

Earth's Magnetism and the Nocturnal Orientation of Migratory European Robins

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The orientation system of nocturnally migrating birds is characterized by the many stimuli that can be used for orientation. Environmental stimuli known to serve as orientation cues include the stars, earth's magnetic field, and setting sun (Able 1980). Nonetheless, the relationship of these cues with each other, and whether experienced migrants use one as a primary directional reference from which orientation responses to the others may be calibrated or influenced, is not completely understood [see Wiltschko (1982), Bingman (1983a, b), and Able and Bingman (1987) for a discussion of the behavior of young, inexperienced migrants].

Much of what is known about this problem stems from the experiments of Wiltschko and Wiltschko (1975a, b), which demonstrated a prominent role of the earth's magnetic field in the orientation system of a number of nocturnal migrant species. European Robins (*Erithacus rubecula*) and Garden Warblers (*Sylvia borin*) repeatedly tested under stars in a shifted magnetic field and subsequently tested in a directionless magnetic field maintained migratory orientation with respect to the previously experienced shifted magnetic field. The authors suggested that the birds transferred directional information from the shifted magnetic field to the stars and used their recalibrated star compass when the magnetic field was made unusable. Support for this interpretation came from experiments demonstrating the ability of European Robins to calibrate an orientation response to stationary, artificial light sources from an ambient magnetic field (Wiltschko and Wiltschko 1976).

These results have served as an important statement on the problem of cue interaction in nocturnal migrants, despite the emergence of possible contradictory results (Wallraff and Gelderloos 1978, Rabøl 1979, Katz 1985) and being subjected to criticism (Able 1980). Criticism has focused on the small number of birds used, the lack of compelling statistical results, and the experimental cage arrangement, which provided the birds with limited visual access to the "competing" orientation stimuli: the stars. Considering the importance of the Wiltschkos' study for current conceptualizations of the orientation system of nocturnal migrants, I attempted to replicate their experiments to address these criticisms.

The test animals used in this study were 15 European Robins captured near Pisa, Italy (44°39'N, 10°18'E)

between 23 February and 29 March 1983. In this area wintering robins are composed of both residents and migrants. Therefore, only birds that displayed demonstrable subcutaneous fat deposits, indicating a higher probability of being migratory, were used. During the course of the experiments the robins were maintained in a stone house where they could not view the sky.

For the orientation tests, which took place at the location of capture, the 15 birds were placed arbitrarily into control ($n = 8$) and experimental ($n = 7$) groups. Orientation tests were performed from 2 March through 20 April on clear, moonless nights only. All tests took place after all visible horizon glow from the setting sun had disappeared. Each test lasted about 90 min. In the first stage of the experiment, tests took place outdoors in two sets of Helmholtz coils, which when turned on produced an ambient magnetic field around the test cages with a horizontal component shifted 120° eastward (clockwise) relative to the local earth's magnetic field. The inclination and intensity of the shifted field were kept at local field values (59°, 0.43 Gauss). Both controls and experimentals were tested in the Helmholtz coils, but only the coils of the experimentals were activated. The activated pair of coils was alternated between test nights. Individual controls and experimentals were tested in the local and shifted magnetic field, respectively, 5-7 times (control RG was tested only once and then escaped) before proceeding to the second stage of the experiment (see below).

After the first set of birds (4 from each group) completed the first stage of the experiment (13 March), one Helmholtz coil pair was altered to produce a vertical ambient magnetic field (the coils were set to null the horizontal component of the local earth's field), i.e. a magnetic field without direction. A perfectly vertical magnetic field could not be made, but for the tests the inclination never went below 89°. Upon completing the first stage of the orientation tests, control and experimental birds advanced to the second stage of the experiment, which involved being tested simultaneously for their orientation in the vertical magnetic field. In the vertical field, individual controls yielded 1, 2, 3, 3, 5, 5, and 6 respective nights with activity, while individual experimentals yielded 1, 2, 2, 3, 3, 3, and 3 respective nights with activity. These tests were performed to examine the effect of the birds' previous magnetic field experience on their subsequent orientation in the absence of a directional magnetic field. At this point new control birds beginning the first stage of the experiment were tested on a wooden platform rather than in the coils. There

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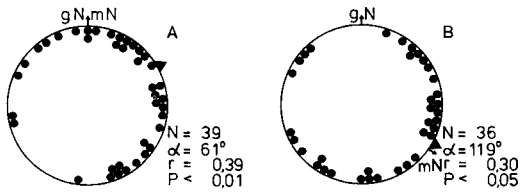


Fig. 1. Migratory orientation of European Robins tested in the local earth's magnetic field (A) and a magnetic field shifted 120° east of the local field (B). Each point represents the mean direction of one bird on one test-night. The black triangle outside each circle represents the distribution mean direction. gN = geographic north, mN = magnetic north. α is a distribution's mean direction, r is the mean vector length, and P is the significance level (Rayleigh test).

was no difference in orientation performance between the controls tested in the coils and those tested on the platform.

Funnel-shaped orientation cages (Emlen and Emlen 1966) were used to record the birds' activity during orientation tests. This was one major change in methodology compared with Wiltschko and Wiltschko (1975a, b), who used automatic radial perch cages. The orientation cages were equipped with shields that restricted a resting bird's view to a symmetrical 120° sector of the overhead night sky. A bird could improve its view of the night sky to 160° by climbing to the top of the funnel. The birds thus were afforded a substantial improvement in visual access to the night sky compared with those of Wiltschko and Wiltschko (1975a, b), whose birds were limited to only a 95° sector. Typewriter correction paper served as the recording medium (Beck and Wiltschko 1981). After quantification of a bird's recorded activity for one night (20 scratches minimum; Beck and Wiltschko 1981), a mean direction was calculated by vector analysis (Batschelet 1981). Mean directions from individual funnels were then pooled for each group for each experimental stage, and group mean directions were calculated. The Rayleigh test and, where appropriate, the V -test were used to test for nonuniformity of the pooled distributions. The nonparametric Mardia-

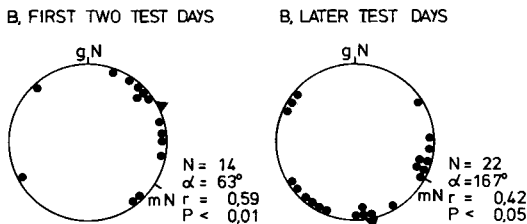


Fig. 2. Orientation of the birds in Fig. 1B partitioned into early and late tests. See Fig. 1 for an explanation of the symbols and abbreviations.

VERTICAL MAGNETIC FIELD

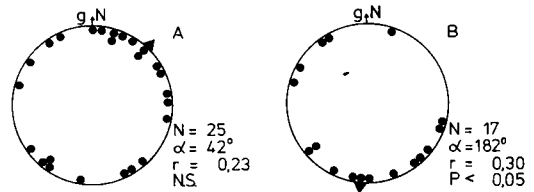


Fig. 3. Orientation of birds previously tested in the local earth's field (A) or shifted magnetic field (B) when exposed to a nondirectional vertical magnetic field. Significance level was obtained with the use of the V -test, using the mean directions of Figs. 1A and 2B, respectively, as the predicted directions. See Fig. 1 for an explanation of the symbols and abbreviations.

Watson-Wheeler two-sample test was used for between-group comparisons. Mean directions of single bird-nights were considered equivalent representations of the birds' directional preferences (Wiltschko and Wiltschko 1978); therefore, second-order statistics relying on mean vector lengths were not used.

The orientation of the control and experimental robins tested in the local earth's magnetic field and the 120° shifted magnetic field, respectively, is plotted in Fig. 1. The controls showed good, seasonally appropriate northeastward orientation with respect to both geographic and magnetic north, which were approximately coincident. Experimentals were east-southeastwardly oriented and northerly oriented relative to geographic and magnetic north, respectively. The difference between controls and experimentals was smaller than would be expected by assuming a simple tracking of the shifted magnetic field on the part of the experimentals, and no statistical difference emerged. At this level of analysis, the results match those of Wiltschko and Wiltschko (1975b) who, after separating the performance of experimentals into early and late tests, found a striking difference in the behavior of controls and experimentals.

The orientation of the experimentals, separating their first two test days with activity from later tests, is plotted in Fig. 2. Initially, the experimentals oriented toward geographic northeast, as did the controls, but in subsequent tests their orientation shifted to geographic south, where the birds maintained a seasonally appropriate northeasterly orientation with respect to the ambient magnetic field. The experimentals' orientation on later test days differed significantly from early test days and from that of controls ($P < 0.01$). A similar division of the control birds' data failed to yield significant orientation differences. The data are consistent with those of Wiltschko and Wiltschko (1975b), who reported a latency of a few days before robins adjusted their orientation to the altered magnetic field.

The orientation of the controls and experimentals

when subsequently tested in the vertical magnetic field, when the only known directional information would have been that of the stars, is plotted in Fig. 3. One notes foremost the poorer performance and the mean directions, which, albeit nonsignificant, correspond to those observed in the directional magnetic fields of stage 1 (the latter part of stage 1 for experimentals). If one takes the mean directions observed in stage 1 (Figs. 1A and 2B) as expected directions for the behavior of birds in stage 2, the orientation of the controls has a probability of uniformity of $0.05 < P < 0.1$, while that of the experimentals is $0.01 < P < 0.05$. Basically, the birds behaved in a manner consistent with the hypothesis that they recalibrated some secondary directional reference, presumably the stars, from the ambient magnetic field they experienced previously. The data indicate the overriding importance of geomagnetism for the migratory orientation behavior of European Robins as described by Wiltschko and Wiltschko (1975b).

Independent of test condition, mean vector lengths of individual bird-nights were variable but generally on the order of 0.40. The average mean vector length of the controls tested in the local earth's field was 0.39 ± 0.21 (SD), and in the vertical field, 0.33 ± 0.17 (SD). The average mean vector length of the experimentals tested in the shifted field was 0.38 ± 0.17 (SD; no difference between early and late tests), and in the vertical field, 0.45 ± 0.20 (SD).

The study reported here took place at a different location, used a different experimental cage, and allowed test birds a more complete view of the night sky than the study of Wiltschko and Wiltschko (1975b). Nonetheless, the results are similar. Within the constraints of the testing paradigm used in this study, therefore, the overriding importance of earth's magnetism for the migratory orientation of European Robins can scarcely be doubted. What remains to be understood, however, is why other testing paradigms fail to reveal such an effect and whether this failure may be attributed to an experimental bias or artifact favoring the use of one orientation cue over another.

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