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RESEARCH ARTICLE

Migratory blackcaps tested in Emlen funnels can orient at 85 degrees but not at 88 degrees magnetic inclination

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ABSTRACT

Migratory birds are known to use the Earth's magnetic field as an orientation cue on their tremendous journeys between their breeding and overwintering grounds. The magnetic compass of migratory birds relies on the magnetic field's inclination, i.e. the angle between the magnetic field lines and the Earth's surface. As a consequence, vertical or horizontal field lines corresponding to 0 or 90 deg inclination should offer no utilizable information on where to find North or South. So far, very little is known about how small the deviations from horizontal or vertical inclination are that migratory birds can detect and use as a reference for their magnetic compass. Here, we asked: what is the steepest inclination angle at which a migratory bird, the Eurasian blackcap (*Sylvia atricapilla*), can still perform magnetic compass orientation in Emlen funnels? Our results show that blackcaps are able to orient in an Earth's strength magnetic field with inclination angles of 67 and 85 deg, but fail to orient in a field with 88 deg inclination. This suggests that the steepest inclination angle enabling magnetic compass orientation in migratory blackcaps tested in Emlen funnels lies between 85 and 88 deg.

KEY WORDS: Bird navigation, Magnetic inclination compass, Functional range, Magnetoreception, Radical-pair mechanism, *Sylvia atricapilla*

INTRODUCTION

For 50 years, it has been known that birds are able to use the Earth's magnetic field for orientation (Merkel and Wiltschko, 1965). In contrast to a man-made compass that works on the basis of the polarity of the magnetic field, the bird's magnetic compass is an inclination compass (Wiltschko and Wiltschko, 1972; Wiltschko and Wiltschko, 1995). This means that birds do not differentiate between North and South but between poleward and equatorward (the direction in which the field lines and the Earth's surface form the smaller angle is defined as equatorward) (Wiltschko and Wiltschko, 1972; Wiltschko and Wiltschko, 1995). Therefore, at the magnetic equator or at the magnetic poles, where the inclination is 0 and 90 deg, respectively, the birds are faced with the problem that the Earth's magnetic field provides no or ambiguous directional information. In other words, there is no larger or smaller inclination angle to detect. Wiltschko and Wiltschko (Wiltschko and Wiltschko, 1992) suggested that for transequatorial migrants, the crossing of the equator serves as a trigger and changes the heading from equatorward to poleward. Cochran et al. (Cochran et al., 2004) suggested that the magnetic compass can be calibrated by celestial cues and that this mechanism might help birds to cross the magnetic equator. Even with these suggestions, an interesting question remains: how wide is the range around the magnetic poles and the magnetic equator where the birds are unable to use their magnetic compass?

Earlier studies showed that migratory wheatears (*Oenanthe oenanthe*) displaced from Sweden (70 deg inclination) to Greenland (81 deg inclination) were still able to orient even under total overcast conditions (Sandberg et al., 1991). Furthermore, Gambel's white-crowned sparrows (*Zonotrychia leucophrys gambelii*) tested in Emlen funnels in the wild were oriented at locations with natural inclination angles up to 88.6 deg, but failed to orient at 89.7 deg inclination (Akesson et al., 2001). We wanted to complement these field-based studies by performing experiments under controlled, constant laboratory conditions. We performed our experiments with Eurasian blackcaps, as the Eurasian blackcap is an iconic species in the study of migration (Berthold et al., 1992; Helbig, 1996; Berthold, 1999), and because it has a more southerly range than the white-crowned sparrows that Akesson and colleagues (Akesson et al., 2001) studied.

Knowing how steep an inclination angle migratory birds can use for magnetic compass orientation under laboratory conditions in Emlen funnels is also important, because 'vertical' fields have often been used in earlier studies whenever a magnetic condition was required that should not provide directional information to the birds (e.g. Bingman, 1987; Able and Able, 1997). But how vertical does a field actually have to be to provide no directional information to the tested birds? This question is particularly relevant because vertical magnetic fields produced by coil systems will inevitably be vertical only in the exact centre of the coils. Birds placed in funnels not located in the exact centre of the coil system would be exposed to magnetic conditions with inclinations, which systematically deviate from 90 deg (Kirschvink, 1992; Mouritsen, 1998). Depending on the dimensions of the coil system used (the bigger and more accurately built the better) and on the number of orientation cages placed simultaneously in each coil system, these deviations from the vertical can become important, so that the birds might in fact have been able to use their magnetic inclination compass in the vertical field condition. Consequently, random orientation might appear, not because no useful magnetic information was available to the birds, but because the magnetic field information pointed in different directions during different tests.

Taking the unavoidable heterogeneities created by any coil system into account becomes particularly important when one wants to test birds' abilities to orient in magnetic fields with very steep inclinations, as even small heterogeneities in the created fields can flip the inclination across the 90 deg point, and thus create a field that should guide the birds in a completely different direction. Hence, the aim of the present study was to use a very accurate, three-dimensional, Merritt four-coil per axis system (Zapka et al.,

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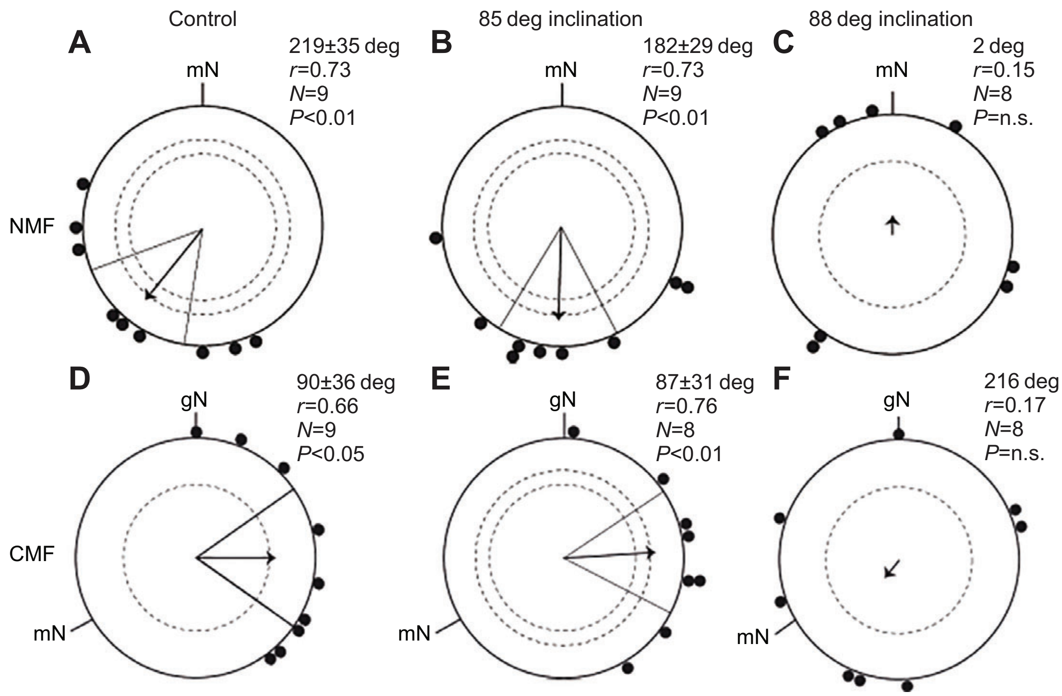

Fig. 1. The orientation of individual blackcaps was tested in magnetic fields with 67, 85 or 88 deg inclination. The birds headed in their appropriate autumn migratory direction towards the Southwest in the naturally directed magnetic field (NMF) with 67 deg (control, A) and 85 deg (B) inclination, and they responded appropriately to a −120 deg horizontal turn of the fields with 67 deg (D) and 85 deg (E) inclination. In contrast, the birds were disoriented in both the normally directed (C) and the −120 deg turned (F) field when the inclination angle was set to 88 deg. mN, magnetic North; gN, geographical North. The arrows indicate the group mean vectors. The inner and outer dashed circles indicate the length of the group mean vector needed for significance according to the Rayleigh test ($P<0.05$ and $P<0.01$, respectively). The lines flanking the group mean vector indicate the 95% confidence intervals for the group mean direction.

2009; Hein et al., 2010) to investigate whether night-migratory blackcaps, *Sylvia atricapilla* (Linnaeus 1758), can use their magnetic compass in a field with 85 and 88 deg inclination angle when they are tested in Emlen funnels inside an electromagnetically screened (Engels et al., 2014) wooden hut without access to any celestial cues.

RESULTS

A group of very well-oriented blackcaps was tested in a magnetic field, which corresponded to the local geomagnetic field [Fig. 1A, control, normal magnetic field (NMF), 67 deg inclination]. They oriented significantly towards their appropriate autumn migratory direction (group mean orientation 219±35 deg, length of the group mean vector r=0.73, N=9, P<0.01, Rayleigh test; Fig. 1A), and significantly turned their orientation as predicted when the horizontal component of the field was turned 120 deg counter-clockwise [group mean orientation 90±36 deg, r=0.66, N=9, P<0.05; Fig. 1D, control, changed magnetic field (CMF), 67 deg inclination]. Their orientation direction was significantly different in the NMF and CMF, as indicated by the lack of overlap of the 95% confidence intervals.

When the inclination was increased to 85 deg, the birds' magnetic compass orientation capabilities were unaffected (Fig. 1B, NMF, group mean orientation 182±29 deg, r=0.73, N=9, P<0.01; Fig. 1E, CMF, group mean orientation 87±31 deg, r=0.76, N=8, P<0.01). The birds' change of orientation between the NMF and the CMF conditions was significant [Watson–Williams F-test (WW): F=24.005, d.f.=1, P<0.001 in the control condition and F=16.152, d.f.=1, P=0.001 for the 85 deg inclination condition]. The orientation was not significantly different under 67 and 85 deg inclination in the NMF (WW: F=2.593, d.f.=1, P=0.127) or in the CMF (WW: F=0.019, d.f.=1, P=0.892) (Batschelet, 1981). The Mardia–Watson–Wheeler (MWW) test confirms these findings (MWW: χ^2=14.664, d.f.=1, P<0.001 in the control condition and χ^2=8.044, d.f.=1, 0.005>P>0.001 for the 85 deg inclination condition, between NMF and CMF, respectively; χ^2=0.985, d.f.=1, 0.5>P>0.25 between NMF 67 deg and NMF 85 deg; χ^2=2.601, d.f.=1, 0.25>P>0.1 between CMF 67 deg and CMF 85 deg) (Batschelet, 1981).

However, when the birds were tested in the magnetic field with an inclination of 88 deg, the birds' orientation was random (Fig. 1C, NMF, group mean orientation 2 deg, r=0.15, N=8, P=0.824; Fig. 1F, CMF, group mean orientation 216 deg, r=0.17, N=8, P=0.738).

During the experiments, we continuously measured the horizontal direction, the inclination angle and the total magnetic field strength that our birds experienced. The magnetic field recordings documented that the magnetic fields our coils produced were extremely accurate and consistent throughout the test periods (see Table 1).

DISCUSSION

Our experiments show that blackcaps tested in Emlen funnels (Emlen and Emlen, 1966; Mouritsen et al., 2009) are able to orient at an inclination of up to 85 deg, but fail to orient at an inclination angle of 88 deg at magnetic field intensities around 49,300 nT (local magnetic field of Oldenburg, Germany). Therefore, a deviation of 5 deg from the vertical still seems to enable blackcaps to use their magnetic inclination compass to choose and maintain migratory orientation in a similar direction and with a similar precision to those at 67 deg inclination (the direction and length of the group mean vector was similar when the same birds were tested with 67 and 85 deg inclination).

Table 1. Variability in the experimental magnetic fields used in the present study

	Magnetic inclination (deg)	Magnetic declination (horizontal polarity) (deg)	Magnetic field intensity (Flux density) (nT)
Control			
Coil center	67.52±0.2	0.005±0.022	49,397±66
All positions	67.7±0.2	0.16±0.55	49,329±53
Condition 85 deg			
Coil center	85±0.02	0.08±1.19	49,257±75
All positions	84.9±0.3	−0.98±2.11	49,275±62
Condition 88 deg			
Coil center	88±0.02	0.12±2.86	49,281±81
All positions	88.0±0.3	−2.7±5.3	49,257±14

Data are means ± s.d.
Coil center: during 10 conducted experiments of condition 85 deg and 88 deg, a magnetometer probe was positioned directly under the test arena in the middle of the coil system, enabling a continuous recording of the displayed magnetic field components. All positions: the displayed magnetic field components of all funnel positions within the test arena were measured and registered after the experiments ended each night.

This is impressive, as it means that their magnetic compass sensory system (Ritz et al., 2000; Mouritsen et al., 2005; Heyers et al., 2007; Zapka et al., 2009; Rodgers and Hore, 2009; Treiber et al., 2012; Mouritsen and Hore, 2012) must be able to either distinguish minute angle differences relative to gravity or detect minute differences in the strength of the horizontal component of the magnetic field relative to the vertical component of the same field. How small these differences are can be illustrated with a few simple biological and trigonometrical considerations.

No matter how the birds' magnetic compass is working, somewhere in the nervous system, the projection of the magnetic vector onto the horizontal (Earth surface) plane or the exact inclination angle relative to gravity needs to be determined in one form or another as the bird must orient in a compass direction that is defined in the Earth surface (horizontal) plane or relative to gravity. Therefore, the Cartesian coordinate system is useful for a principle illustration of why it should be very difficult to determine a migratory direction accurately in a geomagnetic field with very steep inclination. Furthermore, the mean migratory directions seem to be quite precisely inherited (Berthold et al., 1992; Helbig, 1996; Berthold, 1999) and birds' spatiotemporal orientation programs (Mouritsen and Mouritsen, 2000; Mouritsen, 2003) often involve finer changes in migratory directions along their migratory route (Gwinner and Wiltschko, 1978; Helbig et al., 1989; Liechti et al., 2012). It is therefore important to realize that it would most likely not suffice if a magnetic compass sense only distinguishes North from South. Exactly how precisely a night-migratory songbird needs to determine its migratory direction with its magnetic compass in the wild is not known. However, for the purpose of illustration (Fig. 2), we consider two situations: one requiring that birds can determine the difference between North and 15 deg and one requiring that birds can determine the difference between North and 30 deg. In the following calculations, we only consider difficulties originating from the sensory system itself. In nature, additional spread in actual compass headings will be caused by weather, topography, etc.

First, we consider the putative situation where the horizontal component (that is, the projection of the magnetic vector onto the horizontal X–Y plane) is either measured directly by the birds' magnetic sensors or calculated somewhere in the brain. One can visualize the consequences of this by comparing the 'North component' of the projection of the geomagnetic field vector on to the horizontal plane when the bird with its magnetic sensors points towards North with the same value when the bird with its sensors points 15 or 30 deg left or right of North (see Fig. 2).

At 85 deg magnetic inclination, the horizontal component of the field pointing towards North is:

$$x = \cos(\alpha)B\,, \tag{1}$$

where α is the magnetic inclination angle (85 deg) and B is the magnetic field strength (49,300 nT in Oldenburg). Thus, in a 49,300 nT field with 85 deg inclination, x is 4297 nT.

If the bird with its sensors heads 15 deg away from North, x' will be:

$$x' = \cos(\beta)x\,, \tag{2}$$

where β is the horizontal deviation angle (here, 15 deg) from North. Thus, in a 49,300 nT field with 85 deg inclination, x' is 4150 nT. The change (Δx) in the horizontal magnetic field component is:

$$\Delta x = x - x'\,, \tag{3}$$

and therefore just 147 nT in a 49,300 nT field with 85 deg inclination.

At 88 deg inclination, the horizontal component of the field pointing towards North (x in Fig. 2) is 1720 nT, and when the bird with its sensors turns towards 15 deg, it is 1662 nT. The change (Δx) in the horizontal component of the field that would need to be measured is just 58 nT. The values of Δx if we allow for a 30 deg error in the birds' magnetic compass heading are 576 and 231 nT, respectively, at 85 and 88 deg inclination.

Second, we consider the putative situation where the inclination angle relative to gravity is either measured directly by the birds' magnetic sensors or calculated somewhere in the brain. One can visualize the consequences of this by comparing the inclination angle of the geomagnetic field vector when the bird with its magnetic sensors heads towards North with the same value when the bird with its sensors heads 15 or 30 deg left or right of North (see Fig. 2).

The inclination angle (α′) that would be measured if the bird with its magnetic sensors heads 15 deg away from North is:

$$\alpha' = \tan^{-1}\left(\frac{\tan(\alpha)}{\cos(\beta)}\right), \tag{4}$$

which is 85.17 deg for α=85 deg and β=15 deg, and the difference (Δα) from the magnetic inclination (α) experienced if the bird with its magnetic sensors heads towards magnetic North is given by:

$$\Delta\alpha = \alpha' - \alpha\,; \tag{5}$$

that is, just 0.17 deg. Using the same logic, the change in inclination angle (Δα) measured if the bird with its magnetic sensors heads

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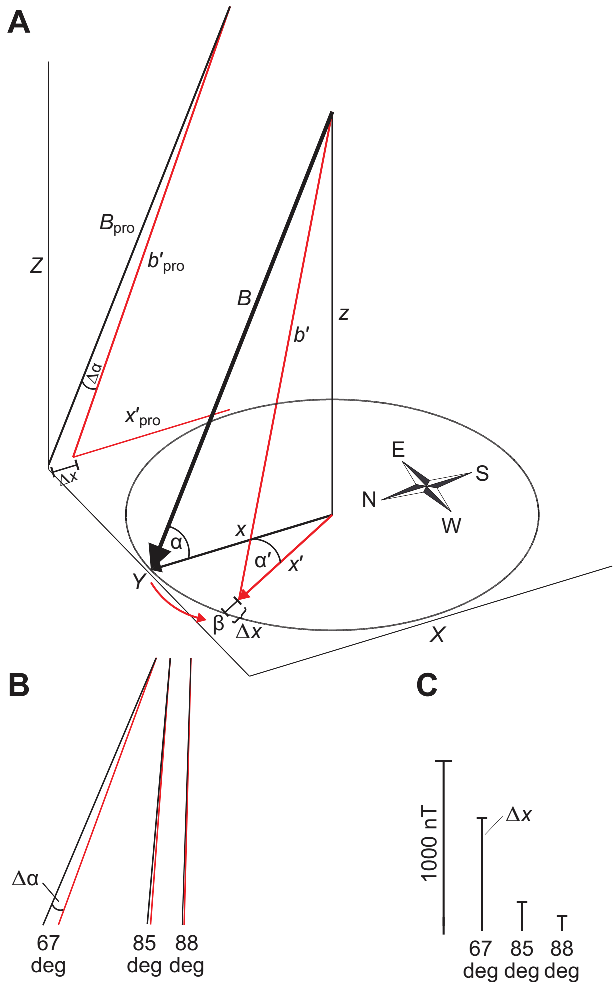

Fig. 2. Scheme illustrating the difficulties associated with using a magnetic inclination compass to accurately determine a compass direction at very steep inclination angles. (A) *B*, the magnetic field vector; *z*, the length of the vertical component of the magnetic field vector; *x*, the true length of the horizontal component of the magnetic field vector; α, the true inclination angle. A turn of the bird with its magnetic sensors by angle β will result in an apparent magnetic field vector *b*′, which results in a change in the perceived horizontal component of the magnetic field by Δ*x* to *x*′ and the angle by Δα to α′. Note that the lines B_{pro}, b'_{pro} and x'_{pro} in the *X*–*Z* plane indicate the projections of *B*, *b*′ and *x*′ back on to the 'North' plane to enable an easier visualization of Δα and Δ*x*. (B) Comparison of the change of Δα experienced when the inclination angle (α) was set to 67, 85 and 88 deg, and when β was set to 15 deg. (C) The bars indicate the size of Δ*x* when the inclination angle (α) was set to 67, 85 and 88 deg, and when β was set to 15 deg. For explanation, see Results and Eqns 1–5.

30 deg away from North instead of North (β=30 deg) is only 0.67 deg. At 88 deg inclination, the change in inclination angle (Δα) that would be measured when the bird with its magnetic sensors points North–South compared with when it is turned 15 or 30 deg away from North would be only 0.07 or 0.27 deg, respectively (see Fig. 2).

We want to stress at this point that the model depicted in Fig. 2, as well as the underlying mathematics, are of course man-made and simple theoretical considerations using a Cartesian coordinate system (or similar to what would be measured by a three-axial magnetometer) only because such considerations are useful to visualize the problems that any magneto-sensory system needing to measure the geomagnetic field vector in 3D space would face at steep inclinations. Fig. 2 and the associated simple calculations, however, help illustrate why separating different compass directions at very steep magnetic inclination angles is difficult. These difficulties become even more obvious when one considers the natural, rather stochastic, variation in the geomagnetic field of typically 30–100 nT in any direction.

Considering these challenges faced at steep inclination angles, birds might have evolved behaviors and/or sensory strategies that would help them detect these minute differences. The magnetic compass of night-migratory songbirds is almost certainly embedded in their visual system (Schulten et al., 1978; Wiltschko et al., 1993; Ritz et al., 2000; Ritz et al., 2010; Mouritsen et al., 2005; Heyers et al., 2007; Zapka et al., 2009; Zapka et al., 2010). Mouritsen et al. (Mouritsen et al., 2004) observed that garden warblers (*Sylvia borin*), a species very closely related to the Eurasian blackcap, performed 'head scans' (subsequent ~90 deg turns of the head, clockwise and counter-clockwise), and that this behavior is correlated with the birds' magnetic compass orientation capabilities. During such a head scan, the putatively hazy, magnetically induced, visual image that the bird would perceive (Ritz et al., 2000; Ritz et al., 2010; Solov'yov et al., 2010; Lau et al., 2012) would move across the retina, and this might facilitate the detection of minute absolute differences by determining a symmetry plane and/or maxima or minima rather than absolute value differences in nanotesla (Mouritsen et al., 2004).

The ability of our blackcaps to use magnetic fields with very steep inclinations is exceeded by the birds tested by Akesson et al. (Akesson et al., 2001): their white-crowned sparrows seemed to be well oriented using their magnetic compass at an inclination angle of 88.6 deg in a 58,100 nT field [fig. 2e in Akesson et al. (Akesson et al., 2001)]. One possible reason for the apparent ability of white-crowned sparrows (Akesson et al., 2001) to utilize steeper inclination angles than blackcaps (this study) could be that it is a biological adaptation to their respective breeding ranges. The white-crowned sparrow's breeding range extends into areas with inclination angles up to 84 deg (Hoyo et al., 1992; Cortopassi and Mewaldt, 1965), whereas the northernmost breeding areas of the Eurasian blackcap (see Fig. 3) feature inclination angles up to 78 deg (Tromsø in Norway) (McLean et al., 2004; Hoyo et al., 1992).

Another possible reason for the apparent difference between the findings of the present study and that of Akesson and colleagues (Akesson et al., 2001) is that we used the strength of the geomagnetic field present in Oldenburg for all inclinations, which is considerably weaker than the polar geomagnetic fields in the experiments of Akesson et al. (Akesson et al., 2001). This difference in field strength would not influence the angle differences that the birds would need to be able to separate, but in the stronger polar field, the absolute magnetic field strength projected down on to the horizontal plane would be larger at any given inclination angle. Thus, everything else being equal, it might be easier to determine a migratory direction in stronger fields with very steep inclinations. Finally, one cannot completely rule out that the single group of birds tested outdoors at 88.7 deg inclination (Akesson et al., 2001) might have had access to additional cues unavoidable in field experiments such as light gradients and olfactory cues. One very practical aspect of our study is that, in experiments where vertical magnetic fields are used, on the basis that they provide no directional magnetic compass information in Emlen funnels, it seems fairly safe to assume that they provide no directional information as long as the deviations from 90 deg do not exceed 2 deg.

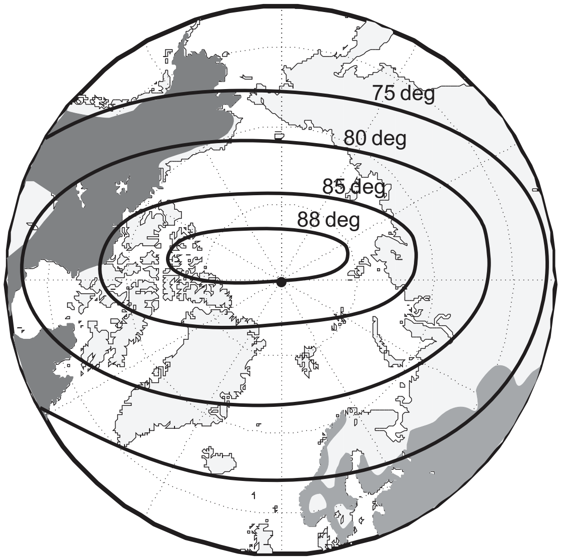

Fig. 3. Polar projection of the most northerly breeding ranges of the white-crowned sparrow (dark gray) and the Eurasian blackcap (mid-gray). The isoclines indicate the angle of inclination of the magnetic fields at a particular point on the map. Note that in contrast to the breeding area of the Eurasian blackcap, in the northernmost breeding range of the white-crowned sparrow, the magnetic inclination reaches up to ~85 deg (Hoyo et al., 1992). The inclination was plotted according to the World Magnetic Model 2010 (McLean et al., 2004) with MATLAB.

MATERIALS AND METHODS

Magnetic fields

The magnetic field conditions were generated by a double-wound, three-axial, Merritt four-coil system (Kirschvink, 1992; Zapka et al., 2009), of 2×2×2 m, operated by high-precision, constant current power supplies (KEPCO BOP 50-4M, Kepco Inc., Flushing, NY, USA). The experiments took place within the center of the coils, where the field homogeneity was better than 99% of the applied field.

Control experiments were performed in a magnetic field that corresponded to the NMF of Oldenburg and in a magnetic field where magnetic North was turned 120 deg counter-clockwise (CMF). In the NMF condition the same amount of current was sent through the coils as in the CMF condition (Engels et al., 2012). The magnetic fields used were very consistent and homogeneous (NMF and CMF: magnetic field strength=49,397±65 nT; inclination=67.5±0.2 deg; deviation from horizontal direction=360±0.02 deg, means ± s.d.). In the experimental conditions, the inclination was changed to 85 or 88 deg, while the total intensity and horizontal direction remained the same as in the equivalent control conditions. All conditions were set and controlled by a custom-written computer script (written in MATLAB). During the experiments with changed inclination (see Table 1), the magnetic field was monitored continuously by a fluxgate magnetometer (Meda FVM-400) and recorded by the software FM 300 Front Panel (Meda, Inc., Dulles, VA, USA) to confirm that all tests were run under stable magnetic field conditions. Because of the slight, unavoidable heterogeneity of the artificial magnetic fields created by the coils, minor deviations from the intended fields could not be avoided (see Table 1).

Animals

Ten blackcaps, *S. atricapilla*, were wild-caught in August 2013 within 1 km of the University of Oldenburg, Germany. The birds were housed indoors, two by two in cages placed in a windowless room under local photoperiodic conditions. The experiments were conducted during the autumn migratory season in September and October 2013 on the Wechloy Campus of the University of Oldenburg. This particular group of birds was unusually well oriented. Therefore, much fewer tests per condition had to be performed in order to get a well-oriented group in the control condition compared with normal (Zapka et al., 2009; Hein et al., 2010; Hein et al., 2011; Engels et al., 2012). All animal procedures were performed in accordance with local and national guidelines for the use of animals in research and were approved by the Animal Care and Use Committees of LAVES (Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit, Oldenburg, Germany).

Behavioral tests

All behavioral tests were performed in wooden huts covered on the inside with electrically connected aluminium plates, which, when grounded, acted as Faraday cages that shielded time-dependent electromagnetic disturbances in the frequency range up to ~20 MHz by approximately two orders of magnitude (Engels et al., 2014). All electrical equipment, such as power supplies, was placed outside the test huts in aluminium shielded shelves to minimize electromagnetic disturbances. Within the test huts, the static magnetic field was the only available cue for orientation.

All experiments started at sunset (±10 min.). One hour before, the birds were placed outdoors in wooden transportation cages fitted with 7 cm diameter mesh-covered peepholes. This enabled the birds to potentially calibrate their magnetic compass from twilight cues (Cochran et al., 2004; Muheim et al., 2006; but see Chernetsov et al., 2011; Schmaljohann et al., 2013). Directly thereafter, the birds were placed in modified Emlen funnels (Emlen and Emlen, 1966), made of aluminium (35 cm diameter, 15 cm high, walls 45 deg inclined). The funnels were covered with scratch-sensitive paper (Blumberg GmbH, Ratingen, Germany) so that the birds' migratory restlessness became visible as scratches on the paper (Mouritsen et al., 2009). All tests were run under dim light conditions (2.5 mW m^{-2}) produced by incandescent bulbs (see Zapka et al., 2009).

Nine blackcaps where tested simultaneously in one hut twice each night. The second test started ~10 min (±5 min) after the end of the first one. In the second round, each bird was tested in a funnel at a different position, preventing any potential remembrance and transfer of room features between tests and conditions.

Orientation data analyses

After the end of the experiments, all the scratch-sensitive paper was evaluated relative to the overlap point. Two researchers, who worked independently from each other, determined the mean direction of each scratch-sensitive paper without knowing the direction of the paper overlap point. The direction of the overlap point was selected randomly each night between the four cardinal directions (N, S, E or W). In cases where the two observers estimated mean directions diverging by more than 30 deg, a third researcher was consulted. If no agreement was attainable, the paper was categorized as random and excluded from further evaluations. Only after the mean direction had been agreed on relative to the overlap direction was this direction revealed and corrected for. Thereby, the true magnetic direction was determined and entered into the calculations of the overall individual mean direction.

We observed that blackcaps placed in Emlen funnels and removed immediately showed less initial escape behavior than, for example, European robins, *Erithacus rubecula*, and that they typically left fewer than 30 scratches on the paper. Therefore, we only considered papers with fewer than 30 scratches as inactive, and these were excluded from further evaluation (cf. Engels et al., 2012; Engels et al., 2014). Only birds that produced at least two oriented data points in the given condition were included in the orientation analyses for that condition. This resulted in slightly different numbers of tested birds in the different conditions. To calculate the individual mean orientation in each test condition, the mean headings of all active and oriented tests of each of the individual birds were added by vector addition. The group mean vector for each condition was calculated by adding up unit vectors in each of the individual mean directions in that condition and then dividing by the number of birds. The group mean vector was tested for significance using the Rayleigh test (Batschelet, 1981). The MWW test and comparison of confidence intervals were used to test for significant differences in orientation direction between groups.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
N.L., D.D. and H.M. conceived and designed the experiments; N.L., D.D. and F.S. performed the experiments; N.L., F.S. and D.D. analyzed the data; N.-L.S. and D.D. provided custom written software; N.L., D.D. and H.M. wrote the paper.

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