

## THE DIRECTION OF CELESTIAL ROTATION INFLUENCES THE DEVELOPMENT OF STELLAR ORIENTATION IN YOUNG GARDEN WARBLERS (*SYLVIA BORIN*)

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### Summary

The study presented here was conducted in order to analyze the role of the direction of celestial rotation in the development of stellar orientation in young migratory birds. The test birds were garden warblers, *Sylvia borin*, which leave their breeding ground on a southwesterly compass course. The birds were hand-raised and, during the premigratory period, exposed to an artificial 'sky' in the local geomagnetic field. For the control group C, the star pattern was rotating in the natural direction, with the centre of rotation and magnetic North coinciding. For the three experimental groups, the star pattern was rotating in the opposite direction; for group E<sub>1</sub>, the centre of rotation coincided with magnetic North, for group E<sub>2</sub> the centre of rotation was at magnetic West and for group E<sub>3</sub> it was at magnetic East. During autumn migration, the birds were tested without magnetic information under the same, now stationary, sky. All four groups were able to use stellar information for orientation, but only the control group

preferred the normal southwesterly course. The three experimental groups, in contrast, all oriented towards a significantly different direction, preferring due south. The results for group E<sub>1</sub> showed less scatter than those for the other two experimental groups.

These results indicate that the direction of celestial rotation is crucial for the development of the normal migratory course with respect to the stars in young garden warblers. Establishing the species-specific southwesterly migratory course requires an interaction between celestial rotation and magnetic cues; this interaction appears to depend on the natural direction of celestial rotation. Rotation in the reverse direction allowed the birds to respond only in a manner that oriented them away from the centre of rotation.

Key words: bird migration, migratory orientation, celestial rotation, magnetic field, ontogeny, garden warbler, *Sylvia borin*.

### Introduction

When young migrants leave for their first migration, they are guided by innate information on the direction of their migration route (for a summary, see Berthold, 1988). Experiments with hand-raised migrants indicated that the genetically coded directional information is transformed into an actual migratory direction by a complex interaction between two cue systems, celestial rotation and the earth's magnetic field (R. Wiltschko and Wiltschko, 1995; Able and Able, 1996; Weindler *et al.* 1996).

The first evidence for the crucial role of the apparent spherical motion of the star patterns in the sky came from a planetarium study: Emlen (1970) demonstrated that young indigo buntings (*Passerina cyanea*) establish a star compass from celestial rotation before they initiate their first migration. His birds oriented away from the centre of rotation, regardless of whether the planetarium sky had rotated around the Pole Star or any other star during the premigratory period. Corresponding experiments using a simple, artificial 'sky' with small lights as 'stars' also emphasized the essential role of celestial rotation: garden warblers (*Sylvia borin*) that had

observed a rotating 'sky' were later able to orient under that stationary 'sky' in the absence of magnetic information, whereas birds that had been exposed to the same, but stationary, 'sky' were not oriented (W. Wiltschko *et al.* 1987). These findings indicate that birds have no innate knowledge about what the sky looks like; they can use any star pattern as long as they have had an opportunity to observe it rotating around a centre (see also Able and Able, 1990).

To analyze the interactions between celestial rotation and magnetic cues during ontogeny, young birds were exposed during the premigratory period to the natural sky or to rotating artificial skies, while magnetic North was altered in various directions. Later, during migration, these birds were tested with only one set of cues available. Birds tested under stars alone preferred southerly directions or corresponding directions away from the centre of rotation (Bingman, 1984; W. Wiltschko *et al.* 1987). Birds tested with the magnetic field as the only available cue, in contrast, were found to have altered their magnetic compass course and preferred a new course that

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depended on the direction of the former centre of rotation (Bingman, 1983; Able and Able, 1990, 1993; Prinz and Wiltschko, 1992). Thus, celestial rotation proved to be the dominant cue; it altered the course with respect to the magnetic field, whereas magnetic information did not seem to affect the course with respect to the stars.

In one of the studies mentioned above, Prinz and Wiltschko (1992) had observed an asymmetry in response: birds raised under the natural sky in magnetic fields altered by 120° changed their magnetic course only when, during exposure, magnetic North had been turned to west-southwest, but seemed disoriented when it had been turned to east-southeast. The authors speculated that possible reasons for this phenomenon might involve the direction of alteration of magnetic North in relation to the direction of celestial rotation.

Although celestial cues appear to dominate over magnetic ones, stellar cues alone do not seem to be sufficient for establishing the appropriate migratory direction. Recent experiments have revealed that garden warblers hand-raised under a rotating artificial sky, but without magnetic information, oriented due south, while their conspecifics raised with both sets of cues available preferred their normal southwesterly course. Genetic information with respect to celestial rotation may be described as 'away from the centre of rotation' only; the establishment of the population-specific migratory direction seems to require additional information from the magnetic field (Weindler *et al.* 1996). This means that celestial rotation and the geomagnetic field appear to be two components of an integrated system.

This leads to the question of how the two types of cues – celestial rotation and magnetic information – are combined to produce the species-specific migratory direction. In view of the asymmetry observed by Prinz and Wiltschko (1992), the role of the direction of celestial rotation became of interest: do birds expect a certain direction of rotation, i.e. do birds born in the northern hemisphere expect a counterclockwise movement around the celestial pole, or can the birds use celestial rotation regardless of its direction and combine it with magnetic information in the appropriate way? Does the directional relationship between celestial rotation and magnetic north affect this process in any way? The present study was designed to answer these questions.

### Materials and methods

The experiments reported here were conducted during autumn migration in the years 1989–1993 in Frankfurt a.M., Germany. They belong to a set of experiments performed in order to gain further insight into the interactions between celestial rotation and magnetic information. Part of this experimental series has been published previously (Weindler *et al.* 1996); the control data for that study and for the present study are the same.

#### *Test birds*

As experimental birds we chose garden warblers, *Sylvia borin* (Bodd, 1783), long-distance migrants that migrate at

night. They breed in central and northern Europe and winter south of the Sahara in tropical Africa between the latitudes 10°N and 30°S. Birds of the central European population appear to migrate in a broad front. Ringing recoveries indicate that, during August and September, they show southwesterly headings that lead them to Spain and Portugal; from October onwards, after passing the Iberian Peninsula, they turn to a more southerly or southeasterly heading to reach their winter quarters in central Africa (Klein *et al.* 1973; Zink, 1973; see also Gwinner and Wiltschko, 1978). This route allows the birds to avoid ecologically unfavourable areas such as the Alps, the Mediterranean Sea and the central part of the Sahara.

The birds used in the present study were taken from their nests in the Bodensee region (southern Germany) at the age of 4–6 days. They were transferred to the Zoological Institute at Frankfurt a.M. and hand-raised until they were self-sufficient.

#### *First summer experience*

During the premigratory period, the birds were housed in wooden huts in the garden of the Institute in the local geomagnetic field (46 000 nT, magnetic North 360°, 66° inclination). Their wooden-framed cages (80 cm×50 cm×40 cm) were covered with netting and were placed so that the birds could see an artificial 'sky' with small lights as 'stars' (as described by W. Wiltschko and Wiltschko, 1976) that was rotating continuously with a rate of one rotation per day.

For group C, the sky was rotating counterclockwise, i.e. in the direction normally observed in the northern hemisphere; the centre of rotation (=rotational North) coincided with magnetic North. This situation mimicked the natural situation outside and served as the control.

The three experimental groups were exposed to an identical 'sky' that was rotating clockwise, i.e. in the reverse direction, with different combinations of the centre of rotation and magnetic conditions: (1) for group E<sub>1</sub>, rotational and magnetic North coincided; (2) for group E<sub>2</sub>, rotational North was in magnetic West; (3) for group E<sub>3</sub>, rotational North was in magnetic East. The different relationships between the centre of rotation and magnetic North were achieved by placing the cages excentrically under the rotating sky (see Fig. 1).

For all four groups, the exposures to the artificial sky lasted for approximately 4 weeks from Mid-July to Mid-August. The birds were then moved into a windowless room inside the Institute, where they were housed in individual cages under a light regime that simulated the local photoperiod.

#### *Orientation tests*

Orientation tests were performed from Mid-August to Mid-November using several wooden huts in the garden as test sites. The test cages stood excentrically under the same, but now stationary, sky in a vertical magnetic field (90° inclination) produced with the help of Helmholtz coils, i.e. directional information from the magnetic field was not available.

The birds were tested in Merkel–Wiltschko orientation cages (1 m diameter, 35 cm high) with eight radially positioned

Data analysis and statistics

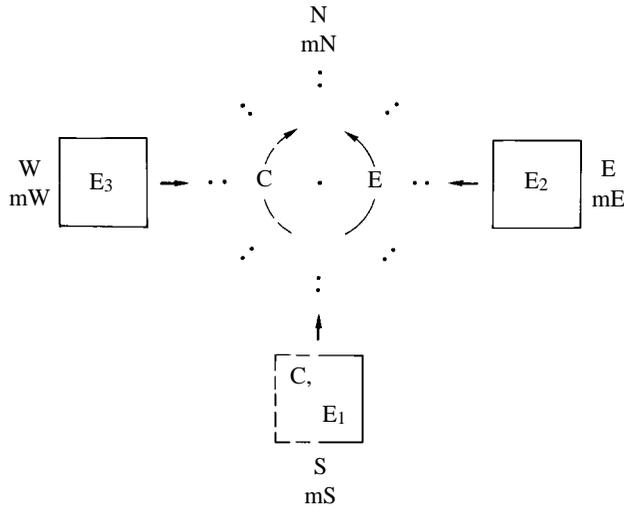


Fig. 1. Schematic view from above showing the rotating artificial 'stars' (dots) and the arrangement of cages during exposure. Solid boxes, experimental groups; dashed box, controls exposed in another room; the position of the control cage corresponded to that of the E<sub>1</sub> group. Note that the counterclockwise rotation in the natural direction as seen from below looks like a clockwise rotation when viewed from above (dashed arrow), and *vice versa*. N, mN: geographic North corresponding to magnetic North of the local geomagnetic field, etc. The small arrows indicate the direction towards celestial rotation for each group of birds.

double perches (for details, see W. Wiltschko, 1968). Their activity was recorded automatically by micro-switches as they jumped on the perches. The test period lasted the entire night.

From the distribution of activity on the eight perches, the heading of each individual bird for each test night was calculated by vector addition. A mean vector was calculated from the nightly headings of each individual bird. Bird nights with less than 20 perch activations were excluded from analysis.

Because garden warblers change direction during the course of their migration, the season was divided in two parts according to the date on which the change is observed in nature, with the data recorded before 30 September representing the first part and the data recorded from 1 October onwards representing the second part of the migratory season (see Gwinner and Wiltschko, 1978). Grand mean vectors were calculated for each test group from the mean directions of the individual birds.

The Rayleigh test was used to test the vectors of individual birds and the grand mean vectors for directional preferences. The Watson Williams test was used to test for differences in preferred directions (Batschelet, 1981), the Wilcoxon test was used to compare the headings of individual birds during the first and the second parts of the season, and the Mann-Whitney *U*-test was used to test individual vector lengths and the deviations of the birds' mean headings from the grand mean in order to detect differences in scatter.

Results

Table 1, 2 give the mean vectors of the individual birds and the grand means of the groups for the first and the second parts of the season.

Table 1. Stellar orientation of the control group C in the absence of magnetic information

Bird	August and September			October and November		
	<i>n</i>	<i>r</i>	$\alpha$	<i>n</i>	<i>r</i>	$\alpha$
1	11	0.80***	225°	14	0.67**	247°
2	10	0.49	341°	2	0.99	333°
3	11	0.80***	240°	7	0.86**	201°
4	13	0.49	122°	11	0.63*	306°
5	10	0.44	286°	10	0.54	176°
6	9	0.59	247°	12	0.52*	174°
7	8	0.68*	242°	13	0.22	1°
8	7	0.64*	235°	5	0.64	259°
9	7	0.65*	221°	5	0.88*	271°
10	7	0.20	262°	2	0.51	307°
11	7	0.88*	211°	3	0.79	292°
12	8	0.35	223°	5	0.50	200°
13	6	0.84*	212°	3	0.66	296°
14	7	0.44	205°	5	0.54	236°
15	6	0.90**	212°	5	0.68	315°
<i>N</i> =15		0.64	232°, 0.76***		0.64	267°, 0.59**

During the premigratory period, the birds had been exposed in the local geomagnetic field to a sky rotating counterclockwise, i.e. in the natural direction. The centre of rotation lay in magnetic North.

*n* is the number of evaluatable nights; *r*, the length of the vector of an individual bird;  $\alpha$ , the heading of the vector of an individual bird.

In the summary line, *N* gives the number of birds; values below *r* indicate the median vector length of the group, whereas values under  $\alpha$  give the direction and the length of the grand mean vector based on the headings of the birds.

Asterisks indicate significance (Rayleigh test): \**P*<0.05; \*\**P*<0.01; \*\*\**P*<0.001.

Table 2. *Stellar orientation of the experimental groups in the absence of magnetic information*

Bird	August and September			October and November		
	<i>n</i>	<i>r</i>	$\alpha$	<i>n</i>	<i>r</i>	$\alpha$
Group E <sub>1</sub> , rotational North coinciding with magnetic North						
1	7	0.86**	171°	12	0.92***	191°
2	7	0.90**	198°	11	0.73**	220°
3	5	0.45	178°	13	0.49*	191°
4	6	0.96**	151°	7	0.38	171°
5	6	0.75*	184°	2	0.89	49°
6	8	0.30	218°	2	0.89	202°
7	5	0.55	181°	5	0.86*	150°
8	5	0.68	163°	10	0.85***	180°
9	5	0.91*	196°	5	0.65	163°
<i>N</i> =9		0.75	182°, 0.95***		0.85	177°, 0.76**
Group E <sub>2</sub> , rotational North in magnetic West						
10	7	0.67	200°	12	0.53*	149°
11	6	0.86**	172°	13	0.57*	205°
12	6	0.83*	199°	13	0.68**	208°
13	6	0.83*	192°	12	0.53*	98°
14	6	0.91**	186°	9	0.57*	146°
15	12	0.27	190°	11	0.15	51°
16	12	0.24	156°	10	0.46	185°
17	10	0.72**	181°	10	0.91**	161°
18	12	0.46	231°	11	0.63**	297°
19	12	0.30	61°	11	0.26	293°
<i>N</i> =10		0.69	184°, 0.79***		0.55	175°, 0.41 <sup>NS</sup>
Group E <sub>3</sub> , rotational North in magnetic East						
20	7	0.46	125°	13	0.68**	88°
21	6	0.45	132°	8	0.29	338°
22	6	0.52	206°	10	0.19	93°
23	7	0.59	162°	11	0.20	64°
24	10	0.64*	115°	7	0.23	85°
25	11	0.29	74°	11	0.51*	265°
26	8	0.42	98°	4	0.64	292°
27	8	0.73*	182°	5	0.32	266°
28	8	0.60	167°	3	0.64	94°
29	8	0.41	142°	5	0.53	159°
30	5	0.42	184°	6	0.38	165°
31	12	0.17	245°	11	0.85**	343°
<i>N</i> =12		0.45	151°, 0.72***		0.44	72°, 0.17 <sup>NS</sup>

During the premigratory period, the birds had been exposed in the local geomagnetic field to a sky rotating clockwise, i.e. in the *reverse* direction.

See Table 1 for details.

NS, not significant.

The garden warblers were tested under a stationary star pattern in the absence of meaningful magnetic information, i.e. they had to rely on the stars alone and on what they had learned during the premigratory period. During the first part of migration, all groups were significantly oriented, but there was a marked difference between the control group C and the three experimental groups (Fig. 2). Only the group C birds that had observed the artificial sky rotating in the natural direction showed the seasonally appropriate tendency

towards southwest. The birds that had experienced a sky rotating in the reverse direction, in contrast, headed due south. The differences between the headings of group C and those of the three experimental groups were significant (C *versus* E<sub>1</sub>,  $P < 0.01$ ; C *versus* E<sub>2</sub>,  $P < 0.05$ ; C *versus* E<sub>3</sub>,  $P < 0.001$ , Watson Williams test), while the three experimental groups did not differ from each other in direction ( $P > 0.05$ ).

Between the first and the second part of migration, when

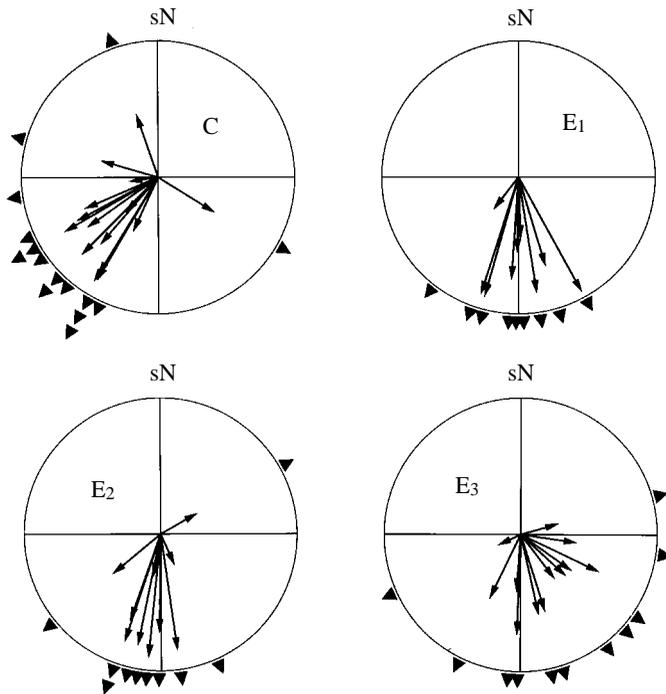


Fig. 2. Orientation of garden warblers during the *first part* of their autumn migration, tested under a stationary artificial sky in the absence of meaningful magnetic information. C, control group exposed to an artificial sky rotating in the natural direction; E, experimental groups that had been exposed to an artificial sky rotating in the reverse direction; see Fig. 1 and the text for details of groups E<sub>1</sub> to E<sub>3</sub>. sN indicates 'stellar north', i.e. the direction that, by the stars, corresponded to the former centre of rotation. The arrows represent the vectors and the symbols at the periphery of the circle indicate the mean headings of the individual birds.

garden warblers have normally changed their course from southwest to southeast, none of the groups showed a significant directional shift ( $P > 0.05$ , Wilcoxon test). The scatter appeared to increase in all four groups in the second part of the season because the vector lengths of the grand means were markedly shorter than during the first part of the season. This was significant for groups C and E<sub>2</sub> ( $P < 0.05$ , Mann-Whitney test). Only groups C and E<sub>1</sub> continued to be oriented (see Tables 1, 2).

Among the experimental groups, E<sub>1</sub>, the group for which rotational North and magnetic North had coincided, seemed to show less scatter than the other two groups. During both parts of the season, the individual vector lengths of the E<sub>1</sub> birds tended to be longer, and the grand mean vector lengths were longer. In particular, the results for group E<sub>3</sub> were much more scattered (see Table 2); the differences between E<sub>1</sub> and E<sub>3</sub> were significant ( $P < 0.05$ , Mann-Whitney test).

### Discussion

Our findings clearly show that the direction of celestial rotation plays an important role in the development of the

population-specific migratory direction with respect to the stars. Orientation in the appropriate southwesterly direction seems to be possible only if, during the premigratory period, the stars have been rotating in the natural direction. After exposure to a 'sky' rotating in the reverse direction, garden warblers preferred directions around due south, i.e. they merely headed away from the centre of rotation and failed to establish their normal southwesterly migratory direction that is adapted to the conditions between the breeding and wintering ground.

In another part of our study (Weindler *et al.* 1996), garden warblers had been raised under the same artificial 'sky' rotating in the natural direction, but without simultaneous access to meaningful magnetic information. In tests with stars as the only cues, these birds also oriented due south, indicating that, during ontogeny, specific interactions between magnetic and celestial cues are necessary to establish the population-specific southwesterly migratory direction. Apparently, celestial rotation only provides a reference direction away from its centre, and some information from the magnetic field must be combined with information obtained from the stars. This information appears to be a deviation from the reference direction provided by celestial rotation, in the case of our garden warblers '50° to the right' (Weindler *et al.* 1996).

Our present findings show that this transfer of information during the premigratory period depends on the direction of rotation and is disrupted when the sky is rotating in the reverse direction. This suggests that the birds have some spontaneous expectation about the direction of celestial rotation which has to be met to allow the normal addition of information from the magnetic field to that obtained from celestial cues. This is remarkable in view of the observation that the appearance of the sky itself and the configuration of the star patterns seem to be totally irrelevant (e.g. W. Wiltschko *et al.* 1987; Able and Able, 1990).

However, even a sky rotating in the reverse direction provides some information for migrating bird, allowing them to set a course with respect to the stars. The three experimental groups all oriented away from the centre of rotation, regardless of the relationship between rotational and magnetic North they had previously experienced. Their responses were therefore no different from that of the birds in the other part of the study that had observed the same artificial sky rotating in the natural direction but in the absence of magnetic information (Weindler *et al.* 1996). This clearly shows that celestial rotation, regardless of its direction, provides a reference direction corresponding to south and can set the star compass accordingly. It appears to be just the interaction between information from the magnetic field and that from celestial cues, establishing the population-specific migratory direction, that is disrupted when the stars rotate in the reverse direction.

In a parallel study with pied flycatchers (*Ficedula hypoleuca*), we also found that the direction of celestial rotation was crucial for the interaction between celestial and magnetic cues. At higher latitudes with a steep magnetic inclination, pied flycatchers hand-raised and tested without access to celestial cues showed a bimodal preference along the

migratory axis, choosing their normal migratory direction and the opposite direction with equal frequency. However, when the birds had been allowed to observe a rotating planetarium sky during the premigratory period, they were unimodally oriented in the appropriate migratory direction (Weindler *et al.* 1995). This change from axial to unimodal orientation also depends on the direction of celestial rotation; it occurs only when the stars rotate in the natural direction (P. Weindler, in preparation).

This leaves the asymmetrical response observed in pied flycatchers when the birds had been exposed to the natural sky while magnetic North was shifted to west-southwest and east-southeast (Prinz and Wiltschko, 1992). In these experiments, an interaction between celestial rotation and magnetic cues reset the magnetic course. The direction of rotation had been normal and, as in our present study, the relationship between the direction of rotation and magnetic North had differed between the experimental groups. Oriented behaviour with the aid of magnetic information was observed only when magnetic North was in the West or, expressed the other way, when rotational North was in magnetic East, while the group with rotational North in magnetic West showed a large scatter. In our present study, the various relationships between rotational and magnetic North did not affect the direction preferred by the experimental groups with respect to the stars, but it seemed to cause differences in scatter that are still unexplained. Interestingly, with the reverse direction of rotation, the group that showed most scatter was the one that had experienced rotational North in magnetic East, just the opposite to what was observed by Prinz and Wiltschko (1992). This suggests that the relationship between the direction of rotation and magnetic North might be involved in establishing the migratory course in a still unknown manner.

In the second part of the season, our birds did not show the directional shift normally observed in garden warblers. In cage studies, this shift was observed only when the birds had access to magnetic information (e.g. Gwinner and Wiltschko, 1978), indicating that the course of the second leg of migration is coded with respect to the magnetic field alone (see also Weindler *et al.* 1996). In pied flycatchers, the seasonal shift in migratory direction was also found to depend on magnetic information; here, orientation during the second part of migration seemed to require magnetic conditions as found in northern Africa (Beck and Wiltschko, 1988). Magnetic information appears to play a role of increasing importance as migration proceeds (for a review, see R. Wiltschko *et al.* 1997). The reasons for this may lie in the changes in the stellar sky that the birds experience as they move southward, whereas the magnetic field becomes more regular at lower latitudes. Our birds, tested with stars as their only cue, lacked the relevant magnetic information; this might have confused them, as indicated by the increase in scatter observed in October and November.

Taken together, all these findings indicate that complex interactions between celestial rotation and the magnetic field occur during the premigratory period when the starting course

for migration is established. The direction of celestial rotation appears to be crucial for these interactions and, thus, for establishing the population-specific migratory direction. However, the direction of rotation does not seem to be important for a star compass to be established: our experimental birds were oriented with stars as the only cues, even if they preferred a direction that was significantly different from their normal migratory direction. Under natural conditions, 'away from the centre of rotation' corresponds to geographic South, which is not a totally inadequate course for autumn migration, as it will always lead the birds to regions with less severe winters. Therefore, the behaviour of the experimental birds might represent some general, fundamental response of migrants to celestial rotation, regardless of its direction. The population-specific courses leading to optimal migration routes, in contrast, seem to require interactions with the magnetic field which, in turn, require celestial rotation in the natural direction.

This raises an interesting point: rotation in the reverse direction in our experiments corresponds to the natural situation south of the equator. Birds breeding in the southern hemisphere must be adapted to this direction of rotation. However, many northern migrants winter beyond the equator, among them garden warblers from eastern European populations. How they respond to celestial rotation and the local geomagnetic field when they start their return journey is not known – problems associated with setting the return course have not yet been analyzed in detail.

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