Batschelet 1981). The Kruskal-Wallis test and a one-way ANOVA were used to analyse differences between the recovery directions and distances between the age groups, respectively. Watson’s U² test was used to evaluate differences between the mean directions (Batschelet 1981). To calculate the differences, I used frequency distributions. The sum of flight directions in each 20° sector was represented as midpoints: 10°, 30°, 50°, etc (Fig 2).

RESULTS

Ringing recoveries
Ringing recoveries of thrushes ringed in eastern Finland showed that the main autumn direction of movement is southwest for Redwings, Fieldfares and Song Thrushes, west-southwest for Blackbirds and south for Mistle Thrushes (Fig 2). The majority of the 4,482 foreign recoveries of thrushes ringed in Finland were found in the southwest quarter of Europe (Table 1), while 97 individuals have been recovered from the southeast quarter (Table 2) and 19 birds from the northwest quarter (Table 3). The age distribution of ringed birds varied considerably between the species (Fig 3) and also between the ringing regions. In general, relatively more adults and first-year birds were ringed in regions with coastlines (Fig 1; areas 1, 2 and 5) than in inland regions (Fig 1; areas 3, 4 and 6), where more nestlings were ringed.

A greater proportion of the Redwings ringed in western Finland were recovered from the southeast quarter of Europe compared to those ringed in eastern Finland (Fig 4). A second ringing recovery data, Redwings and Fieldfares that winter furthest east appeared to come from the more western breeding populations, as represented by the frequency of ringing recoveries in relation to the three ringing regions (Figs 5 & 6).

Birds originating from the same area can also show different migratory movements, as shown by ringing

![Figure 2](image-url). Distribution of foreign ringing recoveries and autumn visible migration flight directions of five thrush species from eastern Finland (area 4; Fig 1), except for ringing recoveries of Mistle Thrushes which illustrate birds ringed in the whole of Finland (areas 1–6; Fig 1). Ringing recoveries are based on the national ringing data of thrushes ringed in eastern Finland during 1927–2000. Autumn migratory directions grouped in 20° sectors are based on observations in eastern Finland during 1996–2001. Minimum number of birds shown in each sector (5–500 individuals) varies between the species. Dashed lines on the figures on the right indicate the direction of main lake districts in eastern Finland. Mean vectors on the figures on the left are drawn relative to the radius ($r$) of the circle = 1. Mean directions ($\alpha$, $\alpha_2$), lengths of vectors ($r$) and axis ($r_2$), and probability levels ($P$, based on number of individuals) according to the Rayleigh test, were calculated by using standard procedures given in Batschelet (1981).
Table 1. Data on five thrush species ringed in Finland and recovered abroad. Recovery percentage within nine months indicates the percentage of Finnish-ringed thrushes recovered abroad during the same autumn or the following winter period (elapsed time less than 270 days, from ringing between 1 July and 31 March). Also shown are mode months for ringing and recoveries (Nest = ringed as nestlings, FG = ringed as fledged birds of all ages). Two-letter country codes are: FR (France), IA (Italy), ES (Spain), PO (Portugal), BL (Belgium), GB (Great Britain), DE (Germany), NO (Norway), AG (Algeria), DK (Denmark), SV (Sweden), NL (Netherlands), GR (Greece), TU (Turkey), AB (Albania) and RU (Russia).

<table>
<thead>
<tr>
<th>Species</th>
<th>Ringing years (total no of birds ringed)</th>
<th>Mode ringing month</th>
<th>N foreign recoveries</th>
<th>Mode recovery month</th>
<th>Recovery % within 9 months</th>
<th>Main recovery countries</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redwing</td>
<td>1913 - 2000 (149,742)</td>
<td>Jun Sep</td>
<td>869 927</td>
<td>Nov Dec</td>
<td>64.7 63.2</td>
<td>FR, IA, ES, PO, BL, GB</td>
</tr>
<tr>
<td>Fieldfare</td>
<td>1913 - 2001 (126,238)</td>
<td>Jun Oct</td>
<td>725 397</td>
<td>Dec Dec</td>
<td>51.0 48.9</td>
<td>FR, IA, BL, DE, GB, N</td>
</tr>
<tr>
<td>Song Thrush</td>
<td>1930 - 2001 (76,659)</td>
<td>Jun Sep</td>
<td>270 865</td>
<td>Oct Nov</td>
<td>54.8 50.1</td>
<td>ES, FR, IA, DE, GB, N</td>
</tr>
<tr>
<td>Blackbird</td>
<td>1930 - 2001 (38,647)</td>
<td>Jun Apr</td>
<td>79 335</td>
<td>Nov Jan</td>
<td>51.9 44.2</td>
<td>PO, AG, DE, GB, FR, DK</td>
</tr>
<tr>
<td>Mistle Thrush</td>
<td>1962 - 1999 (2,232)</td>
<td>Jun Oct</td>
<td>9 5</td>
<td>Feb Nov</td>
<td>55.6 60.0</td>
<td>FR, GR, TU, AB, RU, IA</td>
</tr>
</tbody>
</table>

Table 2. The number of all southeastern foreign recoveries of five thrush species ringed in Finland during 1913–2001. *West of longitude 26° E.

<table>
<thead>
<tr>
<th>Species</th>
<th>No of southeast recoveries</th>
<th>Percent of all recoveries</th>
<th>Recovery sector between birds ringed as nestlings</th>
<th>Percent of southeast birds ringed in the western* part of Finland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redwing</td>
<td>56</td>
<td>3.1</td>
<td>112° – 180°</td>
<td>37.5</td>
</tr>
<tr>
<td>Fieldfare</td>
<td>21</td>
<td>1.9</td>
<td>101° – 180°</td>
<td>28.6</td>
</tr>
<tr>
<td>Song Thrush</td>
<td>7</td>
<td>0.6</td>
<td>100° – 180°</td>
<td>0.0</td>
</tr>
<tr>
<td>Blackbird</td>
<td>7</td>
<td>1.7</td>
<td>97° – 176°</td>
<td>14.3</td>
</tr>
<tr>
<td>Mistle Thrush</td>
<td>6</td>
<td>42.9</td>
<td>141° – 178°</td>
<td>50.0</td>
</tr>
</tbody>
</table>

Table 3. The number of northwestern recoveries of five thrush species ringed in Finland during 1913–2001. Recoveries included are those of movements over 100 km, in a direction between the smaller angle between 270° and 360°, and recovered less than 180 days after ringing. *West of longitude 26° E.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of northwest recoveries</th>
<th>Recovery sector between birds ringed as nestlings</th>
<th>Percent of northwest birds ringed in the western* part of Finland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redwing</td>
<td>7</td>
<td>270° – 324°</td>
<td>50</td>
</tr>
<tr>
<td>Fieldfare</td>
<td>8</td>
<td>273° – 358°</td>
<td>81.8</td>
</tr>
<tr>
<td>Song Thrush</td>
<td>-</td>
<td>315°</td>
<td>100</td>
</tr>
<tr>
<td>Blackbird</td>
<td>4</td>
<td>272° – 343°</td>
<td>14.3</td>
</tr>
<tr>
<td>Mistle Thrush</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
recoveries where migratory directions have been more irregular among Redwings and Fieldfares than among Song Thrushes (Table 4). Mode months for recoveries showed that most of the birds were probably recovered near their wintering areas, and not on their way back to their breeding grounds (Table 1). There were no seasonal differences between the age groups of Redwings in relation to mean distance of recoveries, but some significant differences were found among Fieldfares, Song Thrushes and Blackbirds (Fig 7). Young Fieldfares tended to migrate the shortest distance, while the opposite seemed to be evident among Song Thrushes, where birds ringed as nestlings were recovered furthest away. Alternatively, Song Thrushes ringed as fledged birds may have already undertaken some movement from the natal site.

Flight and wind directions
In comparison with ringing recoveries, the visible migration of four thrush species over eastern Finland showed significantly different directions of movement, mainly towards a west-northwest or along west-northwest
Table 4. Means of differences and confidence interval limits between recovery directions of birds ringed as siblings from the same brood, and recovered during the following winter (35.1% of the sibling pairs) or later. N = number of sibling pairs. Double controls are ringing recoveries of a single bird during subsequent winters. Mean of differences between recovery directions among three thrush species is statistically significant (Kruskal-Wallis test, $\chi^2 = 6.966$, df = 2, $P < 0.05$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Ringing years</th>
<th>Mean of differences</th>
<th>N</th>
<th>N number of double controls</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redwing</td>
<td>1955–1990</td>
<td>13.5° ± 5°</td>
<td>14</td>
<td>2</td>
</tr>
<tr>
<td>Fieldfare</td>
<td>1952–1996</td>
<td>21° ± 10°</td>
<td>15</td>
<td>1</td>
</tr>
<tr>
<td>Song Thrush</td>
<td>1961–1976</td>
<td>4° ± 3°</td>
<td>8</td>
<td>-</td>
</tr>
</tbody>
</table>

to east-southeast axis, ie parallel to the shorelines of the main lake districts (visible movements vs ringing: Redwing, 299° vs 235°, $U^2 = 1.095$, $P < 0.001$; Fieldfare, 292–112° vs 232°, $U^2 = 1.629$, $P < 0.001$; Song Thrush, 287° vs 233°, $U^2 = 1.548$, $P < 0.001$; Blackbird, 311–131° vs 255°, $U^2 = 0.464$, $P < 0.05$; Fig 2). Movements of Mistle Thrushes were similar for visible migration and ringing recoveries (168° vs 188°, $U^2 = 0.108$, $P > 0.05$, Fig 2).

The directions of visible migration were only slightly different between the nine municipal areas reported, generally towards the west or along a northwest to southeast axis. The mean direction for departures was 264° from Ilomantsi (number of birds observed, n = 15), 287° from Joensuu (n = 23,583), 270° from Juuka (n = 24), 135° from Kesälähti (n = 46), 135° from Kiihtelysvaara (n = 1,600), 315–135° from Kitee (n = 890), 232° from Kontiolahti (n = 256), 315° from Lieksa (n = 889) and 315–135° from Rääkkylä (n = 1,467).

Movements of thrushes took place in almost all kinds of wind conditions. The thrushes flew in an inappropriate west-northwest direction on most peak days, regardless of wind direction, though in some cases correspondence with moderately strong head or cross winds was evident (Fig 8).

**DISCUSSION**

There are several potential explanations for the observed patterns of thrush migration over eastern Finland: 1) the birds are heading between west-northwest and northwest, or along the northwest/southeast axis, following the shorelines of the main lake districts; and later, possibly in Scandinavia, change direction towards southwest Europe ('nonsense orientation'); 2) the birds are heading between west-northwest and northwest, following the shorelines of the main lake districts, but only in eastern Finland ('topographical orientation'), and shortly after change their direction towards the southwest; 3) the thrushes seen migrating between west-northwest and northwest over eastern Finland mainly represent birds from the eastern areas, including birds from Russia, while birds originating from eastern Finland do not participate in this migration ('different populations'); and 4) the thrushes are heading between west-northwest and northwest without any substantial influence from weather or winds on their directions.

Since ringing recoveries and observed flight directions are not equally numbered among the species, this discussion will mainly focus on the Redwing and the Fieldfare, for which the largest sample sizes were available.

**Ringing recoveries and visible migration**

In general, all five thrush species ringed in eastern Finland are recovered in areas between the south and west of Europe, where the Blackbird is the most western and the Mistle Thrush the most southern. More differences exist in their directions observed during visible migration. A according to this analysis, flight directions of departing birds do not seem to correspond with the direction of ringing recovery locations. The general southwest distribution of recoveries in Europe predicts a change of direction during the migratory flight, or a lower recovery rate in northwestern and southeastern areas.

While thrushes may choose their migratory directions in coastal areas by taking account of wind conditions upon departure from the mainland (Alerstam 1975, for Redwings), they seem to use a different strategy in inland areas by mainly heading along topographical features, like major lake districts, often showing bimodal orientation. A according to the first explanation for the observed movements, when heading parallel to the shorelines of the major lake districts, birds selecting a direction between west-northwest and northwest, in order to take advantage of topography and prevailing winds, head towards northwest Scandinavia, probably later shifting their direction to the southwest. This kind of orientation, more or less opposite to seasonally appropriate headings, could be included in the 'nonsense' orientation category introduced by Matthews (1968). However, this term does not imply that the orientation direction would not be significant to the birds, only that it seems unreasonable to the experimenter or observer. A shmole (1962) considered the westward autumn migration of Finnish and Swedish Fieldfares and Blackbirds to be a probable adaptation for exploiting the berry crops in Norway, from where most of the birds later migrate between southwest and south-southwest.
Thrushes migrating on preferred tracks between west-northwest and northwest must later change their headings in order to reach their main wintering areas in southwest Europe. It may be difficult to interpret why birds should fly with tail winds in seasonally inappropriate directions when they could instead remain on the ground and wait for more favourable wind conditions. Maybe this results from differences in orientation behaviour between separate populations, which would then be connected to the third explanation, though most northwest recoveries suggest a Finnish origin (Table 3) and so do not support the suggestion. On the other hand, several ringing recoveries have shown that thrushes arrive in Scandinavia from the east during the autumn (Ashmole 1962). Therefore, as proposed in the third hypothesis, a western or northwestern heading of migrating thrushes observed in eastern Finland may also suggest Russian origin. Moreover, current evidence indicates that most Redwings of Russian and Siberian origin winter in western Europe (Milwright 2002).

The second explanation suggests that differences in the direction of migration may result from the topographical features of eastern Finland. A strong leading line effect can be predicted by the thrushes migrating at low to moderate altitudes under the prevalence of head or cross winds, being highly responsive to the topography of the areas. Thus, birds could probably save energy and time by routing migration parallel to lake shorelines. However, it would be unfavourable to follow shorelines extending in a direction largely different from the preferred migratory direction unless it is done in order to increase energy reserves in some other regions. Still, when heading parallel to the lakes, why do they largely choose a northwest instead of a southeast direction? A northwest direction may partly account for the early dispersal of juvenile thrushes (Table 3; particularly Fieldfares), but we need to know much more about the normal direction and dispersal of the first-year birds that show migratory activity.

Figure 5. Same autumn/winter recoveries (recovered less than 270 days from ringing) of Redwings ringed as a) nestlings and b) full-grown birds in relation to ringing regions 2, 3 and 4 (Fig 1) in Finland. The numbers inside the circles indicate the number of ringing recoveries in a given area.

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How does the visible migration towards the west-northwest relate to prevailing winds, reorientation or northwestern recoveries? A correspondence between mean track directions and the orientation of the lake shores, irrespective of wind direction, is what would be expected if complete compensation occurs. This study showed only some influence of autumn wind direction and strength on peak migratory headings (Fig 8), which demonstrates neither drift nor use of winds as orientation cues. Myres (1964) and Lee (1963) found no evidence of wind influence on dawn ascent behaviour during thrush migration, even with strong winds, suggesting that winds of moderate strength may have little inhibitory influence on migratory movements. There are also suggestions that at least some of the migrants, especially Song Thrushes and Redwings, are able to re-orientate their direction towards appropriate wintering areas (Ashmole 1962, Alerstam 1975). The above discussion seems to be consistent with the fourth hypothesis.

The movements reported here from eastern Finland are in good agreement with the observations from central (Björk 1994, pers comm) and southeast Finland (Rokkanen 1999). Many ringing recoveries from Norway show that the westward autumn migration of Swedish and Finnish Fieldfares and Blackbirds, mainly composed of first-year birds, is probably a regular occurrence (Ashmole 1962). Migratory movements in a northwest to westerly direction have also been observed elsewhere, eg in first-year Blackbirds in southern England (Snow 1966), Norwegian thrushes over the North Sea (Lack 1962) and mass migration of Russian Fieldfares in the White Sea area (Kontiokorpi 1996).

I have found evidence to support at least two of the four proposed explanations for the observations of visible migration of thrushes over eastern Finland, ie that the preferred direction of migration is different from that of ringing recovery locations and it is directed towards the west to northwest (explanation 1), and that the thrushes tend to fly in an inappropriate west-northwest direction regardless of wind direction.
Figure 7. The average distance (in km) of recoveries in five thrush species Turdus spp ringed in Finland and recovered abroad during the same autumn or the following winter period (elapsed time < 180, except for Mistle Thrushes < 270 days from ringing). A one-way ANOVA was used to compare recovery distances between the age groups (* indicates statistically significant difference).

(= explanation 4). Thus, west-northwest-oriented migration of thrushes seems to be an important part of their migration strategy in eastern Finland.

A comparison with national ringing data
Most winter recoveries of Finnish-ringed thrushes come from France, Italy, Spain, Portugal, Great Britain and Belgium. A major part of the recovery data is clear evidence of a Finnish origin, as 53% of the birds were ringed as nestlings (Fig 3, Table 1). However, evaluation of the recovery data is complicated by those birds ringed as juveniles or as adults that may have had a different origin.

There are some possible biases in the distribution of ringing effort and subsequent recovery data. More birds have been ringed as nestlings than as adults in some areas,
and vice versa (Fig 3). Some species, or age classes, are more likely to be ringed or recovered than others. For example, the lower number of recoveries of thrushes originating from eastern Finland is partly due to a smaller ringing effort in this area. Much of the variation in recoveries comes from the differences in hunting pressures in different countries and the return rate of the rings. At present, restrictive legislation within the European Union, especially in the Mediterranean region, have decreased hunting pressures and hence the number of recoveries. The recovery rate may also fluctuate according to the severity of the winter in a given area.

Ringing data indicate that thrushes ringed in Finland sometimes winter in areas towards the southeast and south, which is in agreement with some other studies (A shmole 1962, A lerstam 1975, A ndreotti et al 2001, M ilwright 2002). The tendency of southeast migration in Redwings is most intense in southwest Finland, which may be partly due to the leading line effect at coastal areas and greater ringing effort. It has been suggested that part of the northern population of Redwings winters in regions situated in a southeast direction, and that these birds have a Scandinavian origin (A shmole 1962; see also Fig 5 for A 2 birds). In addition, radar studies have revealed that the southeast migration of thrushes generally occurs throughout the whole of northwest Europe (A lerstam 1975, 1976). Moreover, the present study shows that only approximately a quarter of the thrushes recovered in areas towards the southeastern sector were ringed as nestlings (Table 2). Therefore, as A lerstam (1981) has pointed out, the region to the southeast must certainly be a more important wintering area for Redwings than indicated by the number of recoveries.

The rather irregular migratory behaviour of Redwings and Fieldfares is shown by the ringing recoveries of individual birds, or birds from the same brood, in subsequent winters in entirely different areas (Simms 1978; Table 4). Some Redwings and Fieldfares have been found in successive winters at areas up to several thousand kilometres and 1,600 km apart, respectively (A shmole 1962). These irregularities could be explained by drift during migration (A lerstam 1975), movements during hard weather (Lack 1960) or intense nomadic behaviour to exploit variable berry crops. On the other hand, while there are a few double controls of individuals recovered in the same area during subsequent years (two Redwings and one Fieldfare; Table 4), there is no evidence that a population follows the same migratory direction in any one year.

The migration patterns and the distinct wintering areas of different thrush species can be interpreted by climatic conditions on the one hand and by the costs and benefits of migration on the other hand, depending on the severity of the winter and the supply of food resources (Tyrvainen 1975). Thrushes may influence each other during migration through their flocking behaviour; the directions of single birds become more similar to each other. More extensive observations are needed of visible migration from inland sites which collect moderate concentrations of migrating birds. In particular, radar or ceilometer observations would be needed to elucidate the nocturnal patterns of Finnish thrushes during the early stages of their migration.

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