

# A Long-Distance Avian Migrant Compensates for Longitudinal Displacement during Spring Migration

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## Summary

In order to perform true bicoordinate navigation, migratory birds need to be able to determine geographic latitude and longitude. The determination of latitude is relatively easy from either stellar or magnetic cues [1–3], but the determination of longitude seems challenging [4, 5]. It has therefore been suggested that migrating birds are unable to perform bicoordinate navigation and that they probably only determine latitude during their return migration [5]. However, proper testing of this hypothesis requires displacement experiments with night-migratory songbirds in spring that have not been performed. We therefore displaced migrating Eurasian reed warblers (*Acrocephalus scirpaceus*) during spring migration about 1000 km toward the east and found that they were correcting for displacements by shifting their orientation from the northeast at the capture site to the northwest after the displacement. This new direction would lead them to their expected breeding areas. Our results suggest that Eurasian reed warblers are able to determine longitude and perform bicoordinate navigation. This finding is surprising and presents a new intellectual challenge to bird migration researchers, namely, which cues enable birds to determine their east-west position.

## Results and Discussion

Many displacement experiments have been performed with young birds on their first autumn migration [4, 6–10]. The vast majority of these studies suggest that young birds on their first autumn migration use a very simple spatiotemporal navigation strategy, namely, simple vector navigation, also called the clock-and-compass or, better, the calendar-and-compass strategy [11–13]. In contrast to young birds on their first autumn migration, adult birds and young birds returning in spring have personal experience with their goals and might thus use information collected through experience to refine the orientation strategies [5, 7, 10–12]. Unfortunately, very few displacement experiments have been performed in spring. Consequently, our knowledge about the spatiotemporal navigation strategies of experienced migrants in spring is very sparse

and rather speculative. Do birds on return migration in spring perform true navigation toward a specific goal area?

We performed cage experiments under clear natural skies to test whether long-distance avian migrants captured during spring passage and displaced about 1000 km toward the east (Figure 1) are able to compensate for an east-west displacement. Experienced avian migrants are usually assumed to be able to perform true navigation toward the goal of their migration. This notion is based on a few cases of rather high breeding and natal philopatry ([14], but see [5]) and several predominantly north-south displacement experiments during spring passage ([15–17], but see [8]). The hypothesis of true bicoordinate navigation [11, 12] assumes that night-migrating passerine migrants are able to identify at least two coordinates (roughly corresponding to geographic latitude and longitude) globally. Theoretically, migrants can determine geographic latitude from the height of the celestial center of rotation above the horizon and/or from the angle of magnetic inclination or total geomagnetic-field intensity [1–3]. However, the identification of longitude is a problem [5, 18]. Geomagnetic inclination and total intensity could potentially be good map cues [19–21], but in many parts of the world, geomagnetic inclination and total intensity's isolines are almost parallel with latitudes. To use celestial cues for navigation, a bird would need a dual time sense, i.e., two internal clocks, one of which is fixed on home time [4, 5]. However, the internal clock is known to adapt to local time quickly [22–24], and a fixed-time internal clock has never been shown to exist in any animal. Therefore, returning migrants in spring have been suggested to perform one-coordinate navigation, i.e., they know the latitude, but not the longitude, of their migratory destination [5]. Thus, if birds perform one-coordinate navigation on the basis of latitude alone, displaced Eurasian reed warblers (*Acrocephalus scirpaceus*) should not be able to correct for an east-west displacement, whereas they should correct for an east-west displacement if they perform true bicoordinate navigation.

The mean directions shown by spring migratory Eurasian reed warblers on the Baltic coast before displacement were  $\alpha = 26^\circ$ ,  $r = 0.59$ ,  $n = 13$ , and  $p = 0.008$  in 2004;  $\alpha = 57^\circ$ ,  $r = 0.45$ ,  $n = 14$ , and  $p = 0.06$  in 2005; and  $\alpha = 44^\circ$ ,  $r = 0.42$ ,  $n = 25$ , and  $p = 0.012$  in 2007 (Figures 2A–2C). The 3 years were not significantly different from each other (Mardia-Watson-Wheeler [MWW] test:  $W = 2.02$ ,  $p = 0.73$ ), and the pooled sample had a mean direction of  $\alpha = 42^\circ$  (95% confidence interval  $19^\circ$ – $64^\circ$ ),  $r = 0.46$ ,  $n = 52$ , and  $p < 0.001$  (Figure 2D).

The mean vectors shown by the same individuals after displacement to the vicinity of Moscow were  $\alpha = 342^\circ$ ,  $r = 0.50$ ,  $n = 13$ , and  $p = 0.035$  in 2004;  $\alpha = 345^\circ$ ,  $r = 0.42$ ,  $n = 14$ , and  $p = 0.08$  in 2005; and  $\alpha = 322^\circ$ ,  $r = 0.36$ ,  $n = 25$ , and  $p = 0.036$  in 2007 (Figures 2E–2G). The 3 years were not significantly different from each other (MWW test:  $W = 1.88$ ,  $p = 0.76$ ), and the pooled sample showed a mean direction of  $\alpha = 334^\circ$  (95% confidence interval  $308^\circ$ – $360^\circ$ ),  $r = 0.41$ ,  $n = 52$ , and  $p < 0.001$  (Figure 2H). The 95% confidence intervals of the pooled samples before and after the displacement did not overlap, and MWW test also indicated a highly significant difference between the orientation of the birds before and after displacement ( $W = 14.16$ ,  $p < 0.001$ ).

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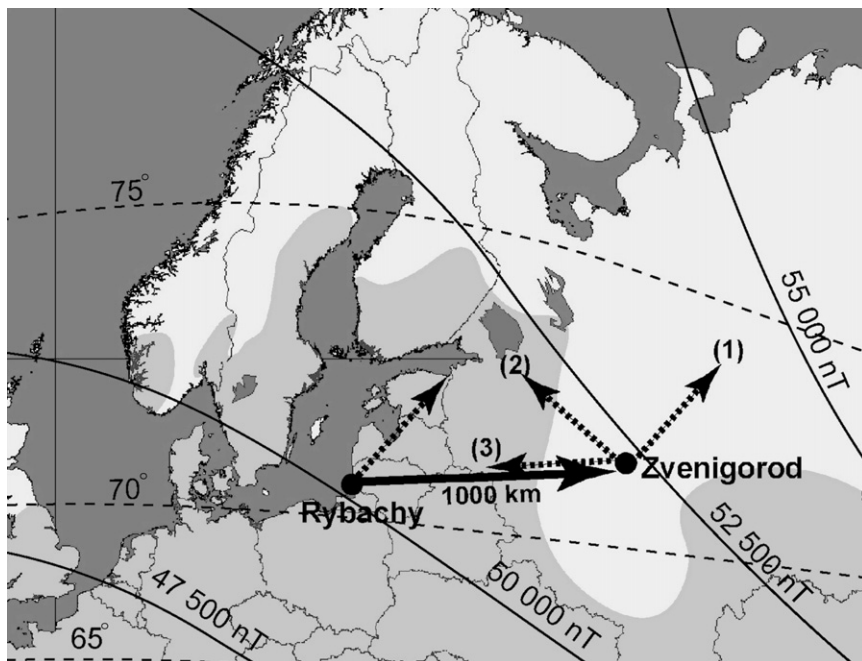


Figure 1. Position of the Study Sites with Isolines of Geomagnetic-Field Total Intensity and Inclination

Map of capture (Rybachy, Kaliningrad region) and displacement (Zvenigorod, Moscow region) sites and the breeding range of Eurasian reed warblers in the region (shaded light gray). Solid arrow shows the displacement direction. The broken arrow at the capture site shows the mean migratory direction, and the broken arrows at the displacement sites show our working hypotheses: (1) no compensation, (2) compensation toward the breeding destinations, and (3) compensation toward the capture site. Solid and broken lines represent the isolines of geomagnetic-field total intensity and inclination, respectively.

Eurasian reed warblers displaced toward the east from their migratory route during spring migration and located southeast of their presumed migratory destinations apparently compensated for the displacement when tested under the natural starry sky in the natural magnetic field. In other words, Eurasian reed warblers seem to be able to perform true bicoordinate navigation during spring migration, i.e., to find their goal without a direct sensory contact with it [25]. By transporting the birds by air, we excluded the possibility that they might have used some positional information for path integration. Our findings refer to birds that were completing their return journey in spring and therefore do not challenge the concept of clock-and-compass strategy in naive first-autumn migrants [5, 12, 26]. Our results are at variance with those by Rüppel [8], who displaced hooded crows (*Corvus corone cornix*) captured during spring migration toward the west. Recoveries suggested

that crows did not correct for displacement but moved in parallel to their normal spring migratory route. However, it should be emphasized that hooded crows are short-distance daytime migrants, whereas our experiments involved a long-distance nocturnal migrant. In contrast, our data are in agreement with recent study performed on experienced white-crowned sparrows during autumn migration [27]. This work strongly suggested that adult migrants in the wild can navigate toward their wintering ground even after an east-west, crosscontinental displacement of about 3000 km toward the east. Taken together, this study and that of Thorup et al. [27] suggest that experienced, night-migratory songbirds can perform true navigation. One possibility is that they use the geomagnetic information. In western Russia, where our experiment was performed, it could potentially be used for longitude identification: total intensity and inclination of the geomagnetic-field changed by approximately 3% between Rybachy and Zvenigorod (Figure 1). Another possibility is that birds determine their east-west position on the basis of time lag: Piggins and Loudon [23] have shown that the circadian clock in the suprachiasmatic nucleus

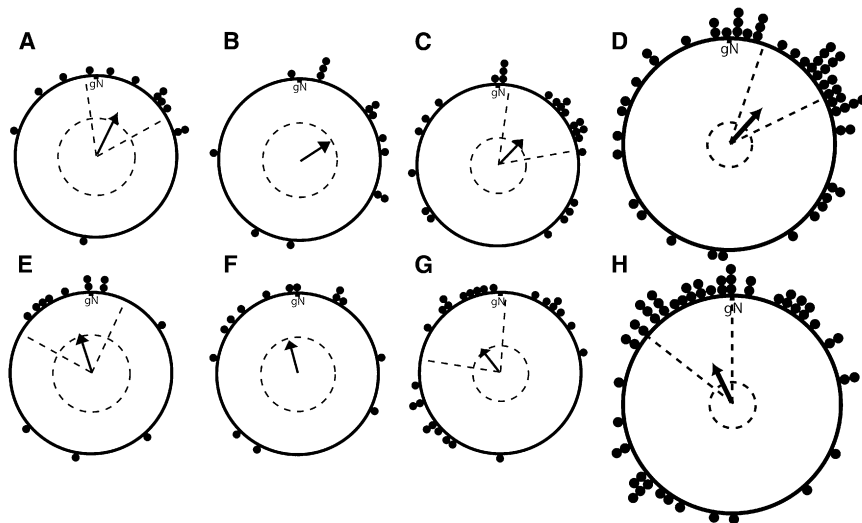


Figure 2. Orientation of Eurasian Reed Warblers during Spring Migration Before and After West-East Displacement

Orientation of Eurasian reed warblers tested at the site of capture during spring migration (A–D) and after displacement 1000 km to the east of the capture site (E–H). All birds were tested in the local geomagnetic field under starry sky. (A–C) Orientation of the experimental birds at the Courish spit in 2004 (A), 2005 (B), and 2007 (C). (D) Pooled orientation of the experimental birds at the capture site. (E–G) Orientation of the experimental birds displaced to the Moscow region in 2004 (E), 2005 (F), and 2007 (G). (H) Pooled orientation of the experimental birds after displacement. Each dot at the circle periphery indicates the mean orientation of one individual bird, arrows show mean bearings, the dashed circle indicates the radius of the group mean vector needed for significance ( $p < 0.05$ ) according to the Rayleigh test of uniformity, and dashed lines give 95% confidence intervals of group mean vectors.

of mammals consists of two substructures, with a ventral core shifting almost immediately after a clock shift and a dorsal shell lagging behind. This difference, if it were possible for individual animals to measure it, would provide the necessary information on the direction and amount of time change and thus indirectly work as a dual-clock system would do. To show what cues the birds use to determine their east-west location will be a big challenge for researchers in this field in the years to come.

#### Experimental Procedures

We captured Eurasian reed warblers at Rybachy (southeastern Baltic coast), tested them in cage experiments, and subsequently displaced them by air to Zvenigorod near Moscow, 1004 km toward the east. We recorded the birds' orientation at the capture site and at the displacement site with Emlen cages. Further information on experimental sites and procedures is given in Figure 1 and in the Supplemental Data available online.

#### Supplemental Data

Experimental Procedures are available at <http://www.current-biology.com/cgi/content/full/18/3/188/DC1/>.

#### Acknowledgments

We are most grateful to Valery M. Gavrilov and Vadim V. Gavrilov, who allowed us to use the facilities of Zvenigorod Biological Station of Moscow State University. Constructive criticism by two anonymous reviewers helped us to improve an earlier draft. Financial support for this study was made available by Heinz Sielmann Foundation, Russian Foundation for Basic Research (grant number 08-04-00242), Russian Science Support Foundation (to N.C.), International Graduate School for Neurosensory Science and Systems (grant and Ph.D. scholarship to D.K.), and a VW-Nachwuchsgruppe and Lichtenberg Grant (to H.M.).

Received: November 1, 2007

Revised: January 14, 2008

Accepted: January 14, 2008

Published online: January 31, 2008

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