

Susanne Åkesson · Lennart Karlsson · Göran Walinder · Thomas Alerstam

## Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia

Received: 11 July 1995/Accepted after revision: 19 November 1995

**Abstract** Extensive ringing data from a coastal site (Falsterbo Bird Observatory) in southwesternmost Sweden were used to investigate the occurrence of reverse autumn migration among 20 passerine bird species of widely different migration categories. The data demonstrate that reverse migration is a widespread and regular phenomenon among nocturnal as well as diurnal migrants and among irruptive migrants, temperate zone migrants, and long-distance migrants destined for tropical winter quarters. The reoriented movements were directed approximately opposite to the normal migration direction, i.e. between NNW and ENE from the coast and towards inland. Median distances of reverse movements varied between 9 and 65 km. Some individuals of irruptive and partial migrants settled to winter in the reverse direction. Bird species with relatively small fat reserves at capture were more likely to perform reverse migratory movements than species with larger fat deposits. In two species birds performing forward migration were significantly heavier within 10 days after capture than individuals performing reverse movements. The reoriented movements probably are of adaptive significance for birds confronted with the sea and pre-disposed to refuelling during migration. A bimodal orientation mechanism will bring the birds from an area with high competition for food and high predation risk to more suitable resting and feeding grounds before resuming migration in the forward direction and crossing the barrier.

**Key words** Autumn migration · Ecological barriers · Orientation · Reverse migration · Ringing recoveries

### Introduction

Migratory flights in the opposite direction of that expected, i.e. away from migratory destinations, have repeatedly been observed during both spring and autumn migration (e.g. von Haartman 1945; von Haartman et al. 1946; Koskimies 1947; Evans 1968; Able 1977; Richardson 1978; Lindström and Alerstam 1986). Orientation errors, effect of wind drift and responses to unsuitable weather have been suggested as possible explanations for reoriented movements. In an extensive analysis of different explanations for reoriented migration flights Richardson (1982) concluded that different causes are involved under different environmental circumstances. In coastal areas reverse migration may be performed by migrating birds that have small fuel reserves when they encounter the sea, in order to refuel before crossing the barrier (Alerstam 1978a). At the coast birds may encounter low food availability as well as high competition for food. The risk of predation may also be higher at the coast compared to inland sites. Support for these suggestions has been found for two species of diurnally migrating finches, which regularly perform reverse movements when confronted with the sea to more suitable stopover sites for restoring fuel reserves before continuing migration (Lindström and Alerstam 1986).

To test whether autumn reoriented migratory movement is a general phenomenon among different categories of migratory birds confronted with a barrier on migration, we analysed ringing recoveries of passerine bird species captured and ringed during autumn migration at Falsterbo Bird Observatory on the southwest coast of Sweden. We were interested in analysing the occurrence of this phenomenon in species and categories of migrants which differ with respect to:

1. Distance of migration (e.g. differences between three categories of migration; irruptive and partial migrants, long-distance migrants with their winter

S. Åkesson (✉) · T. Alerstam  
Department of Animal Ecology, Lund University, Ecology  
Building, S-223 62 Lund, Sweden

L. Karlsson · G. Walinder  
Falsterbo Bird Observatory, Fyren, S-239 40 Falsterbo, Sweden

quarters in the temperate zone and long-distance migrants wintering in tropical zones). A larger fraction of short-distance migrants are expected to be recorded in directions opposite to the normal migration direction shortly after capture compared to long-distance migrants.

2. Time of migration (diurnal vs. nocturnal). Diurnal migrants have the potential to locate suitable resting sites en route and are expected to more often engage in reverse migration compared to nocturnal migrants.
3. Body condition (fat vs. lean birds). Lean birds are expected to reorient away from the coast and head inland for refuelling.

We analysed the direction and distance of movements of birds recovered within a short period ( $\leq 10$  days) after capture compared to birds recovered more than 11 days after capture. The relationship between the birds' fat reserves and body mass and their directions of movement was also analysed.

### Study area and methods

Falsterbo Bird Observatory (55°23'N, 12°50'E) is situated in southwesternmost Sweden (Fig. 1). Birds have been ringed there since 1947 (Roos 1984). Since 1980 a standardized ringing scheme has been in operation (Roos and Karlsson 1981), covering both spring and autumn migration seasons and ringing annually about 23 000 birds. All birds are trapped in mistnets, ringed, measured and thereafter immediately released at the ringing site. Since the 1960s the lighthouse garden, an isolated stand of trees and bushes surrounded

by open area (golf course), has been the main ringing site. During July–September birds are also captured at Flommen, a reedbed area about 1 km north of the lighthouse.

We analysed all autumn ringing recoveries reported to the Swedish Ringing Office from 1960 to February 1995. The selection of recoveries was based on the following criteria: only birds captured and ringed during the autumn migration period and recovered within the same calendar year and at least 3 km from the ringing site were included. Species for which at least five birds were recovered and with at least one recovery within 10 days after capture were included in further analyses.

For analyses of direction and distance of migration, the recoveries were divided into two different groups. The first group includes recoveries reported within 10 days after capture, while the second group involves recoveries reported after 10 days. The ringing recoveries were divided into eight different sectors based on the direction of movement, with sector I representing recoveries in directions between 0° (N) and 44° (NE), sector II: 45°–89°, and so on (cf. Appendix I). Most passerine migrants passing the Falsterbo area in autumn are heading towards the south and southwest (see Roos 1984). We classified directions between 135° and 269° (SE–W) as being in agreement with the expected forward migratory directions (sectors IV, V and VI), while directions between 315° and 89° (NW–E) were considered as reverse migration (sectors VIII, I, and II). All other directions (270°–314° and 90°–134°; sectors VII and III, respectively) were classified as other directions of movement. All directions and distances are given according to calculations for a great circle (orthodrome) route (Imboden and Imboden 1972).

The species included in further analyses were classified in three categories: (1) short-distance, partial or irruptive migrants, which include bird species performing relatively short-distance (<1000–1500 km) or irregular migratory movements, (2) temperate migrants, which regularly migrate to wintering areas located in western or southwestern Europe and (3) tropical migrants, which are long-distance migrants wintering mainly in tropical Africa. The following passerine species included in this analysis (Appendix, where Latin names are also given) could be considered to migrate mainly at night: wren, robin, redstart, song thrush, sedge warbler, reed warbler, whitethroat, garden warbler, willow warbler and goldcrest (Dorka 1966). Mainly diurnal migrants are yellow wagtail, coal tit, blue tit, great tit, jay, starling, greenfinch and siskin. Dunnock and reed bunting probably migrate mainly by day but also at night (Dorka 1966). Migration by day and night may occur in several of the other species studied.

The age of the birds was classified according to criteria given in Svensson (1984) and criteria outlined at Falsterbo Bird Observatory. The median proportion of adults among the migrants captured in recent years varied for the different species from 0% (starling and coal tit) up to a maximum of 44% (siskin). The ringing recoveries show that reverse migration performed by adults occurs in all categories of migrants, but the number of recoveries involving adult birds are too few (1–6 recoveries per species) to allow a critical comparison of the degree of reverse migration between different age groups. The available ringing data are dominated by juvenile birds on their first autumn migration, and the results thus primarily reflect the behaviour of this age group.

Fat deposits on the belly and in the tracheal pit were estimated according to a 10-step scale for visual fat classification (based on Pettersson and Hasselquist 1985, but extended with three fat classes, 7–9, at Falsterbo Bird Observatory). Since 1986, time permitting, birds ringed at Falsterbo Bird Observatory have been classified according to this scale for fat estimation, and morphological measurements and weight have been recorded.

Vector addition was used to calculate a mean angle of orientation based on individual recovery directions for each species for the two different periods (Batschelet 1981). The mean vector length,  $r$ , is a measure of the concentration of the circular distribution ( $r$  ranges between 0 and 1, being inversely related to the angular scatter). We used the Rayleigh test to calculate the significance levels for circular distributions (Batschelet 1981). To achieve the

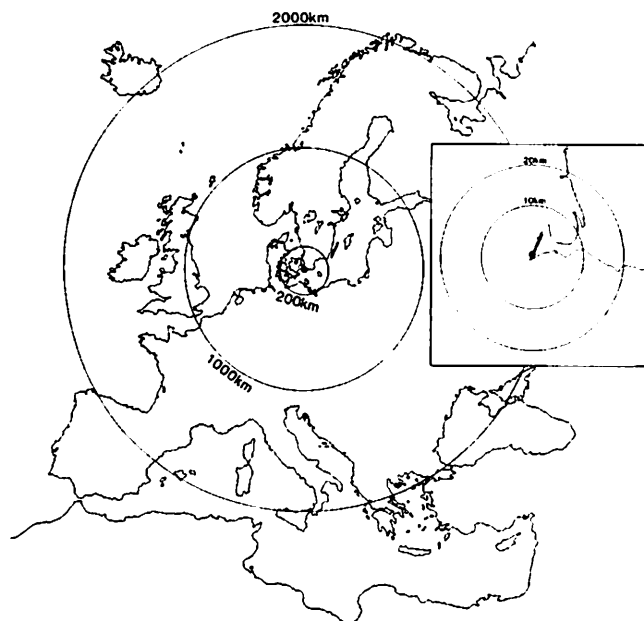


Fig. 1 Two sites are regularly used for capture of birds migrating via the Falsterbo peninsula in southwest Sweden during autumn migration. One site is the lighthouse garden, an isolated stand of trees and bushes, while the other site represents a reedbed. The two sites are only 1 km apart, surrounded by a golf course, at the outermost tip of the Falsterbo peninsula

best description of the angular distributions, we selected the mean axes of orientation when the average vector length resulting from doubling the angles ( $r_2$ ) was larger than the corresponding mean vector length prior to doubling ( $r$ ). To test for differences in scatter between groups we used the test for the homogeneity of concentration parameters (indicated by  $t$ ), while differences in mean angles were investigated by using the one-way classification test ( $F$ ) (Mardia 1972). Spearman rank-order correlation and  $\chi^2$  test were performed with SYSTAT (1992) statistical packages or based on Siegel and Castellan (1988).

## Results

### Direction of migration

A total of 725 recoveries of 20 different passerine species were included in our analyses. The number of recoveries distributed in the eight sectors and reported within 10 days after capture or later during the same year are given in the Appendix for each species. In short-distance or irruptive migrants 43% of the individuals were recovered within 10 days, while the corresponding figures for temperate and tropical migrants were 28% and 48%, respectively. Reoriented migratory movements towards northwest to east (sectors VIII, I and II) were performed by 40% (288) of the total sample of recovered birds and by fully 64% (185) of those recovered within 10 days of capture. The corresponding figures for recoveries in the forward migration directions, southeast to west (sectors IV, V and VI), were 56% (409) of the total sample and 33% (95) of those recovered within 10 days.

The percent and sample size for different categories of migrants performing reverse or forward migration or movements in other directions are given in Fig. 2. Reverse migration occurred more often in the first 10-day period after capture compared to later on. For all three categories of migrants there was a significant difference in the proportion of migrants performing reverse movements, forward migration or movements in other directions between the two periods (short-distance/irruptive migrants:  $\chi^2 = 26.0$ ,  $df = 2$ ; temperate migrants:  $\chi^2 = 112.5$ ,  $df = 2$ ; tropical migrants:  $\chi^2 = 24.2$ ,  $df = 1$ ;  $P < 0.001$  in all cases). There was a significant difference in the proportion of reverse movements between different categories of migrants, within the first 10 days after capture ( $\chi^2 = 6.2$ ,  $df = 2$ ,  $P < 0.05$ ), as well as after 10 days ( $\geq 11$  days after capture;  $\chi^2 = 50.5$ ,  $df = 2$ ,  $P < 0.001$ ). Within the first 10 days after capture, temperate migrants showed a very high proportion of reverse recoveries (75%, cf. Fig. 2), substantially higher than the corresponding proportion among both short-distance and tropical migrants. In the later period ( $\geq 11$  days after capture) the proportion of reverse recoveries was clearly highest among the short-distance migrants (Fig. 2). There was no significant difference in the proportion of reverse recoveries between diurnal and nocturnal

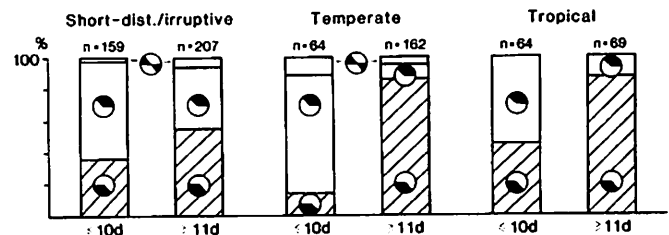


Fig. 2 Proportion of migrants recovered in reverse directions (315°–89°; sectors VIII, I, II) or forward directions (135°–269°; sectors IV, V, VI) or after movements in other directions (sectors III, VII) after capture at Falsterbo Bird Observatory in autumn. Data from six different species are in the category short-distance/irruptive migrants, and from seven species in temperate and tropical migrants, respectively (see Appendix). The dark part of the circle illustrates the direction of movement, and the part of bar indicating the proportion of forward migration is hatched

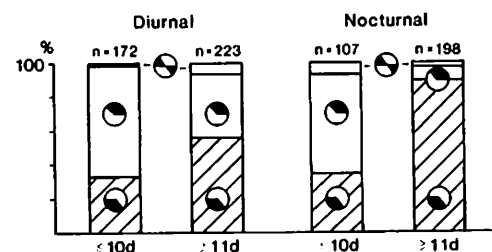


Fig. 3 Proportion of diurnal and nocturnal migrants ringed at Falsterbo Bird Observatory in autumn recovered in reverse or forward directions or after movements in other directions. Included in the category of diurnal migrants are: yellow wagtail, coal tit, blue tit, great tit, jay, starling, greenfinch and siskin. Nocturnal migrants are: wren, robin, redstart, song thrush, sedge warbler, reed warbler, whitethroat, garden warbler, willow warbler and goldcrest. Dunnock and reed buntings are considered as diurnal and nocturnal migrants, and are not included in this analysis. The dark part of the circle illustrates the direction of movement, and the part of bar indicating the proportion of forward migration is hatched

migrants within the first 10 days after capture ( $\chi^2 = 1.3$ ,  $df = 1$ ,  $P > 0.05$ ), but for the complete autumn period there was a significant difference in proportion of reverse recoveries between the two categories of migrants ( $\chi^2 = 41.1$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 3).

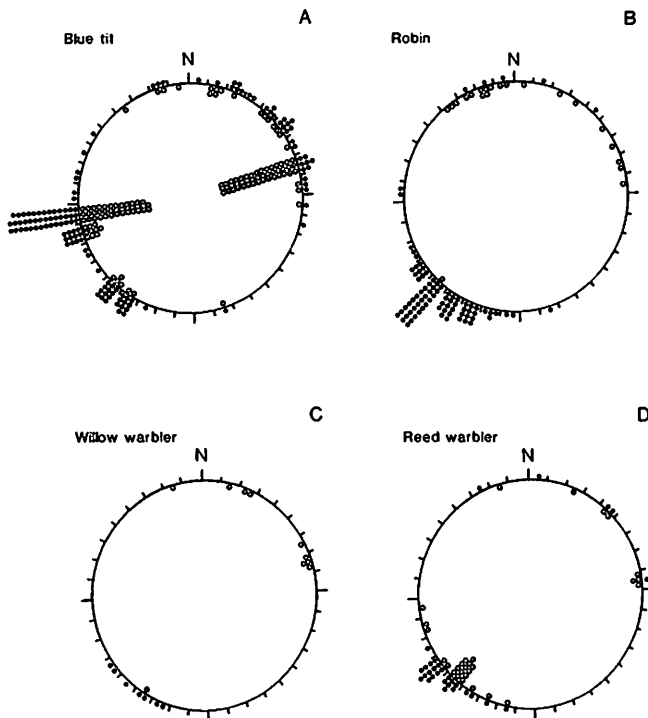
Some examples of migratory directions of different categories of migratory bird species are given in Table 1A (see also Fig. 4). In blue tits the recoveries were bimodally distributed within the first 10-day period as well as later ( $\geq 11$  days after capture) (Fig. 4A). Robins and willow warblers mainly reoriented shortly after capture ( $\leq 10$  days) and were almost always recovered in the expected migratory direction after  $\geq 11$  days since capture (Fig. 4B and C, Table 1A). In contrast, sedge and reed warblers were generally found in the forward migratory direction both shortly after capture and later (cf. test results above; Fig. 4D, Table 1A, Appendix).

Several species showed a significant difference in mean angle of orientation between recoveries reported

**Table 1A** Mean angle of orientation ( $\alpha$ ), vector length ( $r$ ,  $r_2$ ) and number of birds ( $n$ ) recovered within 10 days, or after 11 days or more, according to ringing recoveries from Falsterbo Bird Observatory in autumn. In groups where the axial distributions are more concentrated (higher  $r_2$ ) compared to the unimodal distribution ( $r$ ), values for a bimodal distribution are given. Significance levels are according to the Rayleigh test (Batschelet 1981). **B** Mean angle of orientation, vector length, number of birds and significance levels of all reverse recoveries found in directions between NW and E. Only species with at least five recoveries within sectors VIII, I and II are included

Species	Period	$\alpha$	$r/r_2$	$n$
A Robin	$\leq 10$ days	358°	0.69*** (r)	21
	$\geq 11$	221°	0.86*** (r)	82
Reed warbler	$\leq 10$	51°/231°	0.73*** ( $r_2$ )	29
	$\geq 11$	47°/227°	0.84*** ( $r_2$ )	30
Willow warbler	$\leq 10$	50°	0.66* (r)	10
	$\geq 11$	218°	0.98** (r)	7
Blue tit	$\leq 10$	73°/253°	0.79*** ( $r_2$ )	117
	$\geq 11$	66°/246°	0.66*** ( $r_2$ )	127
<b>B</b>				
Yellow wagtail	All	58°	0.99***	13
Robin	All	8°	0.80***	25
Reed warbler	All	49°	0.80***	13
Willow warbler	All	48°	0.85***	9
Goldcrest	All	30°	0.76***	18
Coal tit	All	70°	0.94***	13
Blue tit	All	59°	0.88***	99
Great tit	All	54°	0.84***	36
Jay	All	40°	0.82***	26
Greenfinch	All	57°	0.67 <sup>ns</sup>	5
Reed bunting	All	65°	0.95**	6

\* $P \leq 0.05$ , \*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ , ns  $P > 0.05$



**Fig. 4** The circular diagrams demonstrate the direction of recoveries for **A** a shortdistance migrant, the blue tit, **B** a temperate migrant, the robin, and two tropical migrants **C** the willow warbler and **D** the reed warbler. The inner circle represents recoveries within 10 days after capture and the outer circle gives the directions of recoveries found at least 11 days after capture. Details of the circular statistics are given in Table 1A

within the first 10 days after capture compared to after at least 11 days (yellow wagtail:  $F_{1,18} = 42.4$ ,  $P < 0.001$ ; dunnoek:  $F_{1,5} = 9.6$ ,  $P < 0.05$ ; robin:  $F_{1,101} = 143.6$ ,  $P < 0.001$ ; song thrush:  $F_{1,23} = 35.7$ ,  $P < 0.01$ ;

whitethroat:  $F_{1,5} = 9.8$ ,  $P < 0.05$ ; willow warbler:  $F_{1,15} = 52.6$ ,  $P < 0.001$ ; goldcrest:  $F_{1,44} = 18.1$ ,  $P < 0.001$ ; reed bunting:  $F_{1,16} = 13.2$ ,  $P < 0.005$ ). These differences in mean orientation are due to the fact that the majority of the migrants are recovered after reverse movements towards northwest to east (sectors VIII, I and II) shortly after capture while recoveries after more than 11 days mostly fall in the normal migratory direction (sectors IV, V and VI). There was a significant difference in scatter between the distribution of recoveries found within the first 10 days after capture compared to later after capture, for blue tit ( $t = 3.1$ ,  $P < 0.05$ ; Mardia 1972), great tit ( $t = 3.2$ ,  $P < 0.05$ ), jay ( $t = 2.4$ ,  $P < 0.05$ ) and siskin ( $t = 10.9$ ,  $P < 0.01$ ). Within the first 10 days after capture these species mainly performed well-defined reverse orientation. After  $\geq 11$  days there was a greater scatter in mean orientation. For all other species studied, there were no differences either in concentration or mean orientation between the two periods (wren:  $F_{1,15} = 2.2$ ; sedge warbler:  $F_{1,11} = 0.2$ ; reed warbler:  $F_{1,57} = 0.6$ ; coal tit:  $F_{1,13} = 0.6$ ; greenfinch:  $F_{1,7} = 1.0$ ;  $P > 0.05$  in all cases). However, redstart ( $F_{1,10} = 3.7$ ,  $P < 0.10$ ), garden warbler ( $F_{1,57} = 0.6$ ,  $P < 0.10$ ) and starling ( $F_{1,7} = 3.7$ ,  $P < 0.10$ ) showed differences, bordering on statistical significance, in the circular distribution of recoveries between the two time periods, demonstrating tendencies of reoriented movements shortly after capture and a dominance of movements in the normal migration direction more than 11 days after capture.

Table 1B gives the mean directions of reverse movements for species with at least five recoveries reported in directions between northwest and east (sectors VIII, I and II). The majority of the mean directions were directed approximately 180° opposite to the normal migration direction. Reoriented movements in robins

and possibly also in goldcrests were directed more to the north compared to the mean orientation of reverse migration in other species ( $P < 0.05$  in 10 out of 16 comparisons between species with at least five recoveries reported in the reverse direction; Mardia 1972). Some species were regularly retrapped by a ringer operating at a locality approximately 9 km ENE of the ringing sites at Falsterbo. Species which were regularly retrapped at this site after reoriented movements were: coal tit ( $\leq 10$  days:  $n = 4$ , making up 67% of all recoveries in the reverse sectors in this species and period;  $\geq 11$  days:  $n = 6$ , 86%), blue tit ( $n = 44$ , 71%;  $n = 5$ , 14%), great tit ( $n = 11$ , 69%;  $n = 8$ , 36%), jay ( $n = 4$ , 30%;  $n = 0$ , 0%) and greenfinch ( $n = 1$ , 33%;  $n = 1$ , 33%). In temperate and tropical migrants only 18% ( $n = 12$ ) of all reorienting birds were retrapped at this site. Yellow wagtails (all) and reed buntings (50%) were mainly retrapped at a roosting site in a reedbed area 10 km northeast of Falsterbo.

### Distance of migration

Distances of reverse and forward migration of the 20 different bird species ringed at Falsterbo in autumn and included in this analysis are given in Appendix. Reverse recoveries (NW–E) were made at distances between 4 and 520 km, while the distances of forward recoveries (SE–W) ranged between 29 and 5625 km. Some examples of unusually long reverse movements are 300 km (reed warbler), 510 km (goldcrest), 520 km (blue tit) and 259 km (jay).

Forward migration involved greater variability in distance, and covered much longer distances in all categories of migrants compared to reverse migration (Table 2; Appendix). Long-distance recoveries in the normal migration direction mainly stem from birds recovered within the normal passage and win-

tering areas in west and southwest Europe and in the Mediterranean area (temperate migrants). Only a few recoveries were from North Africa (redstart, reed warbler and willow warbler) and one yellow wagtail was reported from tropical West Africa (Ghana, 5625 km).

Median reverse migration distances were between 9 and 65 km for the majority of the species during both periods, except for goldcrest with a median distance of 234 km after  $\geq 11$  days since capture (Appendix). Only a restricted number of recoveries were reported in the forward direction of migration during the first ten days after capture, but these were of longer distances than reverse movements during the same period (Table 2).

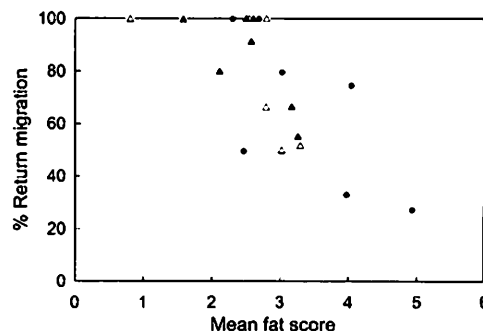
### Effect of body condition on direction of migration

There was a significant negative correlation between the mean fat score at capture (for values see Table 3) and the proportion of reverse migration within the first 10 days after capture among different species (Spearman rank-order correlation:  $r_s = -0.66$ ,  $n = 20$ ,  $P < 0.01$ ; Fig. 5 and Table 3). There were also negative correlations between mean fat score and the proportion of reverse migration within each of the three classes of migrants, but these correlations were not quite statistically significant (short-distance or irruptive migrants:  $r_s = -0.76$ ,  $n = 6$ ,  $P < 0.10$ ; temperate migrants:  $r_s = -0.63$ ,  $n = 7$ ,  $P < 0.10$ ; tropical migrants:  $r_s = -0.68$ ,  $n = 7$ ,  $P < 0.10$ ; different symbols in Fig. 5).

We analysed the directions of movement within the first 10 days after capture in relation to body condition for individuals with mass and fat content registered at capture. Unfortunately, because of sparse data on fat content and mass, only two of the species (blue tit and reed warbler) could be included in this analysis (Table 4). Although showing a tendency for reverse

**Table 2** Range of median distances (in km) covered by different categories of migratory birds performing reverse ( $315^\circ$ – $89^\circ$ ) or forward directed movements ( $135^\circ$ – $269^\circ$ ) after capture. Only median distances of species with at least three recoveries are included. When a median value is available for only one species, this is given in brackets. Data for individual bird species are given in Appendix

Category	Range of medians	
	Reverse	Forward
<b>A. Shortdistance/irruptive migrants</b>		
$\leq 10$ days	9–9	(101)
$\geq 11$ days	9–65	75–725
<b>B. Temperate migrants</b>		
$\leq 10$ days	10–28	(376)
$\geq 11$ days	39–234	393–1547
<b>C. Tropical migrants</b>		
$\leq 10$ days	11–37	710–725
$\geq 11$ days	(34)	776–2394



**Fig. 5** The proportion of reverse migration (%) within 10 days after capture in relation to mean fat score at capture. Each point represents the values for one species. *Open triangles* represent short-distance or irruptive migrants, *filled triangles* temperate migrants and *filled circles* tropical migrants. Values for mean fat class at capture are given in Table 3

**Table 3** Mean fat class at capture (ten-grade scale for visual fat classification). For each species a specific set of years was used for calculations. For details on visual fat classification see Pettersson and Hasselquist (1986). Yellow wagtails, reed warblers, sedge warblers and reed buntings were all captured at the reedbed site. A correlation between the proportion of reverse migration and the mean fat class at capture in different species, given in this table, is presented in Fig. 5

Species	Year	Mean fat class	± SD	n
<b>A. Short-distance/irruptive migrants</b>				
Coal tit	85–93	2.6	1.4	1074
Blue tit	93–94	3.3	1.6	3344
Great tit	93–94	2.8	1.7	706
Jay	80–94	0.8	0.8	1030
Greenfinch	90–94	2.8	1.5	449
Siskin	93–94	3.0	1.8	1768
<b>B. Temperate migrants</b>				
Wren	90–94	3.2	1.4	2863
Dunnock	91–94	2.6	1.8	927
Robin	93–94	2.6	1.5	2989
Song thrush	90–94	2.5	1.4	840
Goldcrest	93–94	3.3	1.6	2445
Starling	85–94	1.6	1.2	64
Reed bunting	93–94	2.1	1.6	664
<b>C. Tropical migrants</b>				
Yellow wagtail	85–94	2.3	1.4	424
Redstart	88–94	2.4	1.7	900
Sedge warbler	93–94	4.0	1.7	1394
Reed warbler	93–94	4.9	2.0	3846
White throat	85–94	2.7	2.3	316
Garden warbler	90–94	4.0	2.0	585
Willow warbler	92–94	3.0	1.9	2620

recoveries to stem from birds with relatively small fat reserves, the data are too meagre to allow a critical test of statistical significance. However, in support of this pattern reorienting individuals were significantly lighter than forward-moving birds [blue tit: reverse mean mass (RM in g) =  $10.4 \pm 0.6$ , forward mean mass (FM) =  $10.8 \pm 0.5$ ;  $t = 1.89$ ,  $n = 31$ ,  $P < 0.07$ ; reed warbler: RM =  $11.9 \pm 1.0$ , FM =  $13.1 \pm 1.4$ ;  $t = 2.16$ ,  $n = 21$ ,  $P < 0.05$ ].

## Discussion

### Direction of migration

The geographical location of Falsterbo Bird Observatory at the southwesternmost point of the Scandinavian peninsula gives a unique opportunity to analyse, on the basis of ringing results, the behaviour and movements of birds reaching the sea after migration flights mainly over land (cf. Fig. 1). Reoriented migration at Falsterbo in autumn has earlier been reported for a restricted number of diurnal and nocturnal passerine migrants (Persson 1972 a, b, c; Alerstam 1978a; Lindström and Alerstam 1986; Sandberg et al. 1988). This study shows that reverse migration is regularly performed by all categories of passerine migrants when confronted with the sea in southwest Sweden on autumn migration. This indicates that preparedness for reverse migration may be a universal feature among migratory passerines. This reorientation possibly represents an adaptation to a situation in which migrants are confronted with an ecological barrier, so that making a temporary retreat to replenish fuel reserves becomes advantageous. Indeed, the high proportion of reverse recoveries within the first 10 days after capture at Falsterbo indicates that the majority of migrants captured at this site may in fact be birds that have just interrupted their forward migration and shifted over to temporary reverse migration, making a brief landfall at the coast in the course of this process.

The proportion of reverse recoveries was also relatively high in the second period ( $\geq 11$  days) for short-distance and irruptive migrants. At least two different causes may explain this pattern. Many partial and irruptive migrants may settle to winter in the reverse direction (Roos 1984; Alerstam 1990a; Ketterson and Nolan 1990). This pattern applies to species such as coal tit, great tit and jay (cf. pp. 173–175 in Alerstam 1990b). In addition, the short-distance migrants (including partial and irruptive migrants) have a much slower migration speed than the other migratory

**Table 4** Fat class at capture of blue tits and reed warblers recovered within 10 days after capture and either performing reverse ( $315^\circ$ – $89^\circ$ ) or forward migration ( $135^\circ$ – $269^\circ$ )

Species	Direction	Fat class										Mean ± SD	Total
		0	1	2	3	4	5	6	7	8	9		
A. Short-distance/irruptive migrant													
Blue tit	Reverse	1	3	2	4	3	1	1	0	0	0	2.8 ± 1.7	15
	Forward	0	0	4	8	4	1	0	0	0	0	3.1 ± 0.8	17
C. Tropical migrants													
Sedge warbler	Reverse	0	1	0	0	0	0	0	0	0	0	(1)	1
	Forward	0	0	0	0	0	1	1	0	0	0	5.5	2
Reed warbler	Reverse	1	0	1	0	0	1	3	0	0	0	4.2 ± 2.6	6
	Forward	0	0	0	1	2	5	3	3	1	0	5.5 ± 1.4	15

categories (for migration speeds see Hildén and Saurola 1982; cf. Fig. 10 in Alerstam and Lindström 1990), and stopover periods in the reverse direction, before fat reserves are restored and forward migration is resumed, may last for a longer time than among other migrants. One should be aware that some birds, irrespective of migration category, may have made their reverse movements in the first 10-day period, although they were not recovered (e.g. reported as long since dead), until later.

Most reoriented movements were directed approximately opposite to the normal southwest migration direction. Robins, and possibly also goldcrests and garden warblers (three recoveries), were found more to the north on reverse migration compared to several of the other species. It has been suggested that this northerly orientation is caused by attraction towards the bright city lights from the Malmö and Copenhagen area (Persson 1972a; Sandberg et al. 1988). However, it is unclear why only some species would be more strongly attracted to lights in this area than other nocturnal bird migrants. The most efficient reverse migration in a coastal area should be directed perpendicularly from the coast, while movements in a 180° reversed migration direction may be facilitated because of the birds' orientation mechanism (Alerstam 1978a). Most birds passing the Falsterbo area on migration probably reach the peninsula from the NE and follow the coasts to the southwestern part (Alerstam 1972; Alerstam and Ulfstrand 1972, 1975), where the two capture sites of the Falsterbo Bird Observatory are located (Fig. 1). In this topographical situation, the most efficient reverse movements from the two coastlines coincide with a 180° orientation reversal towards northeast.

#### Distance of reverse migration

Reverse migration usually covered relatively short distances (9–65 km) for all species studied. These movements were directed towards inland areas where potential resting sites are found. The Falsterbo area is probably not very suitable for refuelling for the majority of passerine migrants. The most suitable stop-over sites are mainly found in northeasterly directions relative to the capture sites and are, for most species, found in forested areas mixed with farmland (cf. map in Alerstam 1978a).

Recoveries of reorienting yellow wagtail, a tropical long-distance migrant, and reed bunting, a temperate migrant, almost exclusively were reported from a roosting site in reedbeds located 10 km towards the northeast in the eastern part of the Falsterbo peninsula. A ringer is regularly operating in this and nearby areas. A great number of short-distance and irruptive migrants were retrapped after reverse movements at a site approximately 9 km ENE of Falsterbo (Persson 1972c). Mainly three species of tits as well as jay and greenfinch were retrapped at this site in high propor-

tions (making up on average 64% and 25% of all recoveries in reverse directions  $\leq 10$  days and  $\geq 11$  days after capture, respectively). This probably reflects an especially low tendency to engage in over-sea flights by these short-distance and irruptive migrants and that reverse migration presumably is performed by short-hop flights. It should be kept in mind that the migrants may be heading for stop-over sites or wintering areas further inland than this nearby ringing site, and that the median distance of reverse movements therefore may be underestimated. The high proportion of retraps at this ringing site may also bias the direction of reverse movements more to the east, especially among the tits, in comparison with the other species.

The location of ringing sites may affect the distribution of recoveries (see discussion above), but a large fraction of the migrants were reported due to other circumstances (e.g. found dead, killed by cat) both in the reverse and the forward direction. The distribution of human activity and settlements may also influence the distribution and the number of recoveries reported. In this study we believe there is no major difference in the probability of receiving reports on recoveries between the densely populated areas of south Scandinavia and northwestern Europe in the reverse and forward migration sectors from the Falsterbo peninsula, respectively. Therefore we believe that the data on direction of movement do indeed reflect a natural behaviour of reverse migration in autumn.

#### Effect of body condition on orientation

Bird species with smaller average fat deposits showed reverse movements more often than species with larger fat reserves (Fig. 5). However, in 14 out of 20 bird species included in this study the average fat score ranged from 2.3 to 3.3 (Table 3), independent of which category of migrants the species belonged to. The average fat score of all species within each category was the same (2.6) in short-distance and temperate migrants and higher (3.3) in long-distance migrants. This demonstrates that most birds captured had relatively modest fat deposits.

One important reason for the pattern in Fig. 5 is presumably that lean birds are more likely to make land-fall at the trapping sites than fat birds. Most migrants arriving at Falsterbo in autumn have been migrating mainly over land with modest fat deposits. It would be expected that the birds with limited reserves would often show reverse movements when encountering relatively limited ecological obstacles (like the Baltic Sea). Robins arriving at Falsterbo in autumn, after having migrated mainly over land, have a higher body mass for each specific fat class compared to conspecifics captured after long-distance migration flights over sea (cf. fat-mass relationship and high liver mass for robins captured at Falsterbo; Karlsson et al. 1988; Åkesson et al. 1992; Ehnborn et al. 1993). This may reflect the

fact that robins arriving at Falsterbo in autumn are physiologically prepared for immediately resuming fuel accumulation after each short flight, with a reduced ability to perform long-distance flights across barriers. This pattern is probably valid for other species too, not only among short- and medium-distance migrants but also in some species with very distant tropical migration goals (e.g. redstart, whitethroat and willow warbler).

The smallest average fat score (0.8) was found in the jay, a truly irruptive species, inhabiting woodland and only seen on migration when the abundance of acorn is very low. Thus, the reason for migration in the jay is lack of food and it is only to be expected that the migrating birds are lean. The high degree of reverse movements may be because of small fuel reserves, but also because of the great hesitation the jays show when confronted with the sea (cf. Enemar 1957; Ulfstrand 1959; Roos 1978). The flocks make repeated attempts to migrate, climbing to several hundred meters just at the shoreline and then turning back. This behaviour is certainly very wasteful of energy, which is inconsistent with low fuel reserves. This behaviour is also seen in other irruptive species like the nutcracker (*Nucifraga caryocatactes*) and (though not so clearly) tits.

Capture data on two species of diurnally migrating finches passing the Falsterbo area on migration have revealed that birds performing reverse movements to resting grounds towards the north and northeast have smaller fat reserves than those moving in the migratory direction (Lindström and Alerstam 1986). A high incidence of reoriented behaviour in lean birds has also been established in orientation cage experiments with nocturnally migrating robins (cf. below; Sandberg 1994). The same relationship was found in this study where birds performing reverse movements were lighter than forward-moving birds (two species) within the first 10 days after capture.

### The adaptive significance of a bimodal orientation mechanism

Migratory birds may travel along coasts to reduce energy expenditure (Alerstam 1978b; Alerstam and Pettersson 1977) and to facilitate orientation and compensation for wind drift. Diurnal bird migrants regularly fly along coasts in large numbers (e.g. Alerstam 1978b; Alerstam and Ulfstrand 1971), and at least low altitude migrants may follow coastlines also at night (Åkesson 1993). This may lead to high concentrations of migrants in coastal areas and at peninsulas protruding in the direction of migration. Therefore high competition and low availability of food combined with high predation risk are to be expected in coastal areas (i.e. Alerstam 1978a; Lindström 1990; Lindström and Alerstam 1986; Moore and Young 1991). To alleviate these problems a bimodal orientation mechanism,

favouring reoriented flights to more suitable resting grounds, may be of selective advantage for birds not prepared to cross the barrier immediately.

Bimodal orientation has repeatedly been observed for different nocturnal bird migrants in orientation cage studies (Able 1977; Bingman 1981, 1983; Bingman and Wiltshko 1988; Sandberg et al. 1988; Sandberg 1994; Able and Able 1990, 1993a, b, 1995; Berthold et al. 1990). The reason for this bimodal orientation has not been explained, but suggests an innate mechanism of axial orientation. This innate directional ambivalence may disappear in experienced wild-caught migrants (see for example savannah sparrows; Bingman 1981, 1983), but does indeed occur in some migrants captured on migration (Able 1977; Sandberg et al. 1988; Sandberg 1994). Axial orientation relative to the geomagnetic field has been demonstrated to be related to the body condition of migratory robins in autumn (Sandberg 1994) in accordance with the results in this study. Birds with large fat deposits oriented towards the normal migration direction while lean birds demonstrated reverse orientation in circular orientation cages. Another alternative explanation for reverse migration may be that birds cannot correctly assess the seasonally appropriate end of the migration axis due to orientation mechanism limitations (cf. Alerstam 1990). However, the location of the capture site and the high proportion of reverse migrants represented by all different categories of migrants speak against this possibility and instead indicate an adaptive explanation. In reality, reverse migration is probably a mixture of many ecological and orientation considerations to be taken into account by the birds. Migratory birds may indeed have use for a universal innate mechanism for reverse orientation, shaped by the forces of natural selection, enabling them to retreat from coasts or other areas bordering on ecological obstacles to more suitable resting grounds before continuing migration.

**Acknowledgements** We are grateful to Frank R. Moore for discussions and comments on the manuscript. We acknowledge all persons taking part in the ringing activity at Falsterbo Bird Observatory throughout the years, for their patient and enthusiastic work. The Swedish Ringing Office supported us with information on ringing recoveries, Vidar Bakken and Gudmundur A. Gudmundsson helped with computer programs and Steffi Douwes drew the illustrations. We are also very grateful to the Associate Editor, W.A. Searcy, and to J.A. Waldvogel and an anonymous referee for suggesting many improvements to the manuscript. Financial support was given by grants from Swedish Natural Science Research Council (to T. Alerstam). This is report no.180 from Falsterbo Bird Observatory.

### References

- Able KP (1977) The orientation of passerine nocturnal migrants following offshore drift. *Auk* 94:320-330
- Able KP, Able MA (1990) Ontogeny of migratory orientation in the savannah sparrow, *Passerculus sandwichensis*: mechanisms at sunset. *Anim Behav* 39:1189-1198



- Able KP, Able MA (1993a) Daytime calibration of magnetic orientation in a migratory bird requires a view of skylight polarisation. *Nature* 364:523–525
- Able KP, Able MA (1993b) Magnetic orientation in the savannah sparrow. *Ethology* 93:337–343
- Able KP, Able MA (1995) Interactions in the flexible orientation system of a migratory bird. *Nature* 375:230–232
- Åkesson S (1993) Coastal migration and wind drift compensation in nocturnal passerine migrants. *Ornis Scand* 24:87–94
- Åkesson S, Karlsson L, Pettersson J, Walinder G (1992) Body composition and migration strategies: a comparison between robins (*Erithacus rubecula*) from two stop-over sites in Sweden. *Vogelwarte* 36:188–195
- Alerstam T (1972) Nocturnal bird migration in Skåne, Sweden, as recorded by radar in autumn 1971. *Ornis Scand* 3:141–151
- Alerstam T (1978a) Reoriented bird migration in coastal areas: dispersal to suitable resting grounds? *Oikos* 30:405–408
- Alerstam T (1978b) Analysis and a theory of visible bird migration. *Oikos* 30:273–349
- Alerstam T (1990a) Ecological causes and consequences of bird orientation. *Experientia* 46:405–415
- Alerstam T (1990b) Bird migration. Cambridge University Press, Cambridge
- Alerstam T, Lindström Å (1990) Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner E (ed) Bird migration. Springer, Berlin Heidelberg New York, pp 331–351
- Alerstam T, Pettersson S-G (1977) Why do migrating birds fly along coastlines? *J Theor Biol* 65:699–712
- Alerstam T, Ulfstrand S (1972) Radar and field observations of diurnal bird migration in south Sweden, autumn 1971. *Ornis Scand* 3:99–139
- Alerstam T, Ulfstrand S (1975) Diurnal migration of passerine birds over south Sweden in relation to wind direction and topography. *Ornis Scand* 6:135–149
- Batschelet E (1981) Circular statistics in biology. Academic Press, New York
- Berthold P, Wiltschko W, Mildenerberger H, Querner U (1990) Genetical transmission of migratory behaviour in blackcaps, *Sylvia atricapilla*. *Experientia* 46:107–108
- Bingman VP (1981) Savannah sparrows have a magnetic compass. *Anim Behav* 29:962–963
- Bingman VP (1983) Magnetic field orientation of migratory savannah sparrows with different first summer experience. *Behaviour* 87:43–53
- Bingman VP, Wiltschko W (1988) Orientation of dunlocks (*Prunella modularis*) at sunset. *Ethology* 77:1–9
- Dorka V (1966) Das jahres- und tageszeitliche Zugmuster von Kurz- und Langstrecken-ziehern nach Beobachtungen auf den Alpenpassen Cou-Bretolet. *Ornithol Beob* 63:165–223
- Ehnbohm S, Karlsson L, Ylvén R, Åkesson S (1993) A comparison of autumn migration strategies in Robins *Erithacus rubecula* at a coastal and an inland site in southern Sweden. *Ring Migr* 14:84–93
- Enemar A (1957) The ringing activity at Falsterbo Bird Observatory 1954–1956 (in Swedish with English summary). *Vår Fågelvärld* 16:20–36
- Evans PR (1968) Reorientation of passerine night migrants after displacement by the wind. *Br Birds* 61:281–303
- Haartman L von (1945) Umschlagende Zugrichtung beim Buchfinken *Fringilla c. coelebs* L., im Herbst. *Ornis Fenn* 22:10–16
- Haartman L von, Bergman G, Koskimies J (1946) Beobachtungen über umschlagende Zugrichtungen der Bachstelze, *Motacilla a. alba* L., im Herbst. *Ornis Fenn* 23:50–62
- Hildén O, Saurola P (1982) Speed of autumn migration of birds ringed in Finland. *Ornis Fenn* 59:140–143
- Imboden C, Imboden D (1972) Formel für Orthodrome und Loxodrome bei der Berechnung von Richtung und Distanz zwischen Beirungs- und Wiederfundort. *Vogelwarte* 26:336–346
- Karlsson L, Persson K, Pettersson J, Walinder G. (1988) Fat-weight relationships and migratory strategies in the Robin *Erithacus rubecula* at two stop-over sites in south Sweden. *Ring Migr* 9:160–168
- Ketterson E, Nolan VJr (1990) Site attachment and site fidelity in migratory birds: experimental evidence from the field and analogies from neurobiology. In: Gwinner E (ed) Bird migration. Springer, Berlin Heidelberg New York, pp 117–129
- Koskimies J (1947) Über den Herbstzug der Bachstelze *Motacilla alba* in der Gegend von Helsinki. *Ornis Fenn* 24:61–79
- Lindström Å (1990) The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. *Behav Ecol* 1:24–35
- Lindström Å, Alerstam T (1986) The adaptive significance of reoriented migration of chaffinches *Fringilla coelebs* and bramblings *F. montifringilla* during autumn in southern Sweden. *Behav Ecol Sociobiol* 19:417–424
- Mardia KV (1972) Statistics of directional data. Academic Press, London
- Moore FR, Young W (1991) Evidence of food-based competition among passerine migrants during stopover. *Behav Ecol Sociobiol* 28:85–90
- Persson C (1972a) Short distance movements of some passerines in south-western Scania during the autumn migration (In Swedish with English summary). *Vår Fågelvärld* 31:163–166
- Persson C (1972b) The annual cycle and the autumn movements of tits (*Paridae*) on Falsterbo Peninsula (In Swedish with English summary). *Vår Fågelvärld* 31:167–177
- Persson C (1972c) Recoveries of *Parus major* and *P. caeruleus*, ringed on Falsterbo Peninsula (In Swedish with English summary). *Vår Fågelvärld* 31:178–182
- Pettersson J, Hasselquist D (1985) Fat deposition and migration capacity of robins *Erithacus rubecula* and goldcrests *Regulus regulus* at Ottenby, Sweden. *Ring Migr* 6:66–76
- Richardson WJ (1978) Reorientation of nocturnal landbird migrants over the Atlantic ocean near Nova Scotia in autumn. *Auk* 95:717–732
- Richardson WJ (1982) Northeastward reverse migration of birds over Nova Scotia, Canada, in autumn. *Behav Ecol Sociobiol* 10:193–206
- Roos G (1978) Visible bird migration at Falsterbo in autumn 1977 (In Swedish with English summary). *Anser* 17:69–89
- Roos G (1984) Migration, wintering and longevity of birds ringed at Falsterbo (1947–1980) (English summary). *Anser* (Suppl 13), Lund
- Roos G, Karlsson L (1981) The ringing activity at Falsterbo Bird Observatory 1980. (In Swedish with English summary). *Anser* 20:99–108
- Sandberg R (1994) Interaction of body condition and magnetic orientation in autumn migrating robins, *Erithacus rubecula*. *Anim Behav* 47:679–686
- Sandberg R, Pettersson J, Alerstam T (1988) Why do migrating Robins, *Erithacus rubecula*, captured at two nearby stop-over sites orient differently? *Anim Behav* 36:865–876
- Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioural sciences. McGraw-Hill, New York
- Svensson L (1984) Identification guide to European passerines. Svensson, Stockholm
- SYSTAT (1992) SYSTAT for Windows, statistics, version 5. SYSTAT, Evanston
- Ulfstrand S (1959) The bird migration at Falsterbo, Scania, SW Sweden, in 1955 (In Swedish with English summary). *Vår Fågelvärld* 18:131–162

Communicated by W.A. Searcy

**Appendix** Number of recoveries and distance in km of reverse (315°–90°) and forward migration flights (135°–270°) of birds ringed at Falsterbo Bird Observatory during autumn migration and recovered within the same calendar year shortly after capture ( $\leq 10$  days) or later ( $\geq 11$  days), respectively. The recoveries are distributed on eight sectors of directions where sector I represents recoveries found between 0° and 44°, sector II = 45°–89°, III = 90°–134°, etc. Proportion of birds performing reverse (315°–90°), forward (135°–270°) or movements in other directions are given for each species

Species	Period (days)	I	II	III	IV	V	VI	VII	VIII	Total	%Reverse (VIII,I,II)	%Forward (IV,V,VI)	%Others (III,VII)	Range (km)	Reverse Median (km)	n	Range (km)	Forward Median (km)	n
<b>A. Short-distance/irruptive migrants</b>																			
Coal tit	$\leq 10$	2	4	0	0	0	0	0	0	6	100.0	0	0	4–16	9	6	–	–	0
<i>Parus ater</i>	$\geq 11$	0	7	0	0	0	2	0	0	9	77.8	22.2	0	9–38	9	7	101–143	122	2
Blue tit	$\leq 10$	7	52	1	1	2	52	0	4	119	52.9	46.2	0.8	7–242	9	63	89–148	101	55
<i>Parus caeruleus</i>	$\geq 11$	10	23	2	1	12	68	6	3	125	28.8	64.8	6.4	7–520	34	36	62–540	101	81
Great tit	$\leq 10$	3	12	0	0	0	0	0	1	16	100.0	0	0	4–45	9	16	–	–	0
<i>Parus major</i>	$\geq 11$	6	11	2	0	0	5	1	3	28	71.4	17.9	10.7	4–50	24	20	40–112	75	6
Jay	$\leq 10$	3	6	0	0	0	0	0	4	13	100.0	0	0	4–67	9	13	–	–	0
<i>Garrulus glandarius</i>	$\geq 11$	5	6	0	0	1	4	2	2	20	65.0	25.0	10.0	26–259	65	13	29–171	91	5
Greenfinch	$\leq 10$	1	1	0	0	1	0	0	0	3	66.7	33.3	0	6–21	14	2	–	(51)	1
<i>Carduelis chloris</i>	$\geq 11$	0	2	0	0	2	1	0	1	6	50.0	50.0	0	6–30	21	3	100–712	195	3
Siskin	$\leq 10$	0	1	0	0	0	1	0	0	2	50.0	50.0	0	–	(7)	1	–	(98)	1
<i>Carduelis spinus</i>	$\geq 11$	1	0	0	1	10	7	0	0	19	5.3	94.7	0	–	(23)	1	98–2466	725	18
<b>B. Temperate migrants</b>																			
Wren	$\leq 10$	0	1	0	0	0	1	0	1	3	66.7	33.3	0	–	(60)	1	38–241	139	2
<i>Troglodytes troglodytes</i>	$\geq 11$	0	0	0	0	8	5	0	1	14	7.1	92.9	0	–	(29)	1	48–1444	914	13
Dunnock	$\leq 10$	2	1	0	0	0	0	0	0	3	100.0	0	0	4–22	16	3	–	–	0
<i>Prunella modularis</i>	$\geq 11$	1	0	0	0	3	0	0	0	4	25.0	75.0	0	–	(16)	1	708–1100	900	3
Robin	$\leq 10$	3	5	0	0	1	0	1	11	21	90.5	4.8	4.8	4–112	28	19	–	(585)	1
<i>Erithacus rubecula</i>	$\geq 11$	1	1	0	1	51	23	2	3	82	6.1	91.5	2.4	4–74	39	5	295–2688	1547	75
Song thrush	$\leq 10$	1	2	0	0	0	0	0	0	3	100.0	0	0	5–111	26	3	–	–	0
<i>Turdus philomelos</i>	$\geq 11$	0	1	0	0	19	3	0	0	23	4.4	95.6	0	–	(7)	1	857–2003	1509	22
Goldcrest	$\leq 10$	4	6	4	0	2	4	2	5	27	55.6	22.2	22.2	47–510	27	14	101–837	376	6
<i>Regulus regulus</i>	$\geq 11$	1	1	1	0	4	8	3	1	19	15.8	63.2	21.0	26–510	234	4	43–1382	708	15
Starling	$\leq 10$	0	1	0	0	0	0	0	1	2	100.0	0	0	6–65	36	2	–	–	0
<i>Sturnus vulgaris</i>	$\geq 11$	0	1	0	0	0	4	2	0	7	14.3	57.1	28.6	–	(14)	1	71–777	393	4
Reed bunting	$\leq 10$	1	3	0	0	1	0	0	0	5	80.0	20.0	0	5–22	10	4	–	(107)	1
<i>Emberiza schoeniclus</i>	$\geq 11$	0	2	0	1	8	2	0	0	13	15.4	84.6	0	5–10	8	2	174–2020	745	11
<b>C. Tropical migrants</b>																			
Yellow wagtail	$\leq 10$	0	11	0	0	0	0	0	0	11	100.0	0	0	10–12	11	11	–	–	0
<i>Motacilla flava</i>	$\geq 11$	0	2	0	0	7	0	0	0	9	22.2	77.8	0	11–11	11	2	800–5625	1820	7
Redstart	$\leq 10$	0	0	0	0	0	1	0	1	2	50.0	50.0	0	–	(61)	1	–	(342)	1
<i>Phoenicurus phoenicurus</i>	$\geq 11$	0	1	0	0	8	1	0	0	10	10.0	90.0	0	–	(11)	1	593–2609	2394	9
Sedge warbler	$\leq 10$	0	2	0	1	2	1	0	0	6	33.3	66.7	0	37–54	46	2	107–1642	725	4
<i>Acrocephalus schoenobaenus</i>	$\geq 11$	0	0	0	2	5	0	0	0	7	0	100.0	0	–	–	0	92–1498	1027	7
Reed warbler	$\leq 10$	2	5	0	0	9	12	0	1	29	27.6	72.4	0	5–300	37	8	102–1460	710	21
<i>Acrocephalus scirpaceus</i>	$\geq 11$	2	2	0	0	7	18	0	1	30	16.7	83.3	0	5–52	34	5	126–3285	776	25
Whitethroat	$\leq 10$	0	2	0	0	0	0	0	0	2	100.0	0	0	10–12	11	2	–	–	0
<i>Sylvia communis</i>	$\geq 11$	0	0	0	0	1	2	0	1	4	25.0	75.0	0	–	(26)	1	869–1443	1191	3
Garden warbler	$\leq 10$	1	0	0	0	1	0	0	2	4	75.0	25.0	0	4–35	33	3	–	(311)	1
<i>Sylvia borin</i>	$\geq 11$	0	0	0	0	2	0	0	0	2	0	100.0	0	–	–	0	891–1710	1300	2
Willow warbler	$\leq 10$	3	5	0	0	1	1	0	0	10	80.0	20.0	0	7–51	16	9	–	(406)	1
<i>Phylloscopus trochilus</i>	$\geq 11$	0	0	0	0	5	2	0	0	7	0	100.0	0	–	–	0	1076–2525	2208	7