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

(Running head: Inclination threshold in blackcaps)

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Summary

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° inclination should offer no utilizable information on where to find North or South. So far, very little is known about how small deviations from horizontal or vertical inclination migratory birds can detect and use as a reference for their magnetic compass. Here we ask: 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°, but fail to orient in a field with 88° inclination. This suggests that the steepest inclination angle enabling magnetic compass orientation in migratory blackcaps tested in Emlen funnels lies between 85 and 88 degrees.

Introduction

Since 50 years it is 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 birds' magnetic compass is an inclination compass (Wiltschko and Wiltschko, 1972; 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; 1995). Therefore, at the magnetic equator or at the magnetic poles, where the inclination is 0° and 90°, 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 (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. (2004) has 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, it remains an interesting question, how wide the range around the magnetic poles and the magnetic equator might be where the birds are unable to use their magnetic compass.

Earlier studies showed that migratory wheatears (*Oenanthe oenanthe*) displaced from Sweden (70° inclination) to Greenland (81° 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°, but failed to orient at 89.7° 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, since 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 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 & 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 90º (Kirschvink, 1991; 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, since even small heterogeneities in the created fields can flip the inclination across the 90º 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. 2009; Hein et al. 2010) to investigate, whether night-migratory blackcaps (*Sylvia atricapilla*) can use their magnetic compass in a field with 85° and 88° 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, NMF, 67° inclination). They oriented significantly towards their appropriate autumn migratory direction (group mean orientation 219 ± 35°, 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° counterclockwise (group mean orientation 90 ± 36°, $r = 0.66$, $N = 9$, $p < 0.05$; Fig. 1d, control, CMF, 67° inclination). Their orientation direction was significantly different in the normal (NMF) and changed magnetic field (CMF), as indicated by the lack of overlap of the 95% confidence intervals.

When the inclination was increased to 85°, the birds' magnetic compass orientation capabilities were unaffected (Fig. 1b, NMF, group mean orientation 182° ± 29°, $r = 0.73$, $N = 9$, $p < 0.01$; and Fig. 1e, CMF, group mean orientation 87° ± 31°, $r = 0.76$, $N = 8$, $p < 0.01$). The birds' change of orientation between the NMF and the CMF conditions was significant (Watson-Williams F-test (WW): $F= 24.005$, $df= 1$, $p< 0.001$ in the control condition and $F=16.152$, $df= 1$, $p= 0.001$ for the 85° inclination condition). The orientation was not significantly different under 67° and 85° inclination in the NMF (WW: $F= 2.593$, $df= 1$, $p= 0.127$) or in the CMF (WW: $F= 0.019$, $df= 1$, $p=0.892$) (Batschelet, 1981). The Mardia-

Watson-Wheeler (MWW) test confirms these findings (MWW: χ^2=14.664, df= 1, p< 0.001 in the control condition and χ^2=8.044, df= 1, 0.005>p>0.001 for the 85° inclination condition, between NMF and CMF respectively; as well as χ^2=0.985 df= 1, 0.5>p>0.25 between NMF 67° and NMF 85°; χ^2=2.601, df= 1, 0.25>p>0.1 between CMF 67° and CMF 85°) (Batschelet, 1981).

However, when the birds were tested in the magnetic field with an inclination of 88°, the birds' orientation was random (Fig. 1c, NMF, group mean orientation 2°, r = 0.15, N = 8, p = 0.824; and Fig. 1f, CMF, group mean orientation 216°, 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 testing periods (see Tab.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°, but fail to orient at an inclination angle of 88° at magnetic field intensities around 49,300 nT (local magnetic field of Oldenburg, Germany). Therefore, a deviation of 5° 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 the ones showed at 67° inclination (the direction and length of the group mean vector is similar when the same birds were tested in 67° and 85° inclination).

This is impressive, since 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 & Hore 2009; Treiber et al. 2012; Mouritsen & Hore 2012) must either be able to distinguish minute angle differences relative to gravity or be able to 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 since the bird must orient in a compass direction, which 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 & Mouritsen 2000; Mouritsen 2003) often involve finer changes in migratory directions along their migratory route (Gwinner & 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 degrees and one requiring that birds can determine the difference between North and 30 degrees. 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 this information is 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 onto 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° left or right of North (see Fig. 2).

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

$$x = cos(\alpha) * B \qquad (1),$$

where α is the magnetic inclination angle (85°) and B is the magnetic field strength (49,300 nT in Oldenburg). Thus, in a 49,300 nT field with 85° inclination, x is 4,297 nT.

If the bird with its sensors heads 15° away from North, $x`$ will be

$$x` = cos(\beta) * x \qquad (2) ,$$

where β is the horizontal deviation angle (here 15°) from North. Thus, in a 49,300 nT field with 85° inclination, $x`$ is 4,150 nT. The change (Δx) in the horizontal magnetic field component is

$$\Delta x = x - x` \qquad (3),$$

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

At 88° inclination, the horizontal component of the field pointing towards North (*x* in Fig. 2) is 1,720 nT, and when the bird with its sensors turns towards 15°, it is 1,662 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° error in the birds' magnetic compass heading are 576 nT and 231 nT, respectively at 85° and 88° inclination.

Second, we consider the putative situation where the inclination angle relative to gravity is either measured directly by the birds' magnetic sensors or this information is 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° left or right of North (see Fig. 2).

The inclination angle ($\alpha`$) that would be measured if the bird with its magnetic sensors heads 15° away from North is

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

which is 85.17° for α =85° and β =15°, and the difference ($\Delta\alpha$) to the magnetic inclination (α) experienced if the bird with its magnetic sensors heads towards magnetic North is given by

$$\Delta\alpha = \alpha` \quad \alpha \qquad (5),$$

That is just 0.17°. Using the same logic, the change in inclination angle ($\Delta\alpha$) measured if the bird with its magnetic sensors heads 30° away from North instead of North (β =30°) is only 0.67°. At 88° inclination, the change in inclination angle ($\Delta\alpha$) that would need to be measured when the bird with its magnetic sensors points North-South compared to when it is turned 15° or 30° away from North would be only 0.07° or 0.27°, respectively (see Fig. 2).

The authors want to stress at this point that the model depicted in Figure 2, as well as the underlying math are by all means 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 which any magneto-sensory system needing to measure the geomagnetic field vector in 3D-space would face at steep inclinations. Figure 2 and the associated simple calculations, however, helps illustrate why separating different compass directions at very steep magnetic inclination angles should be 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 behaviours 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, 2010; Mouritsen et al. 2005; Heyers et al. 2007; Zapka et al. 2009, 2010). Mouritsen et al. (2004) observed that garden warblers (*Sylvia borin*), a species very closely related to the Eurasian blackcap, performed "head scans" (subsequent ~90° turns of the head, clockwise and counter clockwise), and that this behaviour is correlated with the birds' magnetic compass orientation capabilities. During such a head scan, the putatively hazy, magnetically induced, visual image that the bird might perceive (Ritz et al. 2000, 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 abilities of our blackcaps to use magnetic fields with very steep inclinations are exceeded by the birds tested by Akesson et al. (2001): their white-crowned sparrows seemed to be well oriented using their magnetic compass at an inclination angle of 88.6° in a 58,100 nT field (Fig. 2e in 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. White-crowned sparrows' breeding range extends into areas with inclination angles up to 84° (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° (Tromsø in Norway; McLean et al., 2004; Hoyo et al., 1992).

Another possible reason for the apparent difference between the present study and Akesson et al. 2001 is that we used the field strength of the geomagnetic field present in Oldenburg for all inclinations, which is considerably weaker than the polar geomagnetic fields in the experiments of Åkesson 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 onto 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° inclination (Åkesson 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 as providing 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° do not exceed 2°.

Materials and Methods

Magnetic fields

The magnetic field conditions were generated by a double-wound, 3 axial, Merritt 4-coil system (Kirschvink, 1991; Zapka et al., 2009), of 2x2x2 m, operated by high-precision, constant current power supplies (KEPCO BOP 50-4M, Kepco Inc., Flushing, NY, US). 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 natural geomagnetic field (NMF) of Oldenburg and in a magnetic field where magnetic North was turned 120° counter-clockwise (CMF). The used magnetic fields were very consistent and homogeneous (NMF and CMF: MF strength = 49,397 nT ± 65 nT [s.d.]; inclination = 67.5° ± 0.2° [s.d.]; deviation from horizontal direction = 360° ± 0.02 [s.d.]). In the experimental conditions, the inclination was changed to 85° or 88° respectively 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, US) to confirm that all tests were run under stable magnetic field conditions. Due to 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

10 blackcaps, *Sylvia atricapilla*, were wild-caught in August 2013 within 1km 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 to what is normally required (Zapka et al., 2009; Hein et al., 2010, 2011; Engels et al., 2012). All animal procedures were performed in accordance to local and national guidelines for the use of animals in research and approved by the Animal Care and Use Committees of the 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 aluminum plates, which, when grounded, acted as Faraday cages that shielded time-dependent electromagnetic disturbances in the frequency range up to ca. 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 aluminum 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 that, the birds were placed outdoors in wooden transportation cages fitted with 7 cm diameter mesh-covered peepholes. Thereby, the birds were enabled 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 aluminum (35 cm diameter, 15 cm high, walls 45° 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/m²) produced by incandescent bulbs (spectrum in Zapka et al. (2009)).

Nine blackcaps where tested simultaneously in one hut twice each night. The second test started approximately 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 of the scratch sensitive papers were 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°, a third researcher was consulted. If no agreement was attainable, the respective paper was categorized as random and excluded from further evaluations. Only after the mean direction had been agreed on relative to the overlap-direction, this direction was 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 show less initial escape behavior than e.g. European robins, *Erithacus rubeluca* and that they typically leave less than 30 scratches on the paper. Therefore we only considered papers with less than 30 scratches as inactive. Thus, papers with less than 30 scratches were excluded from further evaluation (compare with Engels et al., 2012, 2014). Only birds, which 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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Author Contributions

Conceived and designed the experiments: NL, DD, HM

Performed the experiments: NL, DD, FS

Analyzed the data: NL, FS, DD

Provided custom written software: NLS, DD

Wrote the paper: NL, DD, HM

List of symbols and abbreviations

CMF: Changed Magnetic Field = a magnetic field turned horizontally by -120° from the natural magnetic North Pole

gN: geographic North

MF: Magnetic Field

mN: magnetic North

NMF: Normal Magnetic Field directed towards the natural magnetic North Pole

n.s.: not significant

Competing Interests

The authors declare that no competing interests exist.

Fig. 1. The orientation of individual blackcaps was tested in magnetic fields with 67°, 85° or 88° inclination, respectively. The birds headed in their appropriate autumn migratory direction towards the Southwest in the naturally directed magnetic fields (NMF) with 67° (a) and 85° (b) inclination, and they responded appropriately to a -120° horizontal turn of the fields with 67° (d) and 85° (e) inclination. In contrast, the birds were disoriented in both the normally directed (c) and the -120° turned (f) field when the inclination angle was set to 88°. 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.

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 the angle β will result in an apparent magnetic field vector b`, which result in a change in the perceived horizontal component of the magnetic field by Δx to x` and the angle by Δα to α`. Note that the lines $B_{pro}$ , $b`_{pro}$ and $x`_{pro}$ in the XZ-plane indicate the projections of B, b` and x` back onto the "North"-plane to enable an easier visualization of Δα and Δx . **B:** Comparison of the experienced change of Δα when the inclination angle (α) was set to 67°, 85° and 88° and when β was set to 15°. **C:** The bars indicate the size of Δx, when the inclination angle (α) was set to 67°, 85° and 88°, and when β was set to 15°. For explanation see main text and equations [1]-[5].

Fig. 3. Polar projection of the most northerly breeding ranges of the white-crowned sparrow (dark grey) and the Eurasian blackcap (medium grey). The isoclines indicate the angle of the magnetic fields´ inclination 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 white-crowned sparrow, magnetic inclination reaches up to ~85° (Hoyo et al., 1992). The inclination was plotted according to the World Magnetic Model 2010 (McLean et al., 2004) with MATLAB.

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

Footnotes to the table: [1]Magnetic Inclination [2]Magnetic Declination (horizontal polarity) [3]Magnetic field strength. [4]During 10 conducted experiments of condition "85°" and "88°", 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. [5]The displayed magnetic field components of all funnel-positions within the test arena were measured and registered after the experiments, ended each night.

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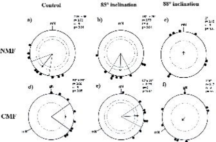
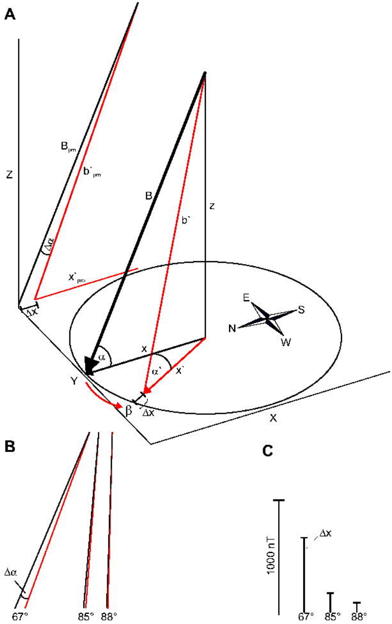
Table 1

Control	Incl[1] Mean	SD	Decl[2] Mean	SD	Strength[3] Mean	SD
Coil-Center[4]	67.515°	0.19°	0.005°	0.022°	49397 nT	65.508 nT
all Positions[5]	67.667°	0.15°	0.161°	0.547°	49329 nT	52.993 nT

Condition "85°"	Incl[1] Mean	SD	Decl[2] Mean	SD	Strength[3] Mean	SD
Coil-Center[4]	85°	0.019°	0.082°	1.194°	49257 nT	74.839 nT
all Positions[5]	84.928°	0.295°	-0.983°	2.114°	49275 nT	62.328 nT

Condition "88°"	Incl[1] Mean	SD	Decl[2] Mean	SD	Strength[3] Mean	SD
Coil-Center[4]	88°	0.022°	0.12°	2.86°	49281 nT	81.497 nT
all Positions[5]	87.956°	0.305°	-2.667°	5.3°	49257 nT	13.903 nT


Control
85° inclination
88° inclination
NMF
CMF
a)
mN
p= 0.01
b)
mN
p= 0.01
c)
mN
d)
gN
mN
p= 0.05
e)
gN
mN
f)
gN
mN


A
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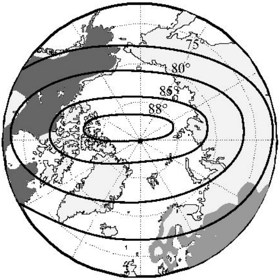
Δx
67°
85°
88°


75°
80°
85°
88°