## Orientation of robins, Erithacus rubecula, in a vertical magnetic field

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It has been known for more than two decades that robins have a magnetic compass (Merkel & Wiltschko 1965). We have recently demonstrated that robins captured as passage migrants at Ottenby Bird Observatory, by the Baltic Sea in south-east Sweden (56°12'N, 16°24'E), use the geomagnetic field as an important orientation cue during the twilight period after sunset (Sandberg et al. 1988a, b). The birds clearly changed their preferred direction when the magnetic field was deflected in orientation cage experiments. However, the robins often adopted a reverse or axial orientation in relation to the magnetic field, suggesting that additional cues (e.g. celestial cues like the sunset direction, skylight polarization pattern or light distribution on the sky) are involved in the orientation process.

To investigate further the roles of the magnetic field and other, mainly celestial, cues for the twilight orientation of robins, we conducted a series of experiments where the birds were tested in a vertical magnetic field and thus were deprived of magnetic directional information.

We carried out the orientation experiments at Ottenby during the autumn (15 September-8 November) and spring (21 April-17 May) migration seasons in 1987 and 1988. The birds were tested outdoors in circular orientation cages surrounded by screens restricting the birds' view of the sky overhead to approximately 90°. The experimental set-up and procedure were as described in Sandberg et al. (1988a, b). Pairs of magnetic coils (cf. Sandberg et al. 1988b) generated a magnetic field that cancelled the horizontal component of the local geomagnetic field. The resulting magnetic field in the orientation cages deviated by maximally 1-2° from the vertical according to inclinometer and magnetometer measurements. The intensity of the resulting vertical field, approximately 46 µT, was slightly lower than the total intensity, approximately 49 µT, of the local geomagnetic field. Registration of the birds' orientation started

10 min after local sunset and lasted for 1 h. Tests were performed under clear skies (less than 5/8 cloud cover) and under simulated overcast skies. In the latter case, a panel of opaque diffusing Plexiglas (strongly depolarizing) was placed on top of the screening tube (Sandberg et al. 1988a).

Each individual was tested only once under a given experimental condition. A mean heading was determined by vector calculation for each test. excluding tests with low activity (fewer than 40 registrations) or a highly scattered and unreliable orientation, where the criterion for exclusion was arbitrarily set to  $Nr^2 < 3.0$  (N = number of counts, r=vector length). Under uniformity the distribution of  $Nr^2$  is independent of the number of counts (N), and values lower than 3.0 are unlikely to occur if the distribution of migratory activity deviates from uniformity (cf. Batschelet 1981). Because the within-test data points are not independent, it was not used as a measure of statistical significance, but simply as a yardstick for exclusion of bird-hours that yielded unreliable estimates of orientation. We excluded 35 tests according to these criteria (27 inactive and eight disoriented). On the basis of individual headings, second-order mean vectors (unimodal mean vector length = r) and axes of orientation (axial vector length calculated from double angles  $= r_2$ ) were determined for each experimental condition according to Batschelet (1981). The Rayleigh test was used to decide whether the orientation results differed significantly from a random circular distribution.

We compare here the results of orientation experiments in a vertical magnetic field (Fig. 1) with the total sample of corresponding control tests with robins in the normal geomagnetic field, available from Ottenby 1984–1988 inclusive. (The major part of the control data have been presented in Sandberg et al. 1988a: Figs 2 and 3.)

Under a clear sky during autumn migration (controls:  $\alpha = 220^{\circ}$ , r = 0.45, N = 129, P < 0.001,  $r_2 = 0.13$ ) the mean direction of controls was

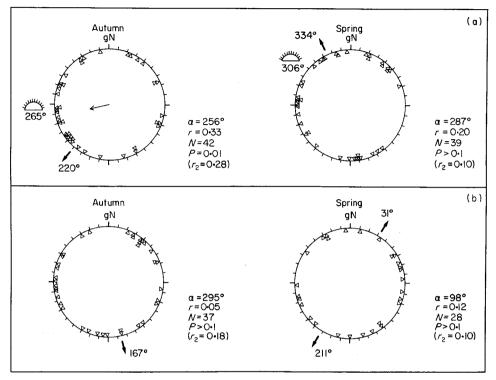


Figure 1. Orientation of robins in a vertical magnetic field under (a) clear skies and (b) simulated overcast skies. Experiments were carried out during the twilight period after sunset. The mean azimuth of the sun 40 min after sunset (in the middle of the test hour) is indicated for clear sky tests. Each symbol represents the mean heading relative to geographical north of an individual. The significant mean vector for the autumn sample in (a) is indicated by an arrow.  $\alpha = \text{mean angle}, r = \text{mean unimodal mean vector length}, N = \text{number of tests/individuals}, P = \text{probability according to the Rayleigh test}, r_2 = \text{axial vector length}$ . Bold arrows outside the circular diagrams indicate the mean orientation of controls, tested in a normal geomagnetic field (cf. text).

significantly different from the average sunset azimuth (P < 0.01), mean sunset position =  $267^{\circ}$ , 99% confidence interval =  $\pm 22^{\circ}$ ). The robins showed a significant directional preference in a vertical magnetic field (Fig. 1), but the orientation was more scattered than that of controls and the mean angle was in a more westerly direction, not significantly different from the sunset position (P > 0.05, 95%) confidence interval =  $\pm 39^{\circ}$ ). The overall orientation performance of experimental birds was significantly different from the corresponding results obtained in control tests  $(P < 0.05, Watson's U^2$ -test; Batschelet 1981).

Under a clear sky in spring (controls:  $\alpha = 334^{\circ}$ , r = 0.35, N = 54, P < 0.01,  $r_2 = 0.13$ ) the orientation in a vertical magnetic field was again highly scattered with a mean angle close to the sunset position. The orientation was not significantly different from random. This is in contrast to the significant north-

northwest orientation under control conditions. There was, however, no statistically significant difference between experimental and control birds  $(P>0.05, \text{Watson's } U^2\text{-test})$ .

In contrast to the significant orientation close to expected migratory directions under overcast control conditions, the robins showed random circular distributions when tested in a vertical magnetic field in simulated total overcast (controls, autumn:  $\alpha=167^{\circ}$ , r=0.39, N=105, P<0.001,  $r_2=0.18$ ; controls, spring: axis = 31°/211°,  $r_2=0.33$ , N=31, P<0.05, r=0.27; Fig. 1). The orientation of the experimental category was significantly different from that of controls in autumn tests (P<0.01, Watson's  $U^2$ -test), but not in spring experiments (P>0.05, Watson's  $U^2$ -test).

The results presented in Fig. 1 confirm the primary importance of the geomagnetic field for the orientation of migrating robins at Ottenby. The

magnetic field probably constitutes the only cue available under total overcast (and without a view of topographical landmarks), and the robins lose their orientation completely when deprived of meaningful magnetic information in this situation (cf. also Wiltschko 1968).

In contrast, under clear skies the loss of magnetic information may affect the birds' orientation in at least three different ways. (1) The birds may maintain their orientation accurately with reference to celestial cues. This has been reported for robins, garden warblers, Sylvia borin, and pied flycatchers, Ficedula hypoleuca, tested in a vertical magnetic field under starry night skies (Wiltschko & Wiltschko 1975a, b; Bingman 1984). Furthermore, Bingman & Wiltschko (1988) showed that dunnocks. Prunella modularis, maintained a well defined orientation, albeit axial, in a vertical magnetic field at the time of sunset. In many of the above cases the birds seemed to have calibrated their celestial compass relative to the geomagnetic field experienced during preceding tests with magnetic directional information available. All robins tested in a vertical magnetic field at Ottenby had prior experience of normal geomagnetic conditions only. Our results indicate that they failed to select a seasonally appropriate orientation on the basis of available celestial cues. It should be noted, however, that the lower portions of the sunset sky were screened off from view in our experiments. The spring data do not allow any firm conclusion since there were no statistically significant differences between experimental and control birds (cf. above).

(2) Without meaningful magnetic information the robins may be attracted towards the brightest part of the sky. Such orientation towards the sunset direction has been demonstrated for robins captured at Falsterbo Bird Observatory in south Sweden. Unlike Ottenby birds, these robins did not respond to shifted magnetic fields (Sandberg et al. 1988a, b). Even if there is a weak attraction towards the sunset sector for Ottenby robins exposed to a vertical magnetic field under clear sunset skies (statistically significant for autumn tests only), the angular scatter is excessive. This should be compared with the concentrated orientation towards sunset by Falsterbo robins, with mean vector lengths in the range 0.53-0.75 (Sandberg et al. 1988a, b). The difference in concentration may be explained by the fact that among the Ottenby robins is a proportion orienting towards sunset like Falsterbo robins, while a majority use the magnetic orientation and show a random scatter in a vertical magnetic field. Alternatively, all individuals at Ottenby may be potentially but only weakly affected by the sunset direction.

(3) The magnetic compass may be of crucial importance, and without it the birds fail to orient properly also under clear sunset skies. Such an effect has been reported by Bingman (1983) for hand-raised savannah sparrows, *Passerculus sandwichensis*, showing disorientation in a vertical magnetic field in outdoor orientation tests at the time of sunset. Our results indicate a similar critical importance of the magnetic field for accurate sunset orientation of robins at Ottenby.

The roles of magnetic and celestial cues for the birds' orientation seem to differ depending on species, migratory dispositions and environmental conditions. This study serves to stress the primacy of the magnetic compass for the robins' sunset orientation in association with migratory flights across the Baltic Sea.

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