RESEARCH ARTICLE

Not all songbirds calibrate their magnetic compass from twilight cues: a telemetry study

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SUMMARY

Migratory birds are able to use the sun and associated polarised light patterns, stellar cues and the geomagnetic field for orientation. No general agreement has been reached regarding the hierarchy of orientation cues. Recent data from naturally migrating North American *Catharus* thrushes suggests that they calibrate geomagnetic information daily from twilight cues. Similar results have been shown in caged birds in a few studies but not confirmed in others. We report that free-flying European migrants, song thrushes *Turdus philomelos*, released after pre-exposure to a horizontally rotated magnetic field, do not recalibrate their magnetic compass from solar cues, but rather show a simple domination of either the magnetic or the stellar compass. We suggest that different songbird species possess different hierarchies of orientation cues, depending on the geographic and ecological challenges met by the migrants.

Key words: migration, birds, orientation, cue calibration.

INTRODUCTION

As early as the 1970s, it became clear that migratory birds are able to use three different reference systems for orientation: the sun and associated polarised light patterns (Kramer, 1950; Moore, 1987; Cochran et al., 2004), stellar cues (Emlen, 1975) and the geomagnetic field (Wiltschko and Wiltschko, 1972; Wiltschko and Wiltschko, 2009). The information from these apparently redundant orientation cues must be integrated.

Most experiments designed to determine the relative importance of compass mechanisms (cue conflict experiments) have been performed in captivity and have resulted in contradictory data. For instance, outcomes of some studies suggest that celestial cues calibrate the avian magnetic compass (Able and Able, 1995a; Able and Able, 1995b); however, other data indicate that migratory birds either calibrate their celestial compass by the geomagnetic field (Bingman and Wiltschko, 1988; Wiltschko et al., 1999; Wiltschko et al., 2001; Sandberg et al., 2002) or, alternatively, show domination of the magnetic compass without any calibration (Sandberg et al., 2002). Thus, no general agreement has been reached regarding the hierarchy of orientation cues (Muheim et al., 2006a; Wiltschko and Wiltschko, 2009). A possible explanation for this discrepancy is that different researchers used different experimental cue conflict designs in terms of the age of the birds tested, cue availability, season and duration of exposure to a cue conflict situation. Additionally, when we consider any orientation data obtained by the Emlen funnel method, we should take into account the fact that (i) not every kind of activity in Emlen cages represents migratory restlessness and, therefore, only second-order individual directions, i.e. those averaged over many orientation tests, can bring biologically relevant data about actual orientation in the wild, and (ii) in an orientation cage a bird has access to a simplified cue environment that may cause artefacts, e.g. phototactic responses.

A growing community of avian biologists supports the idea that cue hierarchy hypotheses should be qualified in the wild on naturally behaving bird migrants. Miniature radio transmitters can help realise this proposal.

To date, the only study performed on naturally migrating radio-tagged birds showed that migratory birds can calibrate their magnetic compass from twilight cues (Cochran et al., 2004). This study has been welcomed and repeatedly cited because of its clear-cut design and conclusions. Results similar to these (Cochran et al., 2004) have recently been found for caged birds in some studies (Muheim et al., 2006b; Muheim et al., 2007; Muheim et al., 2009) but have not been confirmed in others (Wiltschko et al., 2008; Gaggini et al., 2010). Therefore, there is an obvious demand for more field-based cue conflict experiments on different bird migrant species, first, to validate lab-derived cue hierarchy hypotheses and second, to qualify the notion that all bird migrants use a common strategy of cue calibration.

Here, we report the results of the first cue conflict study made on naturally migrating European bird migrants, song thrushes *Turdus philomelos*. In our experiment, we tested the following hypotheses. (i) The magnetic compass is calibrated from twilight celestial cues as shown in the only previous telemetry study (Cochran et al., 2004) (Fig. 1A). (ii) Either magnetic or stellar cues are used separately without transferring reference information to others (simple domination, Fig. 1B). (iii) The stellar compass is calibrated from the magnetic field (Fig. 1C).

MATERIALS AND METHODS
Experimental setup, test animals and release sites

Our experimental setup was similar to that of the previous telemetry study (Cochran et al., 2004): experimental birds (*T. philomelos*, C. L. Brehm 1831) were put into an artificial magnetic field with
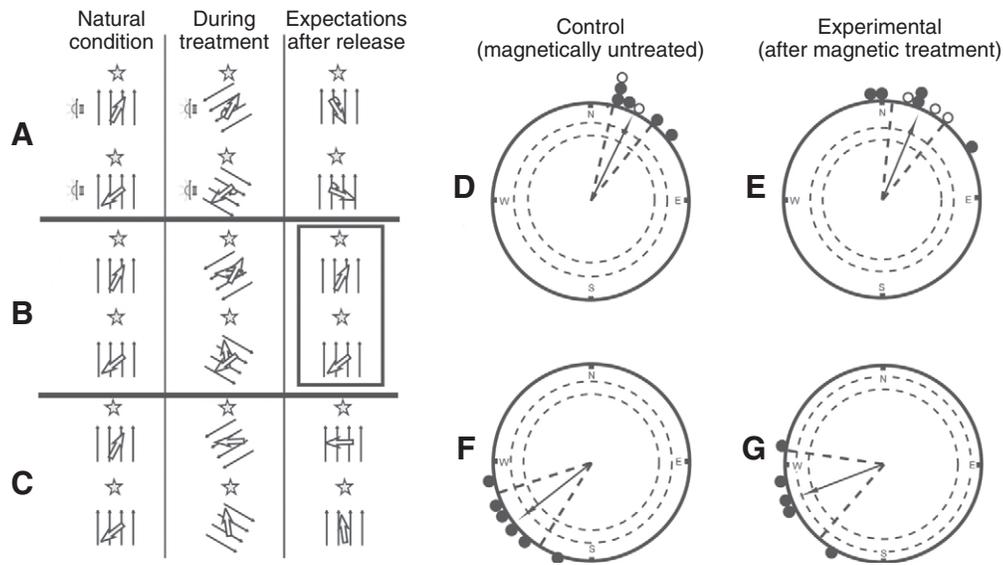
Fig. 1. Predicted orientation responses and results of orientation tests. (A–C) Predicted responses of birds treated with an altered magnetic field according to the proposed hypotheses in autumn (magnetic field deflected 120 deg clockwise) and spring (the magnetic field deflected 120 deg anticlockwise). (A) The magnetic compass is calibrated from twilight celestial cues as previously shown for naturally migrating North American migrants (Cochran et al., 2004). (B) Either the magnetic or the stellar cues are used separately without transferring reference information to other compasses (simple domination). (C) The stellar compass is calibrated from the magnetic field. The case fitting our data is in the rectangle. (A–C) The four thin parallel arrows represent the horizontal direction of the (geo)magnetic field experienced by the birds. The filled half-circle with rays represents the unchanged directional information from the setting sun including polarisation light pattern. The star represents unchanged directional information from the stellar cues. The open arrows represent the expected directions for the birds. (D–G) Bearings of song thrushes kept in the ambient magnetic field (spring D, autumn F) and in the magnetic field deflected 120 deg counterclockwise (spring E) or clockwise (autumn G) prior to release. (D) 26 deg (N=7, r=0.97, P<0.001, 95% confidence interval CI 13–39 deg). (E) 23 deg (N=8, r=0.94, P<0.001, 95% CI 6–39 deg). (F) 232 deg (N=6, r=0.95, P<0.001, 95% CI 212–252 deg). (G) 249 deg (N=5, r=0.92, P=0.006, 95% CI 221–278 deg). Each circle on the circle periphery represents the bearing of the last point at which the bird's radio signal was detected. Filled circles represent data from Rybachy (on the Baltic coast); open circles represent data from Melnikovo (inland). The arrow represents the mean group vector. The inner and outer dashed circles represent the radius of the group mean vector needed for significance (P<0.05 and P<0.01, respectively). The two radial dashed lines flanking the group mean vector represent CI.

magnetic north deflected 120 deg anticlockwise (in spring) or clockwise (in autumn). Control birds experienced the natural magnetic field. All birds were radio tagged. If a bird took off on the night of release, the bearing of the last point at which the bird's radio signal was detected was scored as the departure direction. The distance at which the radio signal vanished was at least 15 km (air to ground signal reception range of our radio transmitters).

All song thrushes were captured during the autumn and spring passage in Rybachy, Kaliningrad Region, Russia (55°09′N, 20°44′E). In autumn, we only tested hatching-year birds; in spring, only second calendar year birds were included. From just after capture until release, all thrushes were kept in cages situated in an outdoor aviary provided with all known orientation cues for several days (at least 1 week) so that the birds could get accustomed to captivity. Thrushes were supplied with food (meal worms) and water *ad libitum*. The birds were regularly weighed and their subcutaneous fat deposits, an important sign of migratory disposition, were checked. To increase the chances of migratory flight on a release night, we chose birds that were most likely to be in migratory condition, i.e. only thrushes that had not lost weight, or had even gained it, and had relatively large fat deposits (subcutaneous fat score ≥2) (Kaiser, 1993).

We performed most of our release tests at the capture site located on the Courish Spit, which is 98 km long, 1–2 km wide and runs from SW to NE (Fig. 2). Several releases were performed on the mainland in Melnikovo, south of the Courish Spit (54°53′N, 20°26′E) to test whether our experimental birds were following the spit, i.e. using landmarks and not a global cue (solar, stellar or geomagnetic) for orientation.

Magnetic coil system and radio transmitters

We used a custom-built magnetic coil system produced by the Pushkov Institute of Terrestrial Magnetism, Ionosphere and Radio Wave Propagation (Russian Academy of Sciences, St Petersburg). The coil was a cuboid with 1 m sides; the release cage was put in the centre of the coil system, so that the artificial magnetic field was uniform within the space available to the experimental birds.

We used radio transmitters (PD-2, Holohil Systems Ltd, Carp, ON, Canada) that allowed us to follow the birds during flight for at least 15 km (air to ground signal reception range) and to record vanishing directions. Transmitters were fitted to their backs *via* a leg-loop harness [a Rappole–Tipton style harness (Rappole and Tipton, 1991)].

Release procedure

Each test night, we released one experimental and one control song thrush. One hour before local sunset, experimental birds were put into a magnetic coil system, whereas control birds were placed into a simulated magnetic coil system made of wood, so that they experienced the natural magnetic field. As they were put in a release cage, the thrushes, which were already accustomed to captivity, quickly calmed down and outwardly were not stressed during the cue conflict treatment. Release cages were placed outdoors, giving the birds a very good view of the sky down to the horizon during the magnetic treatment. All releases were performed when <50% (usually <20%) of the sky was covered by clouds.

We released all birds using a string and pulley setup to gently open the lid of each release cage. Unlike Cochran and colleagues,
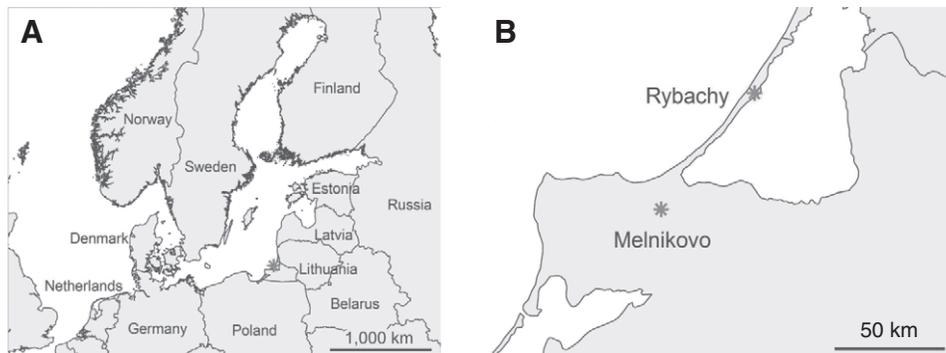
Fig. 2. (A) Map of the study area. The asterisk depicts the place where release sites are situated. (B) The positions of the release sites: Rybachy (on the Courish Spit) and Melnikovo (inland).

who physically threw Swainson's and grey-cheeked thrushes (*Catharus ustulatus*, *C. minimus*) into the air (Cochran et al., 2004), we found that song thrushes thrown into the air invariably grounded in the nearby scrub and did not embark on migratory flight. Therefore, all our birds took off from inside the coil system for their flights unassisted.

All releases took place when the Sun's disc was 12 deg below the horizon, i.e. after the end of nautical twilight. By then, most stars were clearly visible and all traces of polarised light had disappeared from the sky (Cochran et al., 2004), so it was no longer possible for the birds to recalibrate their compasses by the polarised light pattern, and stellar orientation cues were fully available.

RESULTS

Song thrushes in our experiment chose a seasonally appropriate migratory direction regardless of whether they had been subjected to the magnetic treatment prior to release or not, both in autumn and spring. The confidence intervals of the groups overlapped in both seasons, and group mean directions showed no significant difference: Watson–Williams test, spring: $F_{1,13}=0.108$, $P=0.75$; autumn: $F_{1,9}=1.588$, $P=0.24$ (Fig. 1D–G). The 95% confidence intervals of the mean vanishing directions shown by song thrushes following magnetic treatment did not include the mean direction of the control birds deflected by 120 deg either clockwise or counterclockswise that would be expected if the birds calibrate their compasses (Fig. 1A,C). Therefore, the hypothesis that song thrushes, like other free-flying nocturnal songbird migrants tested so far, calibrate their magnetic compass from celestial twilight cues (Cochran et al., 2004; Muheim et al., 2006b; Muheim et al., 2007; Muheim et al., 2009) is not supported; instead, the hypothesis of the magnetic (Wiltschko et al., 2008; Gaggini et al., 2010) or stellar compass dominating is confirmed.

In autumn, the mean migratory direction of song thrushes (232 deg according to our data from control, i.e. magnetically untreated, song thrushes; 222 deg from moon-watching observations on medium-sized songbirds in their natural nocturnal migratory flight) (Bolshakov et al., 2002) is practically parallel to the Courish Spit. So the Courish Spit could therefore be a leading line for migrating thrushes. In spring, the mean direction of free-flying song thrushes is 42 deg (Bolshakov et al., 2002), which differs from the direction of the spit (24 deg). However, in spring the control song thrushes released in Rybachy followed almost the exact direction of the spit (28 deg, $N=5$, $r=0.96$, 95% confidence interval CI 9–47 deg). To test whether our experimental birds were following the spit, we performed spring releases in Melnikovo, on the mainland. Two control song thrushes released there had vanishing directions of 15 and 25 deg; three birds released from the deflected field environment disappeared towards 30, 40 and 15 deg. The

bearings of these birds are shown by open circles in Fig. 1D,E. From these results, we conclude that identical bearings of experimental and control song thrushes did not result from the leading effect of the Courish Spit. Therefore, we pooled the data from the two release sites, i.e. from Rybachy on the Courish Spit and Melnikovo on the mainland.

DISCUSSION

Our results obtained from free-flying birds strongly suggest that neither first-year nor adult song thrushes use the same routine of cue calibration as Swaison's and grey-cheeked thrushes do (Cochran et al., 2004), i.e. song thrushes do not calibrate their magnetic compass from the twilight sunset but, rather, use the geomagnetic or stellar cues alone (simple domination strategy).

One possible explanation for our results may be a biasing influence of the landscape of the Courish Spit on vanishing directions of the birds. However, this explanation is very unlikely because we did not find differences between the results obtained at the Courish Spit and inland, in Melnikovo. It might also be that the thrushes captured at the Courish Spit and released on the mainland, in Melnikovo, might be local birds that, after release, performed homing towards the capture site, not a migratory flight. However, all birds that took off from Melnikovo were fat (see our selection criteria in Materials and methods) and departed by a nocturnal flight, i.e. they were in a migratory disposition (Dolnik, 1975), and probably had a significant distance to go to their breeding sites. We never recorded signal from transmitters of mainland-released song thrushes in Rybachy in subsequent days, and we assume that they significantly overshot Rybachy before ceasing flight. Generally, displaced migrants are known to head towards the goal of their journey, not towards the capture site (Thorup et al., 2007; Chernetsov et al., 2008); the distance between our two release sites, 40 km, was such that the possible difference in direction towards migratory destinations was below the resolution of our method for estimating vanishing directions. Thus, we suggest that song thrushes displaced to the mainland and released there were unlikely to be heading towards the capture site (i.e. towards Rybachy, Fig. 2) and instead were continuing migration towards their, probably distant, breeding destination.

We intentionally used the same cue conflict treatment as in the study of Cochran and colleagues (Cochran et al., 2004). However, there are two differences between our experiment and theirs: (i) we did not follow the released birds but, rather, used vanishing directions on the basis of the last radio signal detected, which was 15 km from the release sites according to the air to ground signal reception range for the radio transmitters we used; and (ii) we used both first-year (in autumn migration) and adult (in spring migration) birds to test the age and season dependency of their cue calibration

strategy. However, we did not find any differences between the ages or seasons.

Our data suggest that one should be cautious when generalising results obtained from individual species to other bird migrants. Simple domination of the magnetic or celestial compass has been found in some orientation cage studies (Wiltschko et al., 2008; Gaggini et al., 2010), whereas different variants of cue calibration have been reported both from the few experiments with free-flying migrants (Cochran et al., 2004; Sandberg and Moore, 1996; Sandberg et al., 2000) and from cage-based tests (Muheim et al., 2006b). It has been suggested that celestial information is given the greatest salience during the pre-migratory period, so it calibrates geomagnetic information in cue conflict, whereas the geomagnetic compass calibrates celestial cues during migration (Wiltschko et al., 1997; Wiltschko and Wiltschko, 1999). An alternative explanation of the observed variation is that the crucial factor is the unrestricted view of the sky down to the horizon rather than the season of exposure to the cue conflict (pre-migratory *vs* migratory) (Muheim et al., 2006a).

We suggest that these varying results could, at least in part, be caused by the variability of cue interactions between different species or maybe even between populations of the same species. Such cue calibration opportunism may arise through different geographic, geomagnetic and ecological situations encountered by avian migrants, with migratory routes of some species or populations demanding more advanced orientation capacities than are sufficient for others. Following Sandberg and Moore (Sandberg and Moore, 1996), we would like to emphasise the importance of ecological context for correct interpretation of the results of orientation tests with migrating birds. Avian species that migrate long distances and have to cross ecological barriers may require very precise orientation capacities: e.g. for bar-tailed godwits (*Limosa lapponica baueri*) that migrate non-stop between Alaska and New Zealand (Gill et al., 2009), an orientation error of a couple of degrees may prove fatal. In contrast, hatching-year song thrushes breeding in northern Europe and wintering in south-western Europe (Bolshakov et al., 2002; Payevsky et al., 2005) may suffer no costs if they deviate from their inherited autumn migratory direction by several degrees. As complex behavioural traits are only supported by natural selection if they provide significant evolutionary benefits, it is possible that such species use simpler orientation rules.

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