

The Influence of Magnetic Total Intensity and Inclination on Directions Preferred by Migrating European Robins

(*Erithacus rubecula*)

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IN THEIR FIRST MIGRATORY PERIOD a simple directional orientation would lead migrating birds to an area appropriate for wintering. The relocation of a specific area, or homing after displacement, however, may need more complex orientation capacities (bicoordinate orientation or true navigation). In this paper I will discuss only directional orientation, which I will call "migratory orientation."

The possibility that birds use the Earth's magnetic field for orientation has often been discussed. Yet the older hypotheses which discussed the role of magnetic cues in bird orientation mostly pertained not to migratory birds, but to homing pigeons (refs. 1 to 4). All these hypotheses were rather speculative and were based upon little or no experimental material. Experiments that tried to influence the directional preference of captive birds by means of artificial magnetic fields lacked conclusive results (refs. 5 and 6), yet the intensity of these artificial magnetic fields is unknown.

Merkel and Wiltschko (ref. 7) and Wiltschko (ref. 8) showed that the directing

cues for migrating European robins are provided by the Earth's magnetic field. Experiments by Southern (ref. 9) showed that the orientation of ring-billed gull chicks is influenced by magnetic disturbances. Experiments using conditioning of the cardiac rhythm show that birds (pigeons) are sensitive to magnetic fields of the same intensity as the Earth's field (ref. 10). An influence of magnetic fields on the orientation behavior of some invertebrate species was described during recent years by Schneider (ref. 11), Becker (ref. 12), and Lindauer and Martin (ref. 13) for insects, and by Brown (ref. 14) for planarians and snails.

In this paper I will try to analyze some magnetic cues which enable birds to select their migratory direction.

MATERIALS AND METHODS

The methods used in my recent experiments were the same as those described in detail in an earlier publication (ref. 8). The orientation cage, made of wood and plastic, was octagonal, 1 m in diameter and 35 cm

high. It contained eight radially positioned perches which were connected to micro-switches that produced a signal for every hop of the bird. These data were punched into a paper tape, which was later processed by computer. I used this automatic method of data gathering so as to avoid subjective mistakes in interpretation.

The Earth's magnetic field in Frankfurt is 0.46 G, magnetic north at $360^\circ =$ geographic north, and $+66^\circ$ inclination. The different magnetic fields used during this study were produced by screening off parts of the Earth's magnetic field by a steel vault and by using Helmholtz coils (2-m diameter and 1-m clearance). The inhomogeneity in such a magnetic field is less than 4 percent in and around the cage. Tests were conducted at field intensities ranging from 0.16 G to 1.05 G in different directions and with inclinations between $+66^\circ$ and $+8^\circ$ and at -66° .

The tests were made in five different places in the Zoologic Institute and the Botanic Garden. During the experiments the test cage was illuminated by a dim, indirect light with an intensity of 0.03 lux, for we found that in complete darkness the birds slept and did not show any restlessness. My test bird is the European robin (*Erithacus rubecula*), a species that can be found in all parts of Europe except in Northern Scandinavia. This species migrates to the Mediterranean and North African countries. I tested more than 200 birds altogether, each test being carried out with only one bird at a time—in one cage where he stayed the whole night.

The mean directions of each night (calculated by computer) are comprised in the mean direction α_m and the concentration a_m of a series. The a_m is tested by the Rayleigh test for directional preference, and differ-

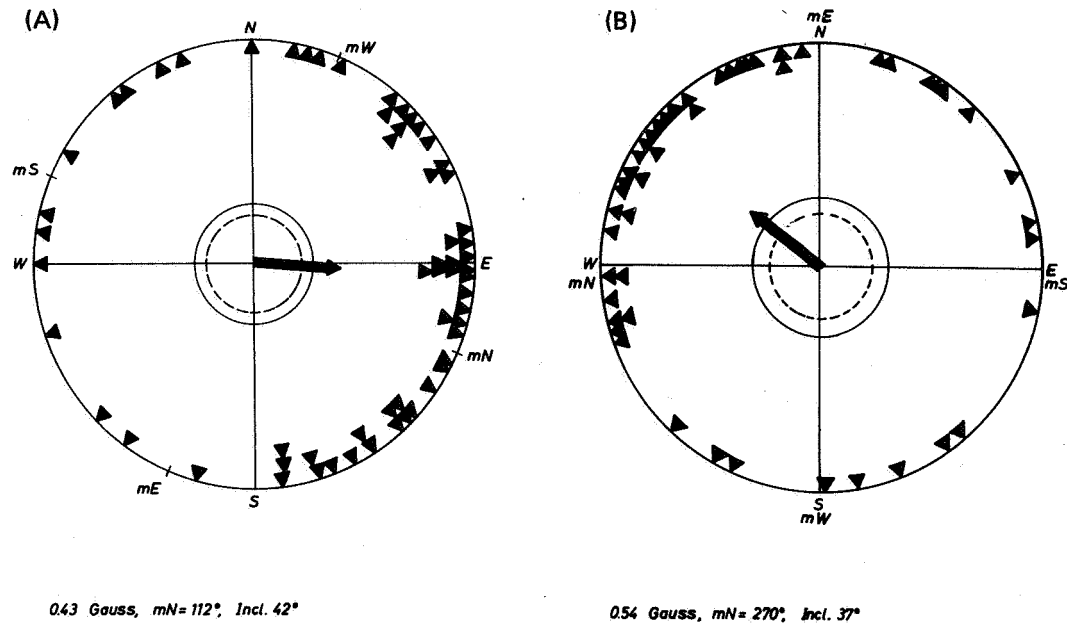


FIGURE 1. Mean directions in spring, magnetic north turned (A) to the ESE and (B) to the W.

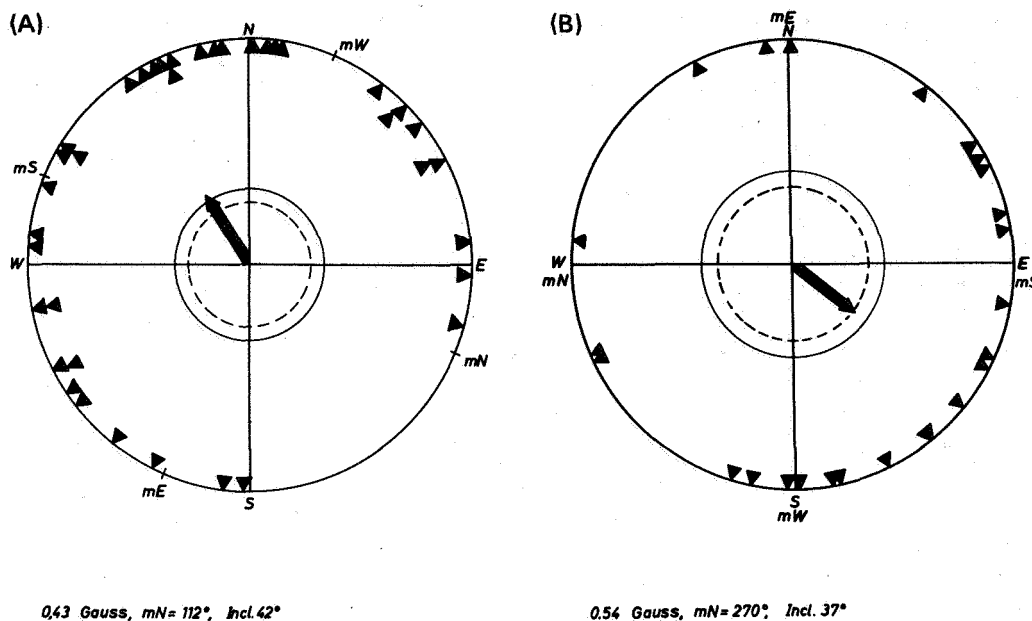


FIGURE 2. Mean direction in autumn, magnetic north turned (A) to the ESE and (B) to the W.

ences in mean directions of different series are tested with Watson and William's test and/or χ^2 test (ref. 15). In this paper's illustrations, the mean direction of single nights are represented by triangles and a circle and the mean direction α_m of the test series is shown as a vector originating from the center. The length of this vector represents the concentration a_m , and the two inner circles are the 5-percent (dotted) and the 1-percent significance border of the Rayleigh test. If the experimental north direction differs from geographic north, it is stated below the diagram and is marked as "mN" on the circle ($0^\circ = 360^\circ =$ geogr. N; $90^\circ =$ geogr. E; $180^\circ =$ geogr. S; and $270^\circ =$ geogr. W).

RESULTS

In order to show that robins use information they derive from the magnetic field for

migratory orientation, I will refer to data from former experiments where I changed the direction of the magnetic field and tried to maintain approximately the normal field intensity (ref. 8).

The migratory direction of robins in spring lies between NW and NE. When the north direction of the experimental magnetic field was turned to ESE (0.43 G, mN = 105° , $I = 42^\circ$) the robins showed a mean direction of 92° during springtime (fig. 1A), which is experimental NNW ($p < 0.01$). Turning experimental north to the west (0.54 G, mN = 270° , $I = 37^\circ$), I found the mean direction at 309° (fig. 1B), which is experimental NE ($p < 0.01$).

In corresponding experiments in the fall the mean direction was 328° , which is experimental SSW (fig. 2A) when magnetic north was in ESE (mN = 105°) ($p < 0.01$); and at 128° , which is experimental SW (fig.

2B) when magnetic north was in W ($mN = 270^\circ$) ($0.05 > p > 0.01$).

In all four cases the birds selected their migratory direction according to the direction of the magnetic field and the season.

It should be emphasized that tests with experimental north in ESE and in W were carried out in an orientation cage which was held in the same position for each individual bird. Only the direction (and to some degree the intensity) of the magnetic field was changed so that the bird could not rely on cues given by the cage itself or by the external environment.

In recent experiments we tried to narrow the limits of magnetic intensity in which the birds are able to select their migratory direction. In the next test the magnetic field intensity was reduced by about 25 percent, experimental north was in geographic north (0.34 G , $mN = 360^\circ$, $I = 57^\circ$). As a control we had a magnetic field of the Earth's

field intensity (0.46 G , $mN = 360^\circ$, $I = 48^\circ$) at the same time in the same room. In the test situation I could not find any directional preference (fig. 3A), whereas the control birds showed a migratory directional preference of $42^\circ = \text{NE}$ ($p < 0.01$) (fig. 3B). Former tests also showed no directional preference at 0.34 G (see table 1 and ref. 8).

In the next test series the field intensity was increased to about 150 percent of the Earth's magnetic field, experimental north remained coincident with geographic north (0.68 G , $mN = 360^\circ$, $I = 25^\circ$). A magnetic field of the same intensity as the Earth's magnetic field again served as the control (0.46 G , $mN = 360^\circ$, $I = 48^\circ$). We found that the birds lost their ability for orientation in magnetic fields of this high intensity, just as they did in fields of low intensity (fig. 4A, control 4B).

Table 1 shows a summary of all experi-

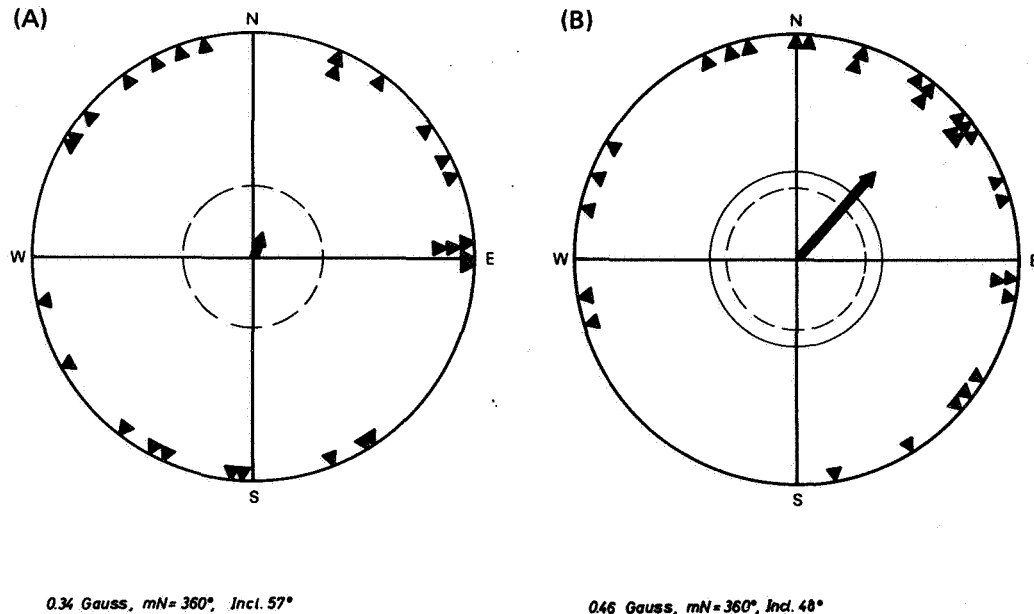


FIGURE 3. Mean directions in spring, (A) reduced field intensity and (B) normal field intensity.

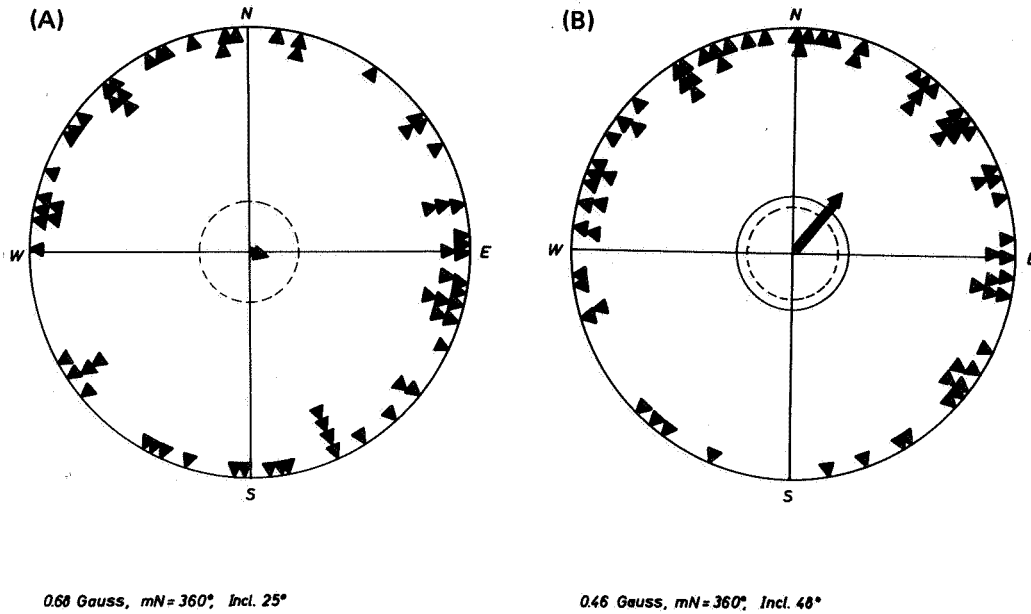


FIGURE 4. Mean directions in spring, (A) increased field intensity and (B) normal field intensity.

ments carried out in Frankfurt. The test series are classified according to the intensity of the magnetic field. This table shows that migratory orientation could be maintained only in the range between 0.34 G and 0.68 G. Further experiments will be conducted to determine whether this range is even narrower.

The range of magnetic intensity in which migratory orientation is possible is very narrow, but during fall and spring migrations the robins might come into geographic latitudes with magnetic intensities outside this range. So it is not surprising that robins, kept more than 3 days in a low field intensity of 0.16 G, again showed a directional preference for their migratory direction: test field 0.16 G, $mN = 360^\circ$, $I = 31^\circ$, mean direction in the fall migration period at 208° , which is SSW ($p < 0.01$) (fig. 5A). As a control, a few tests of the same birds are

TABLE 1.—Summary of All Frankfurt Experiments

Field intensity (G)	Inclination	Season	n	Significant mean direction
0.16	31°	Spring	79
		Autumn	52
0.34	57°	Spring	103
		Autumn	74
0.43	42°	Spring	62	mNNW
		Autumn	38	mSSW
0.46	66°	Spring	83	NNE
		Autumn	42	SW
0.46	48°	Spring	73	NE
		Autumn	18	W
0.54	37°	Spring	49	mNE
		Autumn	35	(mSW)
0.68	25°	Spring	68
0.81	8°	Spring	42
0.82	30°	Spring	28
		Autumn	16
1.05	23°	Spring	50
		Autumn	32

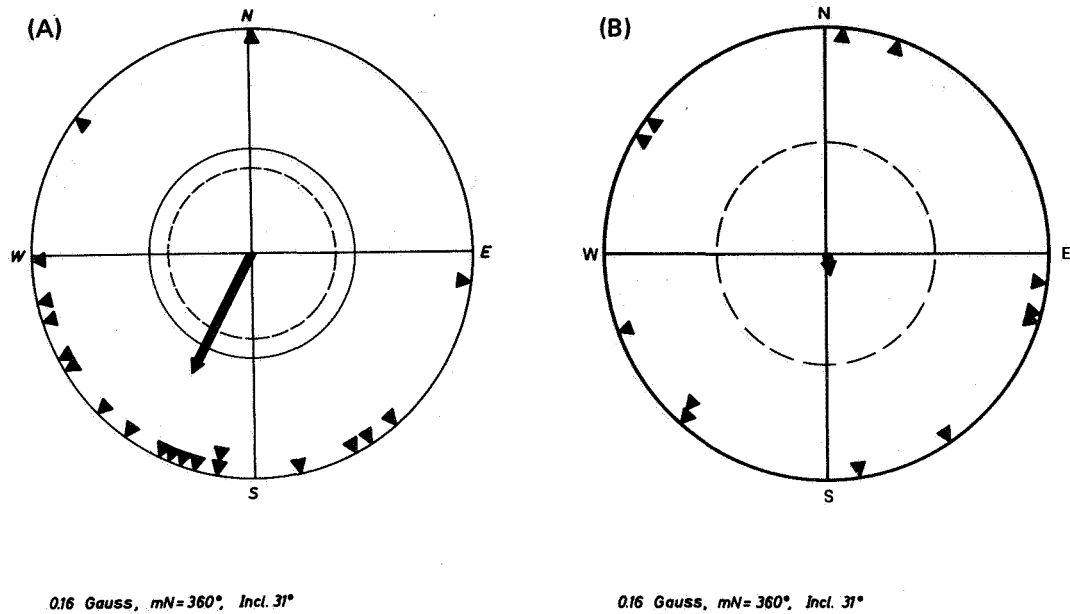


FIGURE 5. Mean directions in autumn at reduced field intensity, (A) birds accustomed to low field intensity and (B) birds housed in normal field intensities.

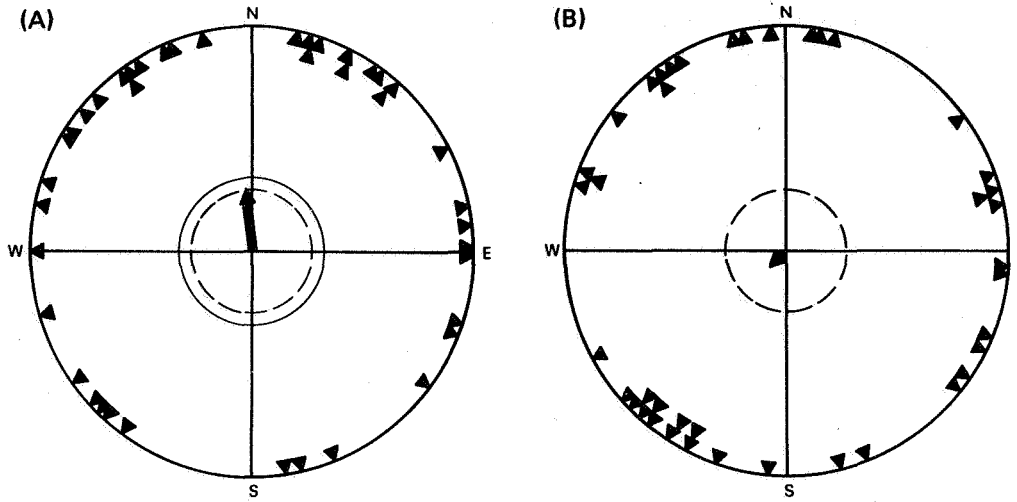
included when they were still kept at 0.46 G and before they were brought to live in this low field intensity (fig. 5B).

Test series that were begun in the spring of this year indicate that, after a period of becoming accustomed, migratory orientation is also possible in fields of high intensity. Birds were kept in a field of 0.81 G for at least 3 days and tested in a magnetic field of the same high intensity (0.81 G , $mN = 360^\circ$, $I = 8^\circ$) (fig. 6A). A directional preference of 354° , which is N, can be observed ($0.05 > p > 0.01$). Tests with birds that were not accustomed to high intensity fields served as controls (fig. 6B).

In the above described experiments the strength of the horizontal component of the magnetic field was varied greatly without influencing the birds' ability of orientation. The question now was whether the magnetic compass of the robin functions as a compass

system in the horizontal plane. A magnetic field was produced in which only the inclination was changed from $+66^\circ$ to -66° , with intensity and north direction remaining the same; i.e., the horizontal component has the same strength and direction as in the Earth's magnetic field. The vertical component also has the same strength, but the opposite direction, since it is now directed upward away from the ground and toward the sky (0.46 G , $mN = 360^\circ$, $I = -66^\circ$). Between the magnetic field lines and the force of gravity there is now an angle greater than 90° , whereas in the Earth's magnetic field this angle is less than 90° . The Earth's magnetic field served as a control (0.46 G , $mN = 360^\circ$, $I = +66^\circ$).

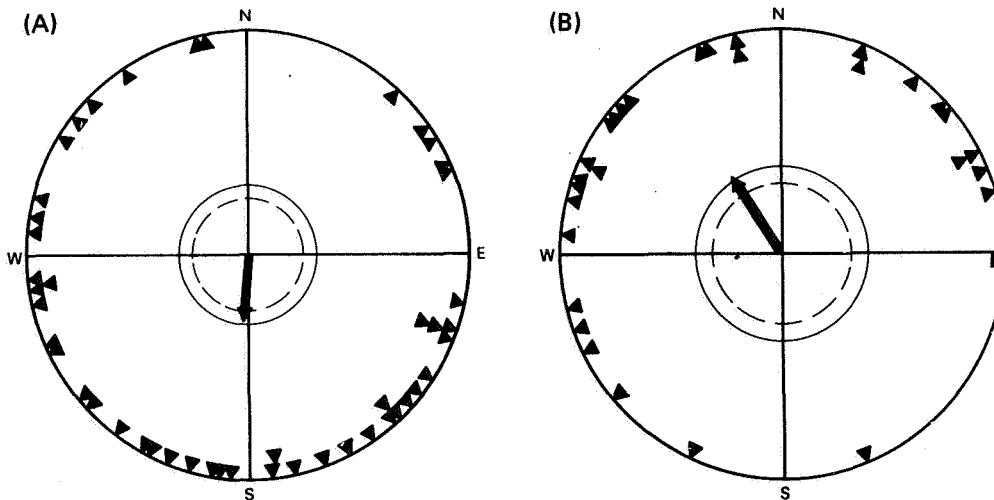
The results of this test were very surprising. The same robins that had showed a mean direction of 327° in the control, i.e., NNW ($p < 0.01$) (fig. 7B), under test con-



0.01 Gauss, $mN = 360^\circ$, Incl. 0°

0.01 Gauss, $mN = 360^\circ$, Incl. 0°

FIGURE 6. Mean directions in spring at increased field intensity, (A) birds accustomed to increased field intensity and (B) birds housed in normal field intensity.



0.46 Gauss, $mN = 360^\circ$, Incl. -66°

0.46 Gauss, $mN = 360^\circ$, Incl. $+66^\circ$

FIGURE 7. Mean directions in spring, (A) inclination negative and (B) normal Earth's magnetic field.

ditions seemed to seek their spring migratory direction in the S at 185° (fig. 7A). The Rayleigh test shows a significance of $0.05 > p > 0.01$ for the test series, yet the fact that the mean directions in test and control originated from different statistical populations is significant with $p < 0.001$.

CONCLUSION

The results show that the magnetic field provides the following cues for migratory orientation: (1) field intensity, (2) direction of the field in the horizontal plane, and (3) inclination equals direction in the vertical plane.

The intensity determines whether the field can be used as a source of information for orientation. By accustoming the birds to intensity values outside the intensity range normally encountered in migratory orientation, the intensity range can be enlarged to lower and, presumably, also to higher values. This may be important for the bird which, during migration, might come to geographic latitudes with other intensity values. The field direction in the horizontal plane provides the bird with a reference direction to orient his migratory direction.

Our tests show the following: (1) within the intensity range which enables the bird to orientate, the angle of inclination does not matter within the positive range (tests were made between $+120^\circ$ and $+66^\circ$); (2) variations in the inclination angle cause significant variations in the horizontal and vertical intensity components of the magnetic field. We can, therefore, assume that none of these components alone is essential for the birds' physiological perception of the magnetic field but only the resultant, total intensity, which can have any direction within the said range.

The last experiment shows the importance

of the direction of the vertical component. A reversal of the vertical component causes the birds to migrate in the opposite direction. The north and the south directions in the relation system given by the direction of the horizontal component are determined by the direction of the vertical component. This means, however, that the bird cannot perceive the polarity of the magnetic field but only the axial direction of the magnetic field lines. We must conclude from this that there is no compass system for the bird in the plane. The axial direction of the magnetic field without its polarity does not, however, permit a clear orientation according to the magnetic field. The bird must still use other information.

According to my present hypothesis, this additional information is provided by the force of gravity, i.e., by the knowledge of up and down. The bird can determine the angle between the gravity direction and the axial direction of the magnetic field. In the northern hemisphere this angle, γ' , is in the northern semicircle always smaller than 90° . The bird looks for the biggest of all angles being smaller than 90° ; this direction points to north.

Mathematically this angle γ can be expressed as follows:

$$\tan \gamma = \frac{H_h}{H_v}$$

where H_h is the horizontal component, positive in the direction of magnetic north, and H_v is the vertical component which is parallel to the force of gravity, positive in downward direction. The bird cannot perceive the direction of the components, but it can measure $\tan \gamma$. The point where $\tan \gamma$ reaches its maximum positive value indicates to the bird the direction of magnetic north (fig. 8A). If we reverse the direction of one

of the components, the sign of $\tan \gamma$ becomes negative (i.e., the angle becomes greater than 90°). But the bird can find an angle with positive $\tan \gamma'$ on the opposite side, and he must look now for his north direction opposite to the original one (fig. 8B).

To confirm this model we are going to make the following tests: (1) reversal of both components — the birds should migrate into the same direction as in the terrestrial field; and (2) production of a field of Earth's intensity but without a vertical component — the birds should not show a clear migratory orientation.

SUMMARY

1. Field intensity determines whether the magnetic field can be used for migratory orientation.

2. The normal intensity range can be enlarged by becoming accustomed to weaker or stronger fields.

3. The birds can perceive the axial direction of the field lines but not their polarity.

4. A discussion of the hypothesis that birds can find the north direction by means of the angle between gravity and magnetic field direction was presented.

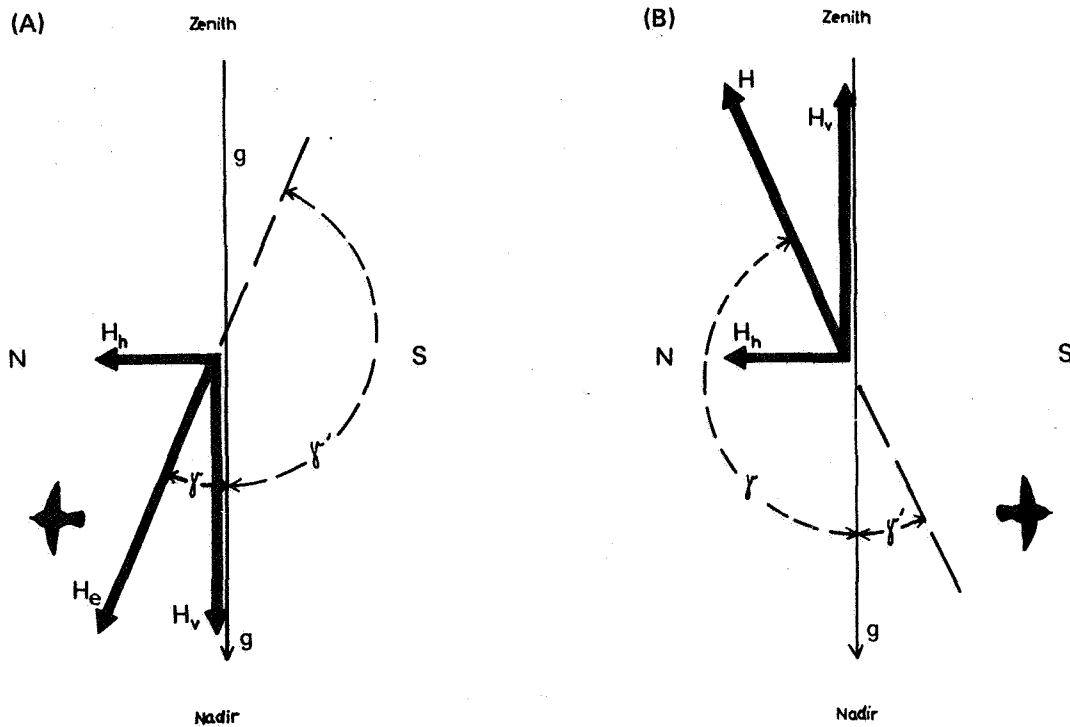


FIGURE 8. Sections through the magnetic field in a plane parallel to the force of gravity and the N-S axis; g = force of gravity; H_e = Earth's magnetic field vector; H = experimental magnetic field vector; H_h = horizontal component; H_v = vertical component; γ = angle between force of gravity and magnetic vector; γ' = supplement angle to γ . (A) Situation in the Earth's magnetic field; (B) situation when the inclination is negative.

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DISCUSSION

QUESTION: What was the average angular deviation for the means of the single nights?

WILTSCHKO: It was about 80° to 65°. We found high activity and directional preference in a single night are negatively correlated. Since we cannot consider the vectors for a single night, we took them all as being equal.

ENRIGHT: What percentage of the individual bird-nights would be statistically significant if you treat each observed perch-hop as statistically independent, which, of course, they are not?

WILTSCHKO: About 60 percent.

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