

## **Bimodal orientation and the adaptive significance of temporary reverse bird migration in autumn**

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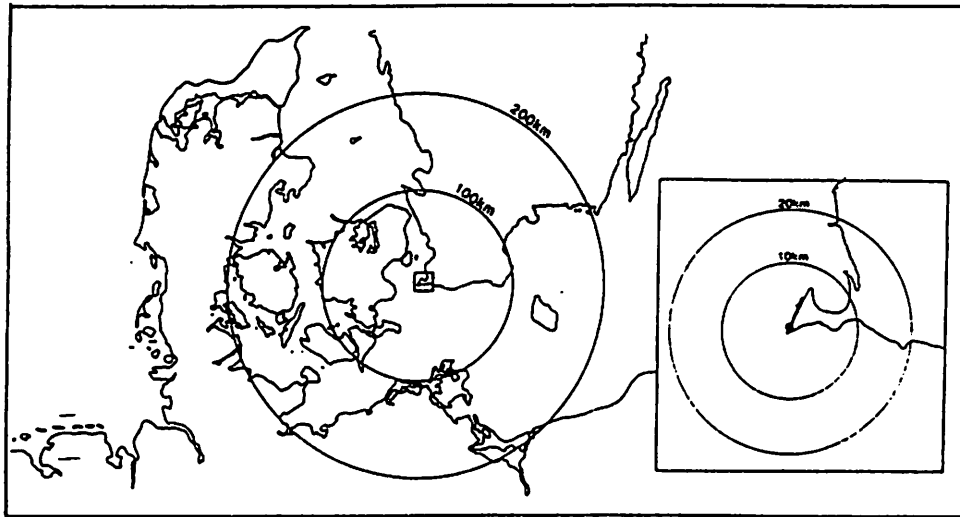
Migratory birds regularly engage in flights opposite to the migratory direction, i.e. away from their migratory destinations, in spring as well as in autumn (e.g. von Haartman 1945, von Haartman et al. 1946, Koskimies 1947, Evans 1968, Able 1977, Richardson 1978, Lindström and Alerstam 1986, Sandberg et al. 1988). The cause of these reverse movements might be different under different environmental circumstances (for review, see Richardson 1982), and factors such as orientation errors, effect of wind drift and unsuitable weather have been proposed to explain this behaviour. In areas bordering to ecological barriers (i.e. coasts and deserts) temporary reverse movements might be performed by birds with small fuel reserves (e.g. Alerstam 1978a). In these areas migratory birds encounter low food availability, high competition for the food and presumably higher risk of predation. Two species of diurnally migrating finches regularly perform reverse movements when confronted with the sea in south Scandinavia (Falsterbo) in autumn (Lindström and Alerstam 1986), and the question is whether temporary reverse bird migration is a general phenomenon in birds arriving at the coast in autumn.

To test this idea, autumn ringing recoveries of 20 different species of passerines ringed at Falsterbo Bird Observatory at the southwestern coast of Sweden were analysed with respect to direction of movement (for extensive analysis, see Åkesson et al. 1996). The occurrence of reverse migration was analysed in species and categories of migrants which differed with respect to: distance of migration, time of migration and body condition. In this paper I report on the direction of movements by migrants recovered within a short period after capture ( $\leq 10$  days) compared to birds recovered more than 11 days after capture and the effect of body condition on direction of migration.

To investigate whether nocturnal passerine migrants passing the Falsterbo area on migration in autumn resume on reverse migration already at night, I have recorded the direction of individual flight paths of free-flying nocturnal migrants (i.e. ceilometer technique; 1-3 hours before local sunrise) at two nearby coastal sites at the Falsterbo peninsula.

### **Study Site and Methods**

Falsterbo Bird Observatory (55°23'N, 12°50'E) is situated at the coast in southwesternmost Sweden (Fig. 1). Bird ringing started 1947 at this site (Roos 1984) and annually about 23000 birds are ringed in spring and autumn. The trapping is performed according to a standardised routine initiated 1980. All birds are captured in mistnets, ringed, measured and thereafter immediately released at the ringing site. The main part of the birds are captured in the lighthouse garden, an isolated stand of trees and bushes surrounded by open area (golf course). During early autumn (July-September) birds are also captured at a nearby reedbed area, located about 1 km north of the lighthouse.



**Figure 1:** The two ringing sites, a lighthouse garden and a nearby reedbed area, at Falsterbo Bird Observatory are located at the coast in southwesternmost part of Sweden.

Autumn ringing recoveries reported to the Swedish Ringing Office from 1960 to February 1995 were included in the analysis. Based on the following criteria birds were selected for further analyses: only birds recovered in autumn within the same calendar year and at least 3 km of distance from the ringing site were included. Species for which at least five recoveries and with at least one recovery within 10 days after capture were selected. For analyses of direction the recoveries were divided into two different groups. The first group represents recoveries reported within 10 days after capture and the second group are birds recovered 11 days or longer after capture. Birds recovered between  $135^{\circ}$  and  $269^{\circ}$  (SE-W) were classified as performing forward movements (see Roos 1984), while recoveries between  $315^{\circ}$  and  $89^{\circ}$  (NW-E) were considered as reverse movements (cf. Fig. 1). All other recoveries (i.e. between  $90^{\circ}$ - $134^{\circ}$  and  $270^{\circ}$ - $314^{\circ}$ ) were classified as other directions.

The species included in further analyses were classified in three different categories based on the distance of migration and the location of their wintering grounds: 1) short-distance, partial or irruptive migrants, which include bird species performing relatively short-distance and irregular migratory movements (<1000-1500 km; coal tit *Parus ater*, blue tit *P. caeruleus*, great tit *P. major*, jay *Garrulus glandarius*, greenfinch *Carduelis chloris*, siskin *C. spinus*), 2) temperate migrants, wintering mainly in areas located in southwestern and western Europe (wren *Troglodytes troglodytes*, dunnoek *Prunella modularis*, robin *Erithacus rubecula*, song thrush *Turdus philomelos*, goldcrest *Regulus regulus*, starling *Sturnus vulgaris*, reed bunting *Emberiza schoeniclus*), 3) tropical migrants, which are long-distance migrants wintering mainly in tropical Africa (yellow wagtail *Motacilla flava*, redstart *Phoenicurus phoenicurus*, sedge warbler *Acrocephalus schoenobaenus*, reed warbler *A. scirpaceus*, whitethroat *Sylvia communis*, garden warbler *S. borin*, willow warbler *Phylloscopus trochilus*). Diurnal migrants are all species in category 1 and the yellow wagtail (dunnoek and reed bunting probably migrate mainly by day but

also at night; Dorka 1966), while the rest of the species are considered mainly as nocturnal migrants. The great majority of the birds were juveniles and therefore the results primarily reflects the behaviour of this age group.

The size of the birds' fat deposits on the belly and in the tracheal pit were estimated at capture according to a 10-step scale for visual fat classification (see Pettersson and Hasselquist 1985, but extended with three classes at Falsterbo Bird Observatory). A mean fat score for each species were used in an analysis of the relationship between degree of reverse migration and body condition.

Observations of free-flying nocturnal passerine migrants were performed at two nearby coastal sites at the opposite sides of the Falsterbo peninsula (for description of sites, see Åkesson 1993) in autumn 1989. The flight directions of individual birds flying through a vertical light beam (i.e. ceilometer) were observed with a pair of binoculars (10x) and were estimated according to a clock-face to the nearest half-hour. Later the flight directions were converted to track directions for individual birds as described by Gauthreaux (1969). The majority of the birds observed were flying at low altitudes, approximately between 10 and 100 m above ground.

Circular statistical methods were applied to calculate a mean angle of orientation based on individual recovery directions for each species for the two different periods and for calculation of mean track directions of free-flying migrants (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). The Rayleigh test was used to calculate the significance levels for circular distributions (Batschelet 1981). Spearman rank-order correlation and  $\chi^2$ -test were performed with SYSTAT (1982) statistical packages or based on Siegel and Castellan (1988).

## Results

### *Direction of migration*

The analysis of ringing recoveries is based on 725 recoveries of 20 different passerine species. The circular distributions of recoveries for different species are given in Åkesson et al. (1996). In short-distance or irruptive migrants 43% of the individuals were recovered within 10 days after capture, while the corresponding figures were 28% of the temperate and 48% of the tropical migrants. Of the total sample of birds 40% (288) performed reverse movements towards northwest to east, and of those performed 64% (185) reverse movements within 10 days after capture. The corresponding figures for recoveries reported in the forward direction, between southeast and west, were 56% (409) of the total sample and 33% (95) for birds recovered within 10 days.

Reverse migration occurred more often in the first 10-day period after capture compared to later on (Table 1). There was a significant difference in the proportion of migrants performing reverse movements, forward migration or movements in other directions between the two periods for all three categories of migrants ( $\chi^2$ -test,  $p < 0.001$  in all cases; see Åkesson et al. 1996).

Some examples of migratory directions of different categories of birds with a similar migration strategy are given in Table 2 and Fig. 2. In three species of tits (coal tit, blue tit and great tit), the recoveries were bimodally distributed in both periods, within 10 days after capture as well as later on (Fig. 2A and B). The distributions of recoveries of temperate migrants

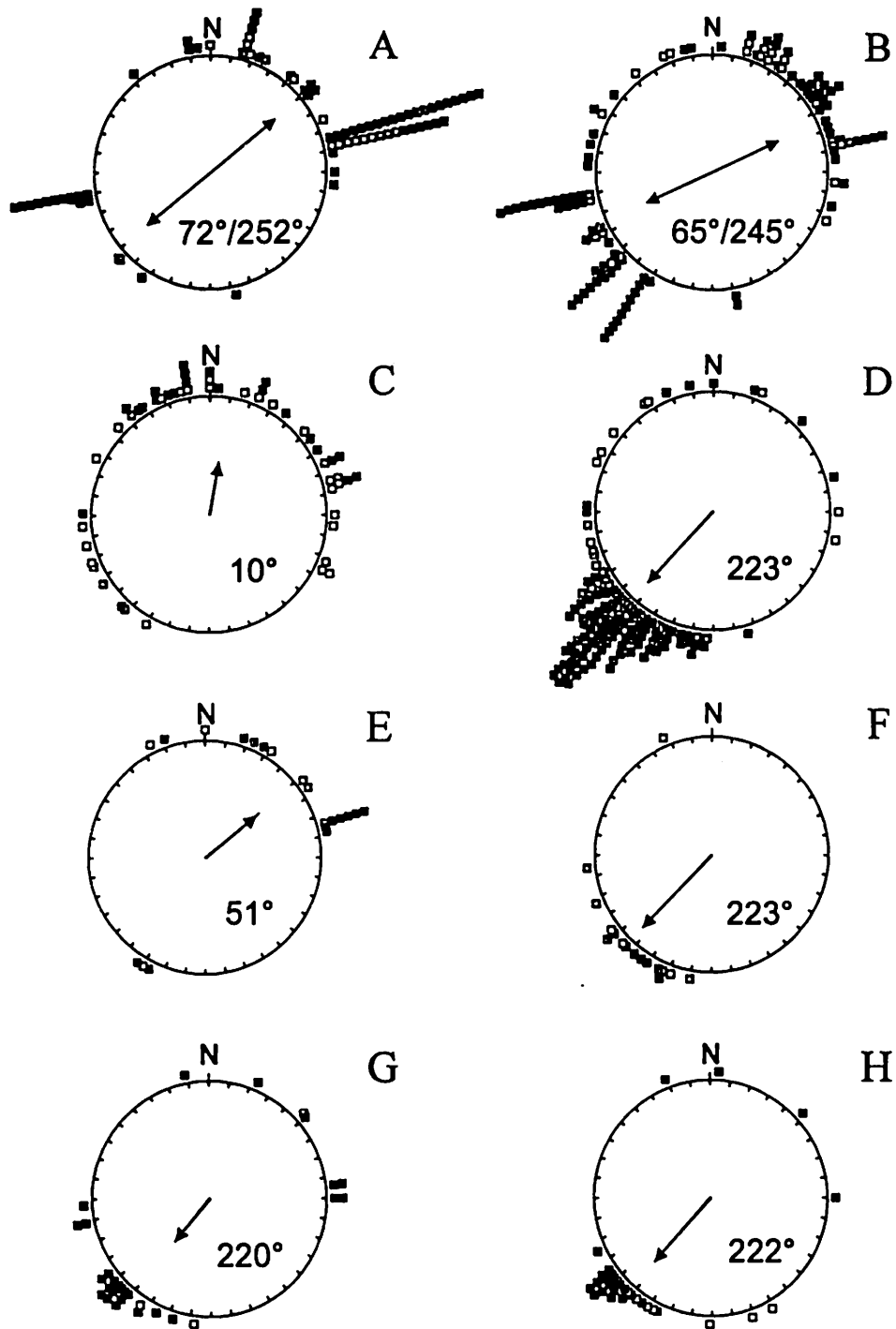
**Table 1:** Proportion and number of migrants recovered in reverse directions (315°-89°) or forward directions (135°-269°) or after movements in other directions after capture at Falsterbo Bird Observatory in autumn. Data from six different species is included in category A and from seven species in category B and C, respectively

Category	Period	Reverse % (N)	Forward % (N)	Other % (N)
A. Short-distance/ irruptive migrants	≤10 days	63.5 (101)	35.8 (57)	0.6 (1)
	≥11 days	38.6 (80)	55.1 (114)	6.3 (13)
B. Temperate migrants	≤10 days	75.0 (48)	14.1 (9)	10.9 (7)
	≥11 days	8.6 (14)	86.4 (140)	4.9 (8)
C. Tropical migrants	≤10 days	54.7 (35)	45.3 (29)	0 (0)
	≥11 days	13.0 (9)	87.0 (60)	0 (0)

**Table 2:** Vector length ( $r$ ,  $r_2$ ) and number of birds (N) recovered within 10 days after capture, or after 11 days or more, according to ringing recoveries from Falsterbo Bird Observatory in autumn. Site 1 and Site 2 represents vector lengths for mean track directions of free-flying migrants recorded at two coastal sites at the Falsterbo peninsula. For highly significant axial distributions ( $r_2$ ), values for a bimodal distribution are given. Significance levels (\*\*\*:  $p < 0.001$ , \*\*:  $p < 0.01$ ) are according to the Rayleigh test (Batschelet 1981). See Fig. 2 and 4 for circular distributions

Species	Period	$r / r_2$	N
A coal tit, blue tit, great tit	≤10 days	0.72*** ( $r_2$ )	109
B <i>Parus ater</i> , <i>P. caeruleus</i> , <i>P. major</i>	≥11	0.63*** ( $r_2$ )	151
C wren, song thrush, goldcrest	≤10	0.45*** ( $r$ )	53
D <i>Troglodytes troglodytes</i> , <i>Turdus philomelos</i> , <i>Regulus regulus</i>	≥11	0.82*** ( $r$ )	141
E whitethroat, garden warbler, willow warbler	≤10	0.57** ( $r$ )	20
F <i>Sylvia communis</i> , <i>S. borin</i> , <i>Phylloscopus trochilus</i>	≥11	0.86*** ( $r$ )	16
G sedge warbler, reed warbler	≤10	0.47** ( $r$ )	29
H <i>Acrocephalus schoenobaenus</i> , <i>A. scirpaceus</i>	≥11	0.73*** ( $r$ )	32
Site 1	Sept-Oct	0.52*** ( $r$ )	71
Site 2	Sept-Oct	0.35*** ( $r$ )	89

given in Fig. 2C and D, were to a high degree found in reverse directions within 10 days after capture and in forward directions 11 days or longer after capture. The two groups of tropical migrants differed with respect to direction of movement within the first period (<10 days). Shortly after capture *Sylvia* and *Phylloscopus* warblers were to a large extent recovered towards northwest to east, while the two *Acrocephalus* warblers mainly moved in directions towards the wintering areas in southwest (Fig. 2E-H). Later after capture (>11 days), the majority of birds from both groups of tropical migrants were recovered in the forward direction. The difference in

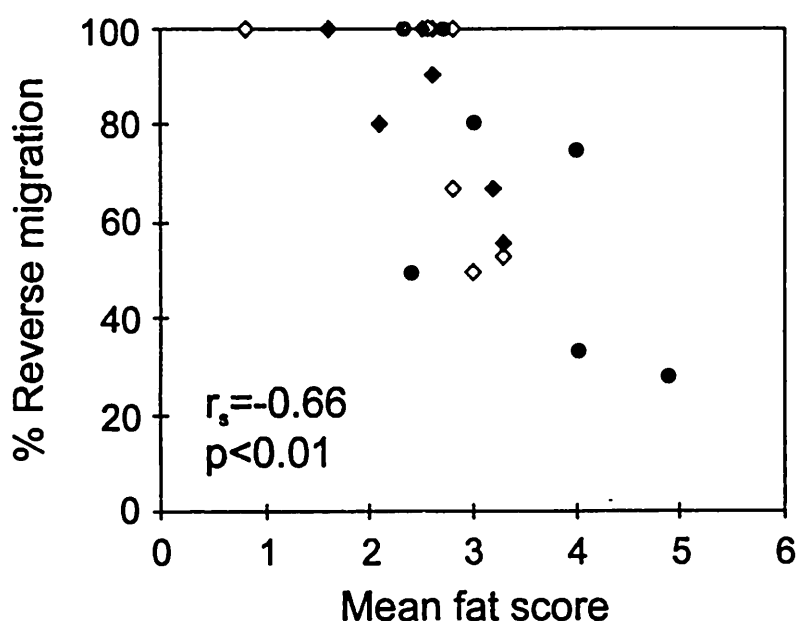


**Figure 2:** The circular diagrams demonstrate the direction of recoveries for A and B) three short-distance migrants (coal tit *shaded squares*, blue tit *filled squares* and great tit *open squares*), C and D) three temperate migrants (wren *open squares*, song thrush *filled squares* and goldcrest *shaded squares*), E and F) three tropical migrants (whitethroat *shaded squares*, garden warbler *open squares* and willow warbler *filled squares*), and G and H) two tropical migrants (sedge warbler *open squares* and reed warbler *filled squares*), respectively. Diagrams to the left show recoveries reported within 10 days after capture and diagrams to the right show recoveries found at least 11 days after capture. Mean angle of orientation is given within the circular diagram. For further information see Table 2.

direction of movement between the two groups of warblers are presumably due to differences in selection of stop-over sites and level of fuel reserves (sedge and reed warblers make stop-over in reedbeds and were caught with relatively large fat reserves, see Åkesson et al. 1996).

#### *Effect of body condition on direction of migration*

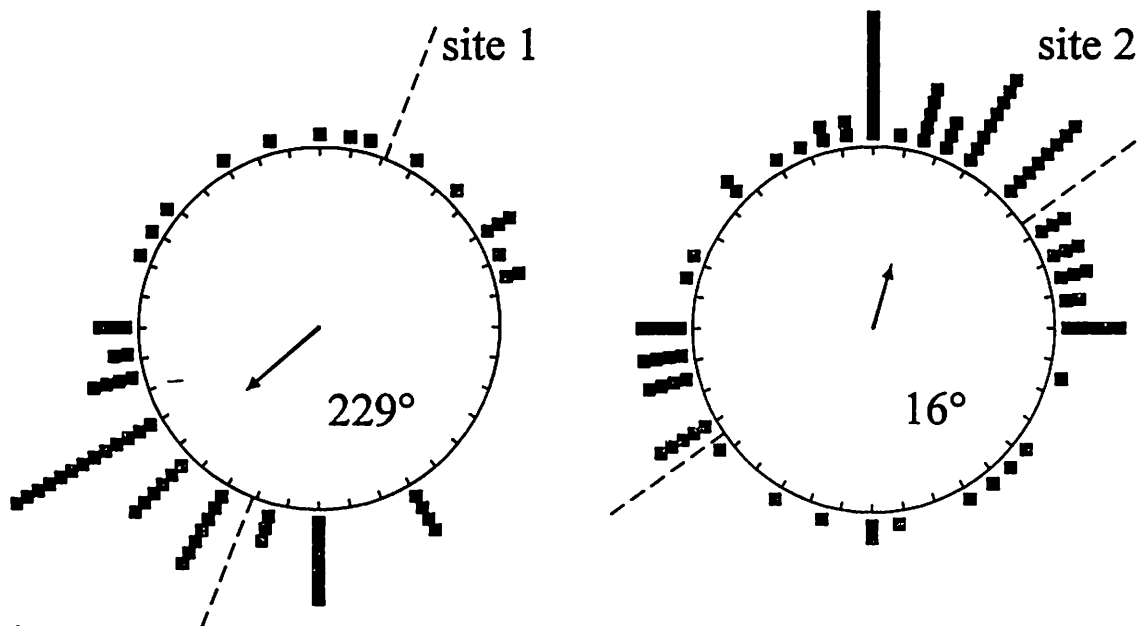
There was a significant negative correlation between the mean fat score at capture and the proportion of recoveries reported in reverse directions within 10 days after capture among different species (Spearman-rank-order correlation:  $r_s = -0.66$ ,  $n=20$ ,  $p<0.01$ ; Fig. 3). Negative correlations, which were quite not statistically significant were also found within each of the three classes of migrants (in all cases  $p<0.10$ ).



**Figure 3:** 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 squares* represents short-distance migrants, *filled squares* temperate migrants and *filled circles* tropical migrants. Values of mean fat class for each species are given in Åkesson et al. (1996). Modified after Åkesson et al. (1996)

#### *Ceilometer observations of free-flying migrants*

The ceilometer observations of free-flying nocturnal passerines showed that birds indeed do engage in reverse flights already 1-3 hours before the local sunrise (Fig. 4). Return flights occurred at both sites, but were most frequent at the most easterly located observation site (site 2). At this site the orientation of the coastline closely agreed with both the expected migratory direction towards southwest and the reverse direction (see also Åkesson 1993).



**Figure 4:** Distribution of mean track directions of nocturnal passerines observed at two coastal observation sites on the Falsterbo peninsula in autumn during the dark 1-3 hours before sunrise. Mean track direction is given within the circular diagram. The orientation of the coastline at the study site is indicated by a broken line. For further information see Table 2 and Åkesson (1993). Modified after Åkesson (1995).

## Discussion

The analysis of ringing recoveries show that migratory birds regularly engage in temporary reverse migration when confronted with the sea in southwest Sweden in autumn. The phenomenon were widespread among all different categories and species of migrants and indicates that the 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.

The majority of the reverse recoveries were reported from directions opposite to the expected migratory direction towards southwest. The most efficient reverse movements in coastal areas should be directed perpendicular to the coast, while movements in a 180° reversed migratory direction may be facilitated because of the birds' orientation mechanism (Alerstam 1978a, Alerstam 1990). The most efficient reverse direction at Falsterbo, perpendicular to the orientation of the two peninsular coastlines coincide with a 180° orientation reversal towards northeast. The ceilometer observations showed that reverse flights at Falsterbo are initiated by passerine nocturnal migrants already before sunrise. The mean track direction towards northeast was approximately parallel with the eastern coastline at the outermost peninsula and directed opposite to the migratory direction observed at this site (cf. Åkesson 1993 and Fig. 1).

The relationship between mean fat score and proportion of reverse migration within 10 days after capture showed that birds with smaller average fat deposits more often engage in reverse

movements compared to species migrating with larger fat deposits (Fig. 3). However, most birds captured had relatively modest fat reserves (mean fat scores 2.3-3.3). The reason for this pattern is presumably that lean birds are more likely to make landfall at the coast than birds with large fat reserves. Capture data on two diurnally migrating finches passing the Falsterbo area on migration in autumn 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 found in orientation cage experiments with nocturnally migrating robins (Sandberg 1994). The same relationship was found in two of the species included in this study (blue tit and reed warbler), in which individuals performing reverse movements were lighter than forward-moving birds within 10-days after capture. Statistics given in Åkesson et al. (1996).

On migration birds may fly along coastlines to reduce energy expenditure (Alerstam 1978b, Alerstam and Pettersson 1977), to facilitate orientation and to compensate for wind drift. Birds do fly along coasts on migration during the day (e.g. Alerstam 1978b, Alerstam and Ulfstrand 1971), as well as during the night (Åkesson 1993). This may lead to large concentrations of migrants in coastal areas and at peninsulas protruding in the direction of migration. Therefore it can be expected that birds will meet high competition and low availability of food combined with high predation risk in coastal areas (i.e. Alerstam 1978a, Lindström 1990, Lindström and Alerstam 1986, Moore and Young 1991). To alleviate these problems an inherited bimodal orientation mechanism favouring reoriented flights to more suitable resting grounds, enabling migrants to retreat from coasts or other areas bordering on ecological barriers, may be of selective advantage for birds not prepared to cross the barrier immediately.

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