Why do migrating robins, *Erithacus rubecula,* captured at two nearby stop-over sites orient differently?

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Abstract. The orientation of robins captured during autumn and spring migration at two different sites, Falsterbo and Ottenby, in southern Sweden was investigated by cage experiments during the twilight period after sunset. The robins were tested under clear skies with skylight from sunset visible, and under simulated total overcast. The robins from the two sites differed in orientation, especially during autumn migration. While robins from Ottenby generally oriented in their expected migratory direction, the birds from Falsterbo under clear skies oriented towards the sunset direction with a narrow scatter in individual mean headings. Under simulated total overcast the robins from Falsterbo preferred northerly directions in autumn. Short-distance recoveries, one or only a few days after ringing, show that robins in autumn regularly fly 20–80 km from Falsterbo on northerly courses, indicating that they have temporarily reoriented from their normal migratory direction when confronted with the Baltic Sea. In contrast, most robins arrive at Ottenby by extensive flights across the Baltic Sea, and rapidly continue their sea crossing in the normal migratory directions. Mean fat deposits in autumn robins were significantly larger at Ottenby than at Falsterbo. These results indicate that migrating birds may show markedly different orientational dispositions depending on body condition and on their situation with respect to preceding and impending migration over land and sea, respectively.

The environment contains numerous cues which may allow migrating birds to obtain directional information. Among these cues the geomagnetic field, the stars and the sunset sky are known to affect the orientation of robins, *Erithacus rubecula,* a common night migrant in Europe (Wiltschko & Wiltschko 1972, 1975, 1978; Katz 1985). It has been suggested that, for nocturnally migrating species, the twilight period between the time of sunset and migratory departure (about 20–45 min later) is of fundamental importance for integrating directional input to determine orientation (Vleugel 1953; Emlen 1980). Using robins captured as passage migrants at the bird observatories Falsterbo (55° 23′N, 12° 50′E) and Ottenby (56° 12′N, 16° 24′E) in southern Sweden to analyse the relative importance of different orientational cues during the sunset period (Sandberg et al. 1988), we noted a distinct tendency for birds from the two sites to orient differently under identical experimental conditions.

This was unexpected because the two trapping sites are situated less than 300 km apart, at localities of a similar character, i.e. southerly or southwesterly protruding points of land in the Baltic Sea, where migrants are captured in the localized wooded vegetation surrounding the Falsterbo and Ottenby lighthouses. Furthermore, according to extensive ringing data (Roos 1984; Liljefors et al. 1985; Pettersson et al. 1986), these two bird observatories are visited by migrating robins from widely overlapping breeding (mainly Fennoscandian) and wintering areas (mainly in southwestern Europe). However, robins from easterly breeding populations in Russia and with winter quarters in southern Europe regularly pass Ottenby, especially in late autumn, while such easterly robins are less frequent at Falsterbo.

The most obvious difference between the two sites is that migrating robins generally arrive at Ottenby after extensive flights over the Baltic Sea, while sea crossings at Falsterbo are much shorter. In fact, during the autumn most robins probably arrive at Falsterbo after overland migration in southern Sweden, and are not confronted with a sea crossing until reaching this site.

In this paper we compare the orientation of robins from Falsterbo and Ottenby by orientation cage experiments. The behaviour of birds allowed to see the sunset sky under clear weather is compared with the orientation of the same birds under simulated total overcast, during both the
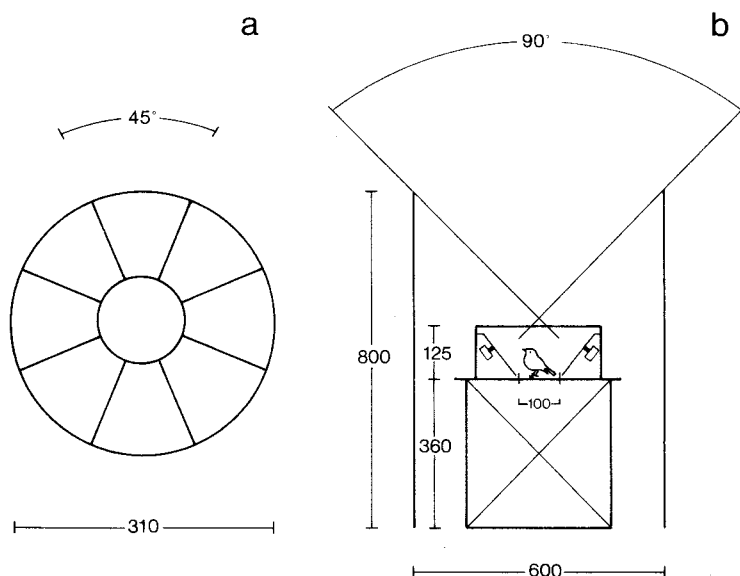
Figure 1. (a) Orientation cage seen from above with eight 45° sectors of sloping walls with automatic registrations. (b) Experimental set-up with a cylindrical plastic shield surrounding the orientation cage and restricting the birds' angle of view to about 90° of the sky overhead. Measurements are given in mm.

autumn and spring migration seasons. The orientation results are evaluated in relation to the recoveries of robins ringed at the two observatories, and possible explanations for changing orientational dispositions of birds in different migratory situations are suggested.

METHODS

Experiments were conducted during the autumn migration period (September and October) 1983–1986 and during spring migration (April and May) 1984–1986. Test birds were captured during the regular ringing schemes at Falsterbo and Ottenby bird observatories (Roos 1984; Pettersson et al. 1986; cf. maps in Figs 4 and 5). After capture, the robins were weighed to the nearest 0·1 g with a 50 g Pesola spring balance. Fat deposits were estimated visually on the bird's bellies and in their tracheal pits following the classification suggested by Busse & Kania (1970) and Pettersson & Hasselquist (1985). The robins from Falsterbo were transported by car approximately 55 km to the northeast to a test site at the ecological field station Stensoffa (55° 42′N, 13° 25′E) close to Lund, while the Ottenby birds were transported by car to a

nearby test site, only 3 km to the north. At the test sites, the robins were housed indoors in spacious individual cages, under the natural photoperiod (cages were placed in rooms with windows) and the local geomagnetic field. Each bird was held in captivity on average 2 weeks, during which time up to six orientation experiments under different conditions were performed. Two of these test conditions are considered in this paper (see below and Sandberg et al. 1988).

The experimental equipment, set-up and procedure were exactly the same at the two test sites. Orientation was recorded in modified 'Emlen-funnels' (Emlen & Emlen 1966) with the sloping walls subdivided into eight 45° sectors (Fig. 1a). A microswitch is placed below each sector and when a bird jumps on one of the sectors, the corresponding switch closes. Each microswitch is connected to a specific counter, and mean vectors of orientation were calculated on the basis of readings from the set of eight counters per cage. The orientation cages are made of non-magnetic materials and covered by a fine-meshed plastic net allowing the bird to see the sky above.

All tests were performed outdoors in open meadows, where the orientation cages were placed inside large plastic tubes in order to screen off
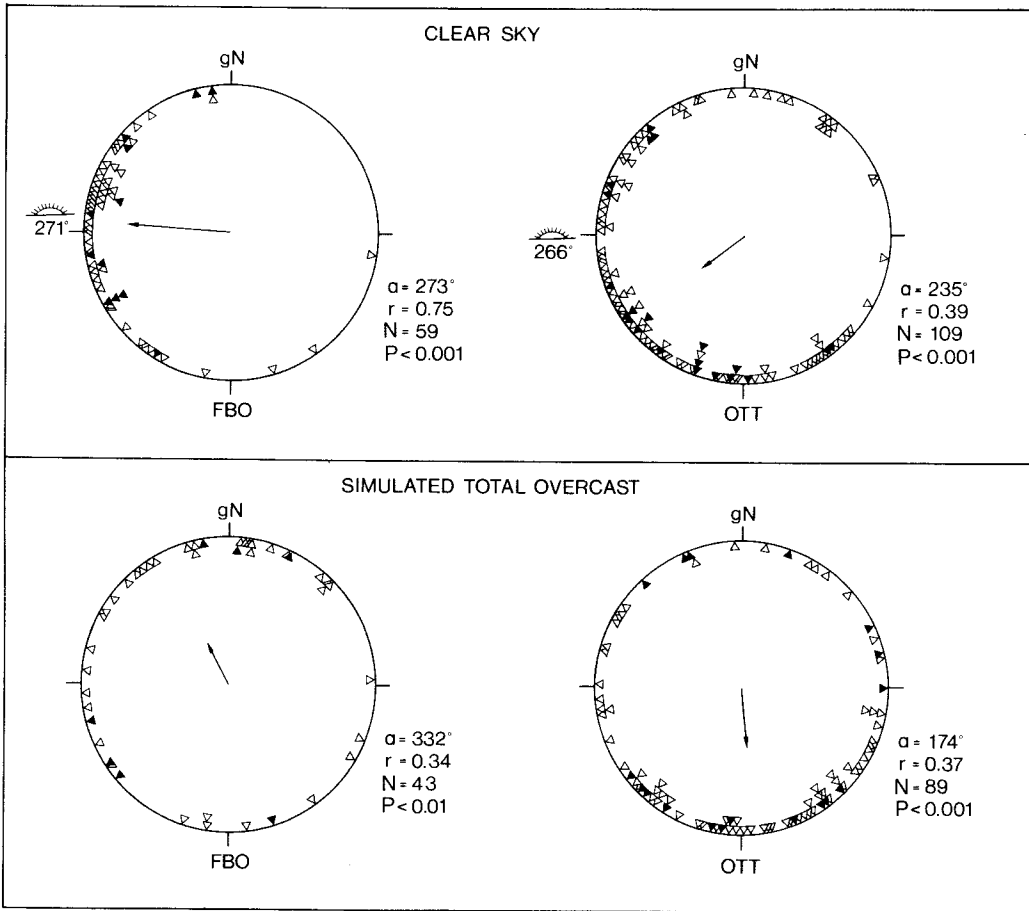
Figure 2. Autumn orientation of robins with (clear sky) and without (simulated total overcast) access to celestial cues at Falsterbo and Ottenby, respectively. The mean azimuth of the sun 40 min after sunset (i.e. in the middle of the test hour) is indicated for clear sky tests. Each symbol represents a mean heading of an individual. Open symbols denote yearlings and closed symbols older birds. Only one test per individual is included for each experimental condition. The mean vector (α) of the sample is represented by an arrow whose length (r) is drawn relative to the radius of the circle = 1. Significance levels are according to the Rayleigh test.

horizon landmarks from view. This arrangement allowed the test birds to see approximately 90° of the sky above (Fig. 1b). The robins were transferred to the orientation cages and carried to the test area about 30 min before sunset. The cages were covered by a piece of cloth while carried to the test grounds, in order to exclude any influence of visual cues during this brief transport. Experiments commenced 10 min after local sunset and lasted for 1 h. Two experimental conditions are analysed.

(1) Orientation under clear skies (less than 5/8th cloud cover), with the skylight from the setting sun clearly visible. However, the brightest part of the sunset sky low over the horizon was screened off from view (see Fig. 1b).

(2) Orientation under simulated total overcast, with a panel of 3 mm opaque diffusing Plexiglas placed on top of the screening tube, preventing the test birds from seeing the sky. Thus, it is improbable that the birds were able to perceive any visual celestial cues under this condition. Measurements showed that the degree of polarization of 100% polarized light is reduced to 7% (blue light, 488 nm)–13% (red light, 633 nm) after passing through such a panel.

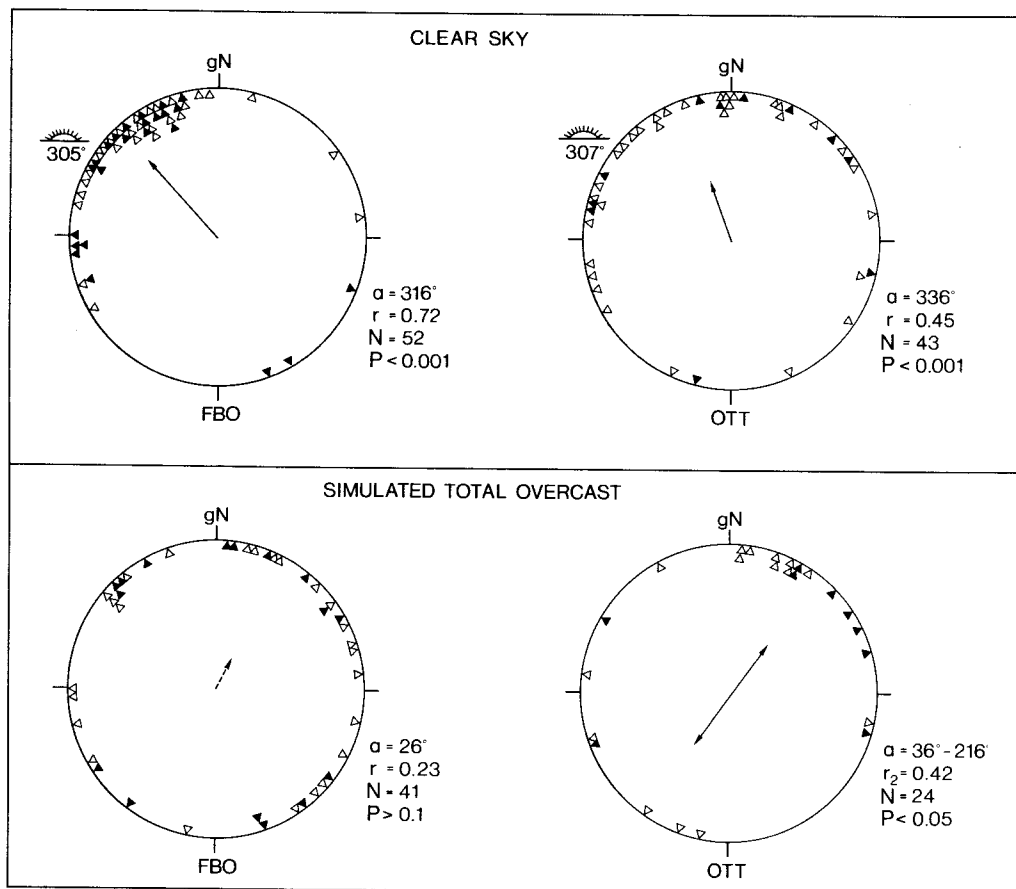Each individual was tested only once per experi-

Figure 3. Spring orientation of robins with and without access to celestial cues at Falsterbo and Ottenby, respectively. See Fig. 2 for details.

mental condition. Vector calculation based on counter registrations yielded a mean heading for each individual and test. Bird-hours with less than 40 counter registrations or a highly scattered and unreliable migratory orientation ($P > 0.05$ according to the Rayleigh test, cf. Batschelet 1981) were excluded from analysis. Because the within-test data points are not independent, the Rayleigh test does not provide correct probability estimates for these tests. Hence, the Rayleigh test was simply used as a yardstick for exclusion of individual bird-hours with the least reliable mean vectors of orientation. The mean activity was normally around 1200 registrations/h (range: 40–5500) under clear skies, and slightly lower, about 1000 registrations/h (range: 40–4000), under simulated total overcast.

On the basis of individual headings, second-order mean vectors and axes of orientation were calculated for each experimental condition according to Batschelet (1981). A mean axis of orientation was used when the mean vector length calculated from double angles (r_2) is greater than the mean unimodal vector (r). The Rayleigh test was applied to determine significant directional preferences. The scatter around the mean angle, as given by mean vector lengths, was compared between different categories by the 'test for the homogeneity of concentration parameters' (Mardia 1972, pp. 165–167). This is a test that allows comparisons of scatter between samples, independently of their mean directions. Differences in mean angles of orientation were investigated by Mardia's (1972, pp. 163–165) one-way classification test. The latter

test can be used for comparing mean angles between two samples with even moderate mean vector lengths, provided the vector lengths are not significantly different.

RESULTS

Orientation under Clear Skies

Autumn

For the orientation experiments under clear skies the mean azimuth towards sunset (the direction towards the position of the sun 40 min after sunset, i.e. in the middle of the test period) was calculated for each experimental group as indicated in Figs 2 and 3. The mean orientation of Falsterbo robins was virtually the same as the sunset direction (Fig. 2). The mean vector of angular differences between a bird's heading and the direction towards sunset at the associated test night was $\alpha = +2°$ (95% confidence interval $= \pm 12°$, $r = 0.75$, $N = 59$). It should be kept in mind that the birds were never allowed to see the disc of the setting sun during tests, and that the sunset sky below about 45° elevation was screened off from view. However, the brightest sectors of the sky overhead, or the polarization pattern (cf. Able 1982), probably indicated to the test birds the sunset direction.

The robins at Ottenby, on the other hand, showed a seasonally appropriate southwesterly mean angle of orientation, which was significantly different from the sunset direction ($\alpha = -31°$, 95% confidence interval $= \pm 20°$, Fig. 2). In addition to the difference in mean orientation between Falsterbo and Ottenby robins, they also differed clearly with respect to the scatter around the mean angles. The orientation of the Ottenby robins was much more scattered than that of the Falsterbo birds, and the difference in mean vector lengths is highly significant ($P < 0.001$).

Spring

The Falsterbo robins showed a northwesterly orientation, which again was not significantly separated from the sunset azimuth (Fig. 3). In contrast, the Ottenby birds oriented in a more northerly direction, significantly to the right of the sunset direction ($\alpha = +29°$, 95% confidence interval $= \pm 26°$, Fig. 3). As in autumn, the robins at Ottenby showed a markedly higher level of orientational scatter than the Falsterbo birds ($P < 0.01$).

Orientation under Overcast

Autumn

During these experiments the birds in the orientation cages were prevented from seeing the sky by panels of opaque diffusing Plexiglas, simulating total overcast. There was a conspicuous difference in orientation between Falsterbo and Ottenby birds (Fig. 2), the former showing a preference for northerly directions, while the latter generally oriented towards the south. The difference between the two mean directions is highly significant ($P < 0.001$). The scatter around the average orientation angles are similar at the two sites under overcast, but significantly less than that shown by Falsterbo birds tested under clear autumn skies ($P < 0.001$).
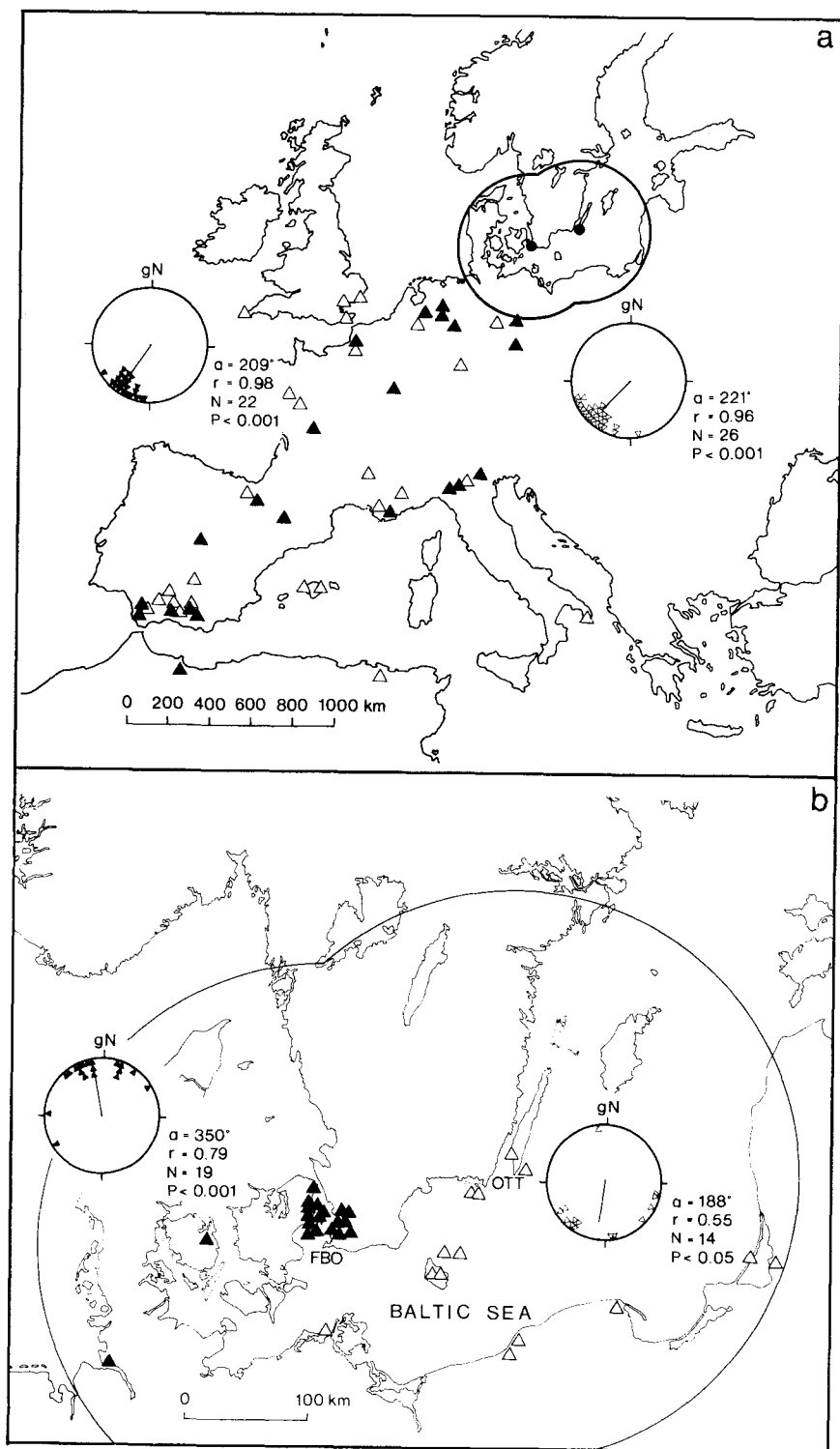
Spring

Without access to celestial cues, many of the robins at Falsterbo as well as Ottenby oriented in a northeasterly direction (Fig. 3). However, the directional choices of Falsterbo birds were too dispersed for the mean orientation to be significantly different from a random distribution ($P = 0.12$, Rayleigh test). Although a majority of the Ottenby robins chose directions in the northeast quadrant, a few individuals preferred southwesterly courses. This resulted in an axis of orientation (see Fig. 3) that provided a slightly better fit to the data than the unimodal mean vector. Still, the latter ($\alpha = 21°$, $r = 0.39$, $N = 24$) was also statistically significant ($P < 0.05$). As in autumn there was no significant difference between mean vector lengths under overcast at the two sites ($P > 0.05$). Both of these vector lengths were, however, distinctly shorter than that shown by the Falsterbo robins under clear spring skies ($P < 0.001$).

Seasonal Changes in Orientation

To investigate whether there were any important changes in orientation within seasons, experiments carried out in the early part of autumn (before 10 October) were compared with those later in autumn, and early spring tests (before 30 April) with experiments later in spring.

Clear skies

The mean azimuth towards sunset was 278°/276° (Falsterbo/Ottenby) for early autumn tests, and 260°/257° for the late autumn tests. The corres-

ponding sunset azimuths during spring were 298°/301° early in the season and 311°/311° in the later part of the season.

The Falsterbo robins showed only very small differences, not statistically significant, in mean angle of orientation between early and late autumn (275°/270°) and between early and late spring (310°/321°). In contrast, the Ottenby birds showed an appreciable and highly significant ($P < 0.001$) intra-seasonal shift in autumn orientation ($\alpha = 267°$, $r = 0.51$, $N = 54$, $P < 0.001$; $\alpha = 198°$, $r = 0.44$, $N = 55$, $P < 0.001$). It is interesting that the mean orientation of early birds was not significantly different from the sunset azimuth (cf. the autumn orientation of Falsterbo robins), whereas the mean directional choice of late robins differed clearly from the sunset position ($P < 0.01$). Hence, this seasonal change in orientation was a contributory cause of the relatively large scatter in overall autumn orientation shown by the Ottenby robins (Fig. 2). In spring, the difference between early and late tests at Ottenby was insignificant (334°/338°).

Overcast

The only indication of possible seasonal changes of any important magnitude is given by the autumn data from Ottenby and the spring data for the Falsterbo robins. In the former case, the early autumn orientation is on average towards the south-southwest with a relatively large scatter between individual headings ($\alpha = 199°$, $r = 0.26$, $N = 43$, $P < 0.05$), while in late autumn the Ottenby birds seem to be less scattered in a south-southeast direction ($\alpha = 162°$, $r = 0.50$, $N = 46$, $P < 0.001$). There is, however, no statistically significant difference either in mean angles of orientation or in scatter ($P > 0.10$ and $P > 0.05$, respectively). In

Figure 4. Ringing recoveries during autumn migration (September and October) of robins ringed previously during the same autumn at Falsterbo (closed symbols) and Ottenby (open symbols). Short-distance recoveries within approximately 300 km radius from the two ringing sites, usually reported within a few days of ringing, are illustrated separately on map b. Recoveries at longer distances (map a) are normally reported 10–40 days after ringing. Compass courses from Falsterbo and Ottenby to the recovery positions were calculated, and mean vectors of these courses are presented, separately for long- and short-distance recoveries in the circular diagrams. The Falsterbo ringing data are from Roos (1984) with complementary unpublished data 1981–1983 communicated by G. Roos, and the corresponding Ottenby data were assembled by J. Pettersson.
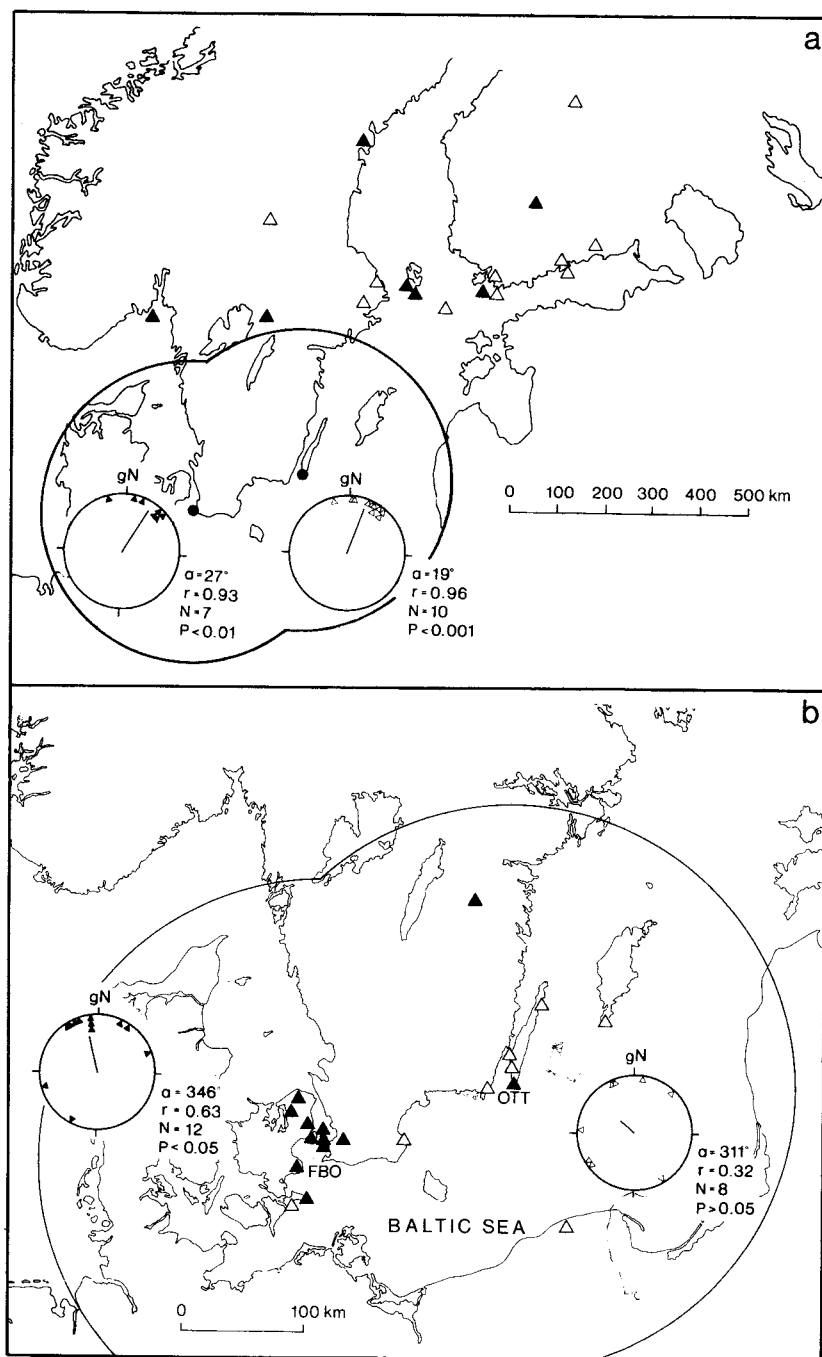
early spring the mean orientation of Falsterbo robins was towards the north-northwest ($\alpha = 332°$, $r = 0.39$, $N = 17$), while late spring tests showed a mean direction towards the east-northeast ($\alpha = 71°$, $r = 0.32$, $N = 24$). However, both of these mean vectors fall short of significance according to the Rayleigh test ($P > 0.05$).

Orientation of Adults and Juveniles

In Figs 2 and 3 birds in their first year, i.e. on their first autumn or spring migration, are distinguished from older individuals (cf. Karlsson et al. 1986). First years and adults generally oriented in a similar way and there are no significant differences, except for the autumn experiments under clear skies at Ottenby. During these latter tests, juveniles show a larger scatter in orientation ($\alpha = 240°$, $r = 0.33$, $N = 87$, $P < 0.001$) than the adults ($\alpha = 225°$, $r = 0.66$, $N = 22$, $P < 0.001$). The difference in mean vector length between the two categories is statistically significant ($P < 0.05$). Unfortunately, the number of adult Falsterbo robins tested under overcast in autumn is too small to indicate whether there is a difference in orientation between age groups under non-visual conditions.

DISCUSSION

Evidence from Ringing Recoveries

The orientation experiments with robins from Falsterbo and Ottenby should be interpreted in the light of ringing results from these two sites. Figures 4 and 5 show the recoveries of migrating robins ringed during autumn and spring, respectively, at Falsterbo and Ottenby and recovered during the same season.

The distribution of long-distance recoveries from the two ringing sites are very similar, with a mean direction towards south-southwest/southwest in autumn and northeast/north-northeast in spring. Figure 4 gives the impression that Ottenby robins may migrate along slightly more westerly courses than the birds passing Falsterbo. However, this does not hold true if recoveries after October, in late autumn and winter, are included in the analysis. In late autumn, robins from easterly breeding populations with winter quarters in southern rather than southwestern Europe pass Ottenby, especially during periods with easterly

Figure 5. Recoveries during spring migration (April and May) of robins ringed previously the same spring at Falsterbo (closed symbols) and Ottenby (open symbols). Short- and long-distance recoveries are plotted on different maps. See Fig. 4 for details.

Table I. Comparison of capture mass and fat load of robins at Falsterbo and Ottenby during autumn and spring, respectively

Site	Fat score							Mean fat load		Mean mass (g)	
	0	1	2	3	4	5	6	N	$\bar{X} \pm$ SD	N	$\bar{X} \pm$ SD
Autumn											
Falsterbo	2	21	12	8	9	5	0	57	2·3 ± 1·4	66	16·0 ± 1·3
Ottenby	0	6	33	35	13	15	0	102	3·0 ± 1·1	102	15·9 ± 1·2
Spring											
Falsterbo	1	0	6	6	6	6	0	25	3·4 ± 1·3	62	15·7 ± 1·2
Ottenby	0	1	4	18	33	18	0	74	3·8 ± 0·9	74	16·2 ± 1·3

The data relate to robins used in the orientation experiments presented in this paper. Fat scores are according to a visual scale (see Methods). The distribution of fat scores was significantly different between the experimental robins from Falsterbo and Ottenby during the autumn ($P < 0.001$, Kolmogorov–Smirnov two-sample test) but not during the spring ($P > 0.05$).

winds, to a higher extent than Falsterbo (Högstedt & Persson 1971; Pettersson & Lindholm 1983). Consequently the overall mean direction of all autumn and winter recoveries of robins ringed at Ottenby lies slightly more to the south than the corresponding direction of Falsterbo robins (cf. Roos 1984; Pettersson et al. 1986). Furthermore, the inclination to report discoveries of ringed birds differs widely between eastern and western Europe which introduces a westerly bias in the distribution of ringing recoveries.

Mean directions as well as the scatter in recovery directions differ between short- and long-distance recoveries. Most remarkable is the fact that a majority of short-distance reports of robins ringed at Falsterbo in autumn are from areas in northerly directions, in southwestern Scania and eastern Zealand. These regions are densely populated, especially at the cities of Copenhagen and Malmö, a fact that may bias the distribution of recoveries (increased probability of reports). In addition, some of the recoveries (but far from all, cf. Roos 1984) have been reported by local bird ringers operating just outside Copenhagen and Malmö. In spite of the possible sources of bias mentioned, the short-distance recoveries still provide clear evidence that northward autumn flights from Falsterbo must occur regularly. In fact, we cannot exclude the possibility that such reoriented flights are carried out by a majority of the robins ringed at this site in autumn.

A circumstance that seems to stress the particular relevance of recoveries in eastern Zealand and southwestern Scania for robins interrupting their autumn migration at Falsterbo is the total absence of recoveries from this region of robins ringed at Ottenby, despite the fact that this region is within the normal range of autumn migratory directions from Ottenby.

The short-distance recoveries of Ottenby robins in autumn indicate that most birds proceed directly from this site by crossing the Baltic Sea on widely different courses in the southeast and southwest quadrants.

Short-distance recoveries in spring show that the robins generally depart with northerly headings both from Falsterbo and Ottenby, although there are cases of retreat migration in directions between south-southeast and west. Reports of Falsterbo robins recovered at short distances in spring show a concentration in eastern Zealand, along a mean direction towards north-northwest whereas the Ottenby robins are widely dispersed (Fig. 5).

Causes of Differences in Orientation

There is a striking similarity between the directions of short-distance recoveries in autumn and the orientation results under simulated total overcast: robins from Falsterbo show a northerly orientation while birds at Ottenby choose directions towards the south. We presume that the orientation experiments under overcast force the test birds to use non-visual cues for their direction finding (Sandberg et al. 1988). Thus, the chosen

directions under overcast are likely to reflect the robins' intended orientation at the capture sites.

When the robins are tested in orientation cages under clear sunset skies, the results may be biased by a tendency for the birds to move towards sunset, perhaps an escape response directed towards the brightest part of the sky. This tendency may be stronger the less motivated the birds are for an immediate continuation of their migratory journey. Hence, for the Falsterbo robins in autumn, orientation directed at sunset seems to overrule completely the normal migratory orientation, while the Ottenby birds are only influenced to a limited degree by this bias. Such a difference between the two categories of robins offers a possible explanation for the low degree of scatter in orientation shown by Falsterbo robins under clear skies as compared to Ottenby birds. Further, it may account for the failure of Falsterbo robins, unlike the birds from Ottenby, to respond to changes in the magnetic field when tested under clear autumn skies (Sandberg et al. 1988).

Why then do the autumn robins at Falsterbo lack the disposition to continue migration (no intra-seasonal differences) in the normal southerly or southwesterly direction, like the birds do at Ottenby, and instead are inclined to reorient towards the north? Persson (1972) suggested that the short-distance ringing recoveries of Falsterbo robins in northerly directions are due to the fact that the migrants are attracted by the nocturnal sky glow from the city lights of Copenhagen and Malmö. However, this cannot explain the preference for northerly directions by the Falsterbo robins deprived of visual celestial cues in the orientation cages.

A more plausible explanation is that robins reaching Falsterbo in autumn to a large extent have migrated across land in southern Sweden by short hops on low fat reserves. When confronted with the Baltic Sea, they reorient in northerly directions to find suitable resting grounds for refuelling before crossing the sea barrier (Alerstam 1978). After having stored enough fat reserves enabling them to depart southwards from eastern Denmark and western Scania, they probably pass over Falsterbo and the surrounding sea areas.

In contrast to the situation at Falsterbo, autumn robins generally arrive at Ottenby after extensive flights across the Baltic Sea. Except for a minority landing with depleted fat reserves, these birds seem to be prepared to continue their sea crossing on the next night affording favourable flight conditions (Pettersson & Hasselquist 1985). Some of the robins captured during early autumn at Ottenby may originate from nearby breeding areas, which can help to explain why these birds oriented close to the sunset azimuth. Alternatively, in early autumn the birds may still have plenty of time to complete their migratory journey, and therefore are more prone to show non-migratory orientation responses.

The above interpretation is supported by the fact that, among autumn robins used in our orientation experiments, the birds captured at Falsterbo had significantly lower fat reserves than the Ottenby birds ($P < 0.001$, Kolmogorov–Smirnov two-sample test, see Table I) according to a visual scale of fat classification (Busse & Kania 1970; Pettersson & Hasselquist 1985). However, in spite of the difference in fat loads, the mean body masses of Falsterbo and Ottenby robins were practically the same. This is probably due to significant differences in body composition, perhaps in the water balance (cf. Torre-Bueno 1978), between birds that have recently landed after extensive migratory flights (Ottenby), and birds about to build up larger fat reserves before departing on migratory flights over longer distances (Falsterbo; Karlsson, unpublished data). The adaptive significance of reoriented migration by individuals with small fat reserves has been demonstrated for finches by Lindström & Alerstam (1986).

This conclusion is also partly consistent with Baker's (1978) concept of exploratory migration. In his model, Baker interprets reversed migration as exploration back along the migration track for suitable stop-over sites, which the birds may already have noticed when passing over on their preceding migratory flights in the standard direction. However, if connected with recently overflown potential refuelling areas, we would expect to find a majority of short-distance ringing recoveries in the northeast quadrant and not, as is the case, in the northwest quadrant (Fig. 5).

During spring migration, differences in orientation between robins from Falsterbo and Ottenby were less pronounced than in autumn: Falsterbo robins were attracted towards the sunset direction under clear spring skies, to a higher degree than the Ottenby birds, and under overcast the Falsterbo birds failed to show a significant orientation. These differences in spring orientation may be related to the possibility that more of the Falsterbo robins are of a local southwest Scandinavian breeding origin

in comparison with those captured at Ottenby. Furthermore, spring migration is on average earlier at Falsterbo than at Ottenby, and birds arriving early may show a greater readiness to interrupt migration than later during the spring.

The above explanations for the unexpected differences in orientation between migrating robins captured at Falsterbo and Ottenby are hypothetical, and important questions remain to be answered. Could the transportation of the robins to test sites at different distances from the two capture sites have affected the orientation results? If Falsterbo robins in autumn reorient in northerly directions (i.e. roughly opposite to the seasonally appropriate directions) to find suitable areas for fat deposition before departing southwards again, we would expect an increased number of individuals to change their orientation towards the south as they gained in fat load and body mass when kept and fed at our test site. However, no such tendency was found among the Falsterbo robins, although gains in fat reserves and body mass before the orientation tests were sometimes substantial. Why did the Falsterbo robins with increased fat loads fail to adopt a seasonally appropriate orientation?

The finding that migrating birds of the same species from two nearby stop-over sites show fundamentally different orientation behaviour has important implications for the interpretation of orientation experiments. Due consideration must be given to the fact that individuals may show different orientational dispositions depending on preceding and impending topographical circumstances of their migratory journey, and on body condition and time schedule.

ACKNOWLEDGMENTS

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