Do migrant European chats and warblers use magnetic gradient navigation?

Jørgen Rabøl

(Med et dansk resumé: Navigerer trækfugle ved hjælp af Jordens magnetfelt?)

Abstract Compass orientation in reference to the magnetic field is a well established behaviour in birds and other animals. On the other hand, the presence and significance of magnetic gradient navigation is more controversial though the time-trend is towards increasing confidence. In this study, 478 passerine migrants were funnel-tested on 29 nights with the purpose to elucidate the possibility of magnetic navigation following simulated displacements towards N and S. No indications of magnetic navigation were found. Furthermore, a thorough reconsideration on claimed cases of magnetic navigation in migrant birds, pigeons and other animals revealed no unambiguous evidence of magnetic navigation.

Introduction

The question is whether nocturnal migrant European passerines make use of magnetic gradient navigation as recently indicated in Grey-breasted Silvereyes *Zosterops lateralis* and Reed Warblers *Acrocephalus scirpaceus* (Fischer *et al.* 2003, Deutschlander *et al.* 2012, Kishkinev *et al.* 2013). Magnetic gradient navigation has also been suspected or claimed in pigeons (e.g. Walker 1998, Wiltschko & Wiltschko 2003), newts (e.g. Fischer *et al.* 2001, Phillips *et al.* 2002a), turtles (e.g. Lohmann & Lohmann 1994, 1996, 1998, Lohmann *et al.* 2001), alligators (Rodda 1984) and spiny lobsters (Boles & Lohmann 2003).

As emphasized by e.g. Rabøl (1998), simulated geographical displacements is the strongest tool to demonstrate navigational significance and influence of one or another potential navigational cue. Using simulation, Rabøl (1998) found evidence that the starry sky provided both N/S and E/W navigational information in passerine migrants. In the present paper, I present results from simulated geographical displacements (autumn) by change of the magnetic field towards a stronger intensity and steeper inclination in one group, and a weaker intensity and a more shallow inclination in another group of passerine migrants. In the first group, the inclination roughly simulated a displacement from Denmark (56° N) to a latitude at about 68° N, running through northern Norway, and in the second group to a latitude of about 38° N (Sicily). The intensity changes simulated the conditions near the magnetic North Pole and the magnetic equator, respectively. As the actual goal area of the birds in (at least the first part of) the test period was supposed to be northern France, the prediction of a system based on magnetic navigation is that the birds tested under the S condition should orient more or less NW, whereas the birds tested under the N condition, and the controls tested in the local magnetic field, should orient about SSW and SSW-SW, respectively (Fig. 1).

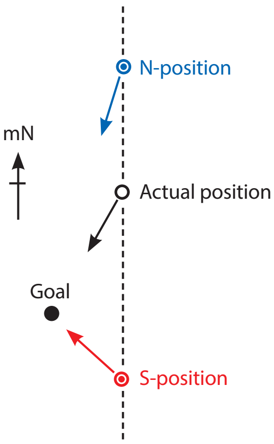

Fig. 1. Expected orientations at actual position (controls) and following simulated displacements towards magnetic N and S along a gradient based on magnetic intensity and/or inclination. The birds are navigating towards the goal area (Goal). The reaction towards magnetic W is (supposed to be) based on another navigational gradient (running E/W) which could be non-magnetic or partly magnetic (e.g. the declination).

Den forventede orientering af kontroller (actual position) og ved simuleret forflytning mod magnetisk N og S.

Experiments in 2004 and 2005

All birds were trapped as grounded migrants in autumn on Christiansø (55° N, 15° E) in the Baltic Sea and then transported about 300 km W to Endelave (55° N, 10° E). Experiments were carried out on 17 nights with 15 to 20 birds per night. A total of 286 tests (bird-nights) were carried out (154 controls, 132 experimentals).

Following the displacement to Endelave, 16 birds – the experimentals – were placed in outdoor cages within artificial magnetic fields; half of them (named the N experimentals) experienced a stronger and steeper magnetic field than the natural (designated the N condition), the other half (named the S experimentals) a weaker and more shallow magnetic field (the S condition). The remaining birds, the controls were placed in outdoor cages within the natural magnetic field.

Each of eight coil systems (quadratic 80 × 80 cm, 45 cm in between) produced a magnetic vector of $\sqrt{2}$ times the local horizontal vector component of the geomagnetic field. If such a vector is added vertically downwards to the local magnetic vector (inclination 70°, intensity 48 μT), the resultant will be a downward directed vector of about 76.5° inclination and an intensity of 70 μT. If it is added vertically upwards, the resultant is an upward-directed vector of about 53° inclination and an intensity of 27 μT. The homogeneity of the resultant magnetic field in the central part within the coils (where the cages and funnels were placed) was high, with a variation of less than 1% (Rabøl *et al.* 2002), i.e. probably less than in the fields of Wiltschko (1968), Wiltschko & Wiltschko (1972) and Sandberg *et al.* (1988).

My magnetic fields were restricted to express only two different vectors, the one mentioned above, or a vector two times the size of the vertical component of the magnetic field in Denmark. Clearly, the first-mentioned vector was the most appropriate one used to simulate reasonable magnetic displacements on Earth.

The birds were caged two by two in conical plastic baskets (diameter 30 cm at the bottom, 40 cm at the top, height 40 cm). There was a free view almost down to the horizon in most directions (towards W all the way down to the horizon) through the lattice structure at the sides of the basket. The top was covered with a cloth-net, and two wooden sticks were set across horizontally through the basket (one close to the ceiling, in order to offer the bird a good view of the sky through the cloth-net). The birds were tested singly in plastic funnels with a side slope of 45° and measuring 30 cm in upper diameter. The funnels were placed horizontally on wooden boards, and in the experimentals each funnel was placed in the central part of the coil system. The inner slope of the funnel was painted with a thin layer of chalk where the hopping and fluttering bird left its feet marks.

When placed outdoors on the boards, the cages were covered on the top with a wooden plate measuring 60 × 60 cm. The intention was to shield against strong sun and rain, but also to limit the birds' view of the stars – since the focus was on magnetic and not stellar navigation. On the other hand, it was considered important that the birds were offered the possibility of *maintaining* the course in reference to the stellar compass *after* (the possible) *establishment* of the compass course following a navigational process rooted in magnetism. Therefore, the birds were allowed (when possible) to see the sun and stars from their cages during the sunset and early night phase, and also when tested in the funnels during the first part of the night, which is why the wooden plates on top of the cages were removed at sunset/early night, and when birds were tested in the funnels. The early night phase started about half an hour before local sunset and lasted at least until one and a half hour after local sunset. The test phase started at least two hours after local sunset and lasted for 75-105 minutes.

Experiments with artificial magnetic fields on Christiansø. Photo: Brian Stigfeldt.

The orientation and amount of activity of the individual birds were estimated as previously described by Rabøl (1979, 1993, 2010). The pattern of scratches was carefully inspected from above to determine the direction of the maximal and minimal activity. The mean direction was estimated to the nearest 5°. In case of a clear bimodal pattern, both peaks were recorded (see Figs 2-8). The concentration of scratches around the mean direction was estimated as high (3), medium (2), low (1) or disoriented (dis). The number of scratches was not counted (this is normally impossible because of too much scraping in some areas), but the amount of activity was estimated as zero (–), very small (VS), small (S), medium (M), large (L) or very large (VL). The significance of the sample mean vector was found by application of the Rayleigh test. I also used the confidence interval test and the Watson-Williams (or the Mardia-Wheeler-Watson) test for testing the difference between two dependent and independent samples, respectively. Furthermore, I used the parametric test for the concentration parameter (Batschelet 1981).

Generally in this paper, sample mean vectors are denoted by their direction and concentration, e.g. 208° – 0.768 or, for a bimodal distribution, e.g. 208°/(28°) – 0.543 (208° major peak) or 208°/28° – 0.543 (two approximately equal peaks). The number of individual directions (n) contributing to the sample mean vector is given in brackets, and if less than 0.05 the statistical significance of the mean vector is given as *, **, or ***, meaning $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively. Instead of bimodal, the designation axial is perhaps better for indicating the focus on 180° between the modes. Consider the following example: Five birds in a sample orient towards 10°, 30°, 50°, 185°, and 215°. Clearly there are two opposite modes (centered about 30° and 200°). However, the sample mean vector calculated in the traditional way comes out as 49° – 0.207 ($n = 5$), and clearly offers a poor description of the bimodal distribution. If the five angles are doubled (into 20°, 60°, 100°, 370° (10°), and 430° (70°)) the bimodal distribution is transferred transformed to a unimodal distribution, and the sample mean vector is calculated as 52° – 0.840* ($n = 5$). Now 52° has to be transferred back into two axial directions. The angle is halved (into 26°), and 180° has to be added as the other mode. The axial distribution is now presented as 26°/(206°) – 0.840* ($n = 5$) fitting the intuitive impression of an bimodal distribution with peaks around 30° (main peak) and 200° (minor peak).

Forsøg med kunstige magnetfelter på Christiansø. Foto: Brian Stigfeldt.

It is normal practice to select and present the bimodal sample mean vector if the sample concentration (here 0.840) exceeds the sample concentration (here 0.207) of the distribution treated as unimodal.

Juvenile Common Redstarts and Pied Flycatchers

Sixteen juvenile Common Redstarts *Phoenicurus phoenicurus* and fourteen juvenile Pied Flycatchers *Ficedula hypoleuca* were trapped on Christiansø on 3-4 September 2004. Following strong SW and W winds on the previous days, many migrants arrived on these days in weak NW winds, suggesting an origin from the north. Thus, in all probability the birds could be considered a homogenous sample (according to experience we should expect no significant deviation in orientation between the two species at this stage).

On 6 September, the 30 birds were transported to Copenhagen and transferred to cages three by three. The following day they were transported to Endelave and transferred to cages two by two. On the nights of 6 and 7 September, the birds were placed inside a house in the local magnetic field, without sight of the sunset and starry sky. On the afternoon of 8 September, the 15 cages were placed outdoors on boards. Seven cages (14 birds, the controls) experienced the local magnetic field, whereas four cages (8 birds) were placed within Helmholtz coils contributing to a resultant magnetic field stronger and steeper than the local field, and four other cages (8 birds) were placed within Helmholtz coils contributing to a resultant field weaker and shallower than the local field. In the evening, the birds were exposed to a clear sunset and starry sky until two hours before midnight, but no tests were carried out.

Experiments were carried out on the clear and starry nights of 9, 10, 19 and 21 September and on the cloudy night of the 16th, where only a few stars were occasionally visible; on this latter night it was probably not possible for the birds to use the stars for establishing or maintaining a compass course. Normally, sixteen birds (8 controls and 8 experimentals were tested in funnels for about 90 minutes, beginning two hours after sunset when no trace of the sunset was visible on the sky. On most other nights the weather was too windy, overcast or rainy for experiments; in fact, from late afternoon 12 September to mid-afternoon 16 September, and again from mid-afternoon 20 September until early afternoon 21 September, the weather was so bad that the cages with birds were taken indoors. On these occasions, all groups experienced the local magnetic field.

The experimentals were caged in the changed magnetic field from late afternoon on the 8th until taken indoors in the late afternoon of 12 September. The individual birds spent all the time within the same field except for the two times 10 minutes when exchanged between cage and funnel, or when the other bird in the same cage was tested. Here, the birds spent about two hours in a dark tent in the local magnetic field. Following the transfer back to the outdoor boards in the afternoon of 16 September, the experimentals formerly experiencing a strong and steep magnetic field were now placed in a weak and shallow field and vice versa. These positions were retained also after the short interruption when placed indoors from the afternoon of the 20th until the afternoon of the 21th September.

Juvenile European Robins

Thirty-one juvenile European Robins *Erithacus rubecula* were trapped on Christiansø on 1 October 2004, following a significant arrival of birds. The wind was NE, 8-9 m/s, the sky half covered with clouds and the visibility 25 km. The birds probably came from the eastern part of Sweden. On 4 October, the birds were transported to Copenhagen and the following day to Endelave, where they were caged two by two in plastic baskets and spent the night and most of the next day inside a house. In the afternoon of 6 October, all baskets were in position on the boards at the experimental site. Eight birds in four baskets were placed within a resultant magnetic field stronger and steeper than the local field, and another eight birds in four baskets were placed within a resultant magnetic field weaker and shallower than the local field. Thirteen birds in seven baskets were placed on a table in the local magnetic field and acted as controls. Until the last experiments were carried out on 11 October, the birds were retained at these positions.

Following a calm 5 October, the weather was windy on 6-7 October, the cloudiness shifted between 1/8 and 7/8 with a few showers, and no experiments were carried out on 7 October. The top of the baskets were covered with a wooden plate (60 × 60 cm) from late afternoon on 6 October until half an hour before sunset on 8 October. On the next three sunsets and nights this procedure was repeated, so that the birds were exposed to a clear sunset and early night sky in the baskets before they later during the night were tested in the funnels. On all these evenings and nights the cloudiness was 0/8 or 1/8, and the stars and Milky Way were prominent.

Adult Common Redstarts, Garden Warblers, Pied Flycatchers and Spotted Flycatchers

Five adult Common Redstarts, three adult Garden Warblers *Sylvia borin*, 15 Pied Flycatchers (11 adults, 4 juveniles) and seven adult Spotted Flycatchers *Muscicapa striata* were trapped as grounded migrants on Christiansø during 17-25 August 2005. In this period, high temperatures and weak, mostly easterly winds suggested arrivals from N (Sweden) or NE (Finland; an adult Pied Flycatcher with a Finnish ring was trapped on 23 August), and in all probability the birds could be considered as a rather homogenous sample although the standard direction of Garden Warblers and Spotted Flycatchers is about S, whereas the standard direction of the two other species is SSW to SW (Bønløkke *et al*. 2006). On Christiansø, the birds were caged outdoors two by two in plastic baskets, and during night they were covered and unable to see the sky.

On 26 August, the 30 birds were transported to Copenhagen and the following day to Endelave and transfered to cages two by two. Birds of different species were distributed as evenly as possible between three treatment groups, except that the four juvenile Pied Flycatchers were all placed in the control group. On the nights of 26, 27 and 28 August, the birds were in a house experiencing the local magnetic field and with no view of the sunset and starry sky. On the afternoon of 29 August, the 15 cages were placed outdoors on boards. The birds were able to observe the sun, sunset and starry sky through the lattice structure of the sides of the baskets, whereas the top of each basket was covered by a wooden plate allowing no view of the starry sky overhead. Thirteen birds (the controls) in seven cages experienced the local magnetic field, whereas four cages (8 birds) were placed within four Helmholtz coils contributing to a resultant magnetic field stronger and steeper than the local field, and four other cages (likewise 8 birds) were placed within four Helmholtz coils contributing to a resultant field weaker and shallower than the local field. Late afternoon on 30 August, the wooden plates were removed, so that the birds for the first time since capture were exposed to a clear sunset and starry sky. Expositions and experiments were carried out on the clear and starry nights of 30 and 31 August and 3, 4, 6, 8, 10 and 12 September, and on all these nights the birds also experienced a clear and uncovered sunset in their baskets. On all test nights, the stars and the Milky Way were clearly visible.

Three treatments were carried out. First, the experimentals were caged and tested within their resultant magnetic fields from late afternoon on 29 August until late afternoon on 6 September. The individual birds spent all the time within the same field except for the two times 10 minutes, when exchanged between cage and funnel, or on the two occasions where they spent about two hours in the local magnetic field (in a dark tent, while the other bird in their cage was tested). Secondly, in the sunset/early night basket phase of 6 and 8 September, and while being tested in the funnels, the experimentals formerly experiencing the strong and steeper magnetic field were now placed and tested in the weak and shallower field and vice versa. After testing, these birds were transferred back into their normal coil-fields. And thirdly, from the sunset/early night phase on 10 September, and for the rest of the period I interchanged the experimentals and controls: eight well and steadily oriented control birds were chosen as new experimentals, while 12 out of 16 experimentals were selected as new controls and caged and tested in the local magnetic field.

Experiments in 2007

In 2007, experiments were carried out on Christiansø using the same method as on Endelave in 2004/2005, except that on Endelave the birds were caged for several days or even weeks. On Christiansø, I used birds trapped on the same day as the experiment, or on the preceding day, and the birds were tested only once. The birds were transferred to cages within the altered fields 1-2 hours before sunset and were placed into the funnels about two hours after sunset. During the cage-phase the top of the cage was covered by a wooden plate, because I wanted to limit the influence of the starry sky, which might possibly mask the influence of the magnetic field. During tests, the top was uncovered (leaving the tested bird with the option of using the starry sky as a 'maintaining' compass, after the possible navigatory process based on magnetic clues). As mentioned, the birds on Endelave in 2004/2005 were allowed to see the stars also when caged during sunset/early night.

During 9 August – 5 September, 192 experiments were carried out on twelve nights:

- 9 August: 6 Pied Flycatchers + 2 Garden Warblers (controls), 4 Pied Flycatchers + 4 Garden Warblers (experimentals).
- 10 August: 2 Pied Flycatchers + 6 Garden Warblers (controls), 2 Pied Flycatchers + 6 Garden Warblers (experimentals).
- 12 August: 8 Pied Flycatchers (controls), 8 Pied Flycatchers (experimentals).
- 13 August: 1 Pied Flycatcher + 2 Garden Warblers + 5 Common Whitethroats *Sylvia communis* (controls), 8 Garden Warblers (experimentals).
- 14 August: 5 Pied Flycatchers + 3 Garden Warblers (controls), 8 Pied Flycatchers (experimentals).
- 17 August: 8 Pied Flycatchers (controls), 8 Pied Flycatchers (experimentals).
- 18 August: 8 Pied Flycatchers (controls), 8 Pied Flycatchers (experimentals).
- 20 August: 8 Pied Flycatchers (controls), 8 Pied Flycatchers (experimentals).
- 21 August: 8 Pied Flycatchers (controls), 8 Pied Flycatchers (experimentals).
- 22 August: 5 Pied Flycatchers + 3 Garden Warblers (controls), 4 Pied Flycatchers + 4 Garden Warblers (experimentals).
- 4 September: 3 Pied Flycatchers + 2 Common Redstarts + 3 Blackcaps *Sylvia atricapilla* (controls), 8 European Robins (experimentals).
- 5 September: 2 Pied Flycatchers + 2 Common Redstarts + 1 Blackcaps + 3 European Robins (controls), 2 Common Redstarts + 2 Blackcaps + 4 ER (experimentals).

The 96 controls were 64 Pied Flycatchers, 16 Garden Warblers, 5 Common Whitethroats, 4 Blackcaps, 4 Common Redstarts and 3 European Robins. The 96 experimentals were 58 Pied Flycatchers, 20 Garden Warblers, 12 European Robins, 2 Blackcaps and 2 European Redstarts. I have no reason to believe that there is any significant difference between the species concerning the orientation and reaction to the magnetic field.

The experiments on Christiansø were carried out on Dronningens Bastion in the SE-corner of the island; here, direct light from the island's lighthouse (towards NW-NNW) is screened away by the barren top of the island, and although the passing light beam in the sky is visible, it is mostly faint and supposed not to have any effect on the birds' orientation in the funnels. As on Endelave, all experiments were carried out on moonless nights. From their position on Dronningens Bastion, the birds could see the sky almost down to the horizon. Until transferred to the baskets on the experimental site, the birds were caged in a shielded garden, two by two in plastic baskets covered on top by a plywood plate.

As on Endelave, I intended to carry out the night tests in the funnel under a starry sky, but this was not always possible. On the three first nights (9, 10 and 12 August), the night sky was almost totally overcast with only few stars occasionally visible. The three sunsets were also mostly cloudy, but the position of the sunset was visible. Also, during the three nights of 20, 21 and 22 August, the night sky was initially overcast, but changed to half-covered in the course of the test.

Results

Juvenile Common Redstarts and Pied Flycatchers (2004)

The orientation and activity of each individual is given in Appendix 1. The orientations on all five nights compiled are shown in Fig. 2. Clearly, the sample orientation on the N condition is much more dispersed than that of the controls and of the experimentals on the S condition,

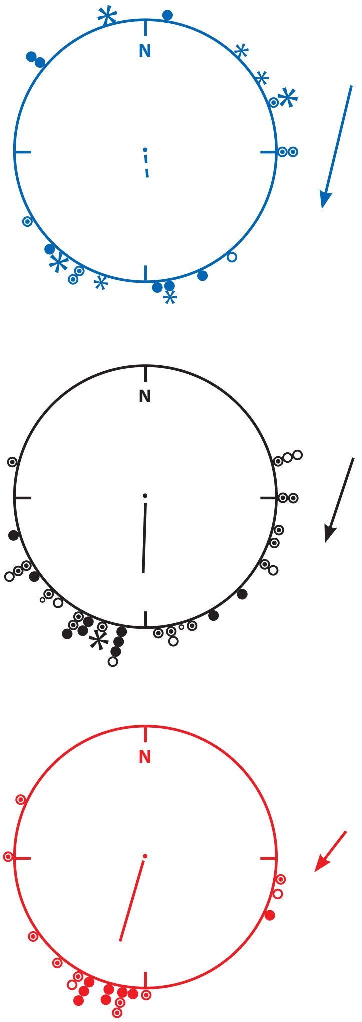

Fig. 2. Orientation of juvenile Common Redstarts and Pied Flycatchers 9-21 September 2004 under a clear starry sky. The orientation and amount of activity of the individual birds are shown as the mean direction estimated to the nearest 5°. In case of a clear bimodal pattern, both peaks were recorded, and the major peak – if there was one – is denoted by a large cross. In case the two peaks in a bimodal distribution were about the same size these are denoted as two medium sized crosses.
The concentration of scratches around the mean direction was estimated and given as high, medium and low concentration, respectively. At very small activity, the mean direction is denoted as a small circle. The lines pointing out from each centre denote the mean vector of directional activity. The line is dashed in case of statistical insignificance (P > 0.05). If two lines point in opposite directions, the group has a tendency for two-directional activity. The upper figure shows the orientation under the N condition with a sample mean vector of 174° – 0.203 (n = 17), or after doubling the angles 209° (9)/29° (8) – 0.168. The middle figure shows the controls with a sample mean vector of 181° – 0.616*** (n = 34), or 182° – 0.629*** (including the two smaller white dots, n = 36). The lower figure shows the orientation under the S condition with a sample mean vector of 197° – 0.720*** (n = 19). The lengths and slope of the arrows besides each circle are measures of the magnetic intensity and inclination under the N, control and S conditions, respectively.
Orienteringen af Rødstjerter og Brogede Fluesnappere (ungfugle) i 2004 under en stjerneklar himmel. Følgende tekst gælder generelt for Fig. 2-8. Hver prik på cirklerne viser gennemsnitsretningen af én fugl anbragt i en tragt. Sorte, plettede og hvide prikker viser tiltagende variation af tragt-aktiviteten omkring gennemsnitsretningen. Små prikker viser meget lav aktivitet. Store krydser viser den største aktivitets-top i en to-toppet aktivitet, medens to ens, mindre krydser viser to-toppet aktivitet med ca. lige meget aktivitet i de to toppe. Stregen udgående fra centrum viser gruppe-gennemsnits-vektoren baseret på retningen af prikker og krydser. Hvis stregen er prikket, er den ikke statistisk signifikant (P > 0,05). Hvis stregen er rettet i to modsatte retninger, viser gruppen tendens til to-toppet aktivitet. Kontrollerne er vist i midten og den simulerede N- og S-betingelse henholdsvis øverst og nederst. Længden og hældningen af pilene ved siden af hver cirkel er et udtryk for den magnetiske intensitet og inklination under de tre betingelser.

● High concentration
⊙ Medium concentration
○ Low concentration
∘ Very small activity
✱ Bimodal, major top
✱✱ Bimodal, two tops

both showing a significant southern orientation close to the standard direction.

Considered in more detail, the orientation of the N experiments on the N condition on the first two starry nights (9 and 10 September) after the displacement from Christiansø, was 79° – 0.359 (n = 8), or after doubling the angles 71°/(251°) – 0.262. The controls showed 162° – 0.675*** (n = 14), and the S experiments on the S condition 211° – 0.666* (n = 8). When applying the Mardia-Wheeler-Watson test, the differences between the N experimentals and both of the other groups were significant at the 0.05 level. The difference between the controls and the S experimentals was not significant (P > 0.05).

On 16 September, under an almost overcast sky (only few stars high up in the sky were occasionally visible) the orientations were: N condition 202° – 0.413 (n = 4), controls 171° – 0.552 (n = 7) and S condition 207° – 0.943 (n = 4). Recall that the (former) S experiments were now tested on the N condition and vice versa. Clearly, there are no significant differences between these orientations. If the three samples are summed, the mean vector is 191° – 0.592** (n = 15).

The orientation on the last two starry nights (19 and 21 September) were as follows: 217° – 0.614 (n = 5, N condition), 204° – 0.716*** (n = 15, controls) and 174° – 0.746* (n = 7, S condition). Remember that the N experimentals on 9 and 10 September were now caged and tested on the S condition and vice versa. There is no significant difference between the three sample mean vectors.

Obviously, there are no clear differences between the orientation on the overcast night 16 September and the four starry nights.

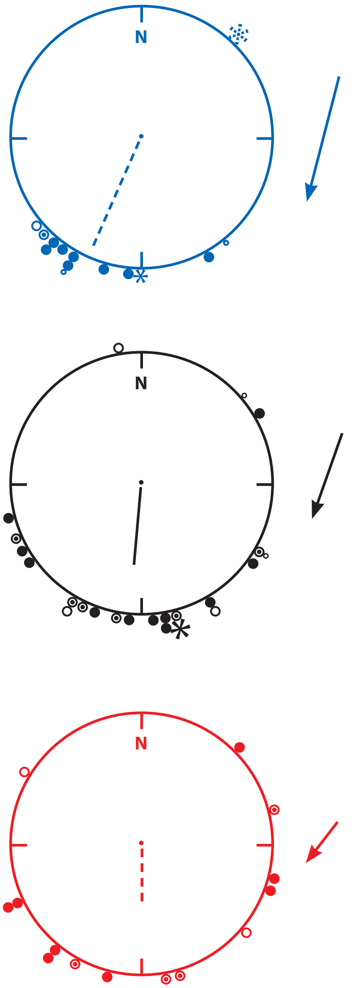

Fig. 3. Orientation of juvenile Robins 8-11 October 2004. The upper figure shows the orientation of the N experimentals with a sample mean vector of 204° – 0.924*** (n = 11), or 190° – 0.765*** (two smaller white dots and the dotted big cross included, n = 14). The middle figure shows the controls with a sample mean vector of 185° – 0.647*** (n = 21), or 178° – 0.582*** (two smaller white dots included, n = 23) and the lower figure the S experimentals with a sample mean vector of 179° – 0.424 (n = 14). See Fig. 2 for further explanation. *Orienteringen af unge Rødhalse i 2004. Se Fig. 2 for yderligere forklaring.*

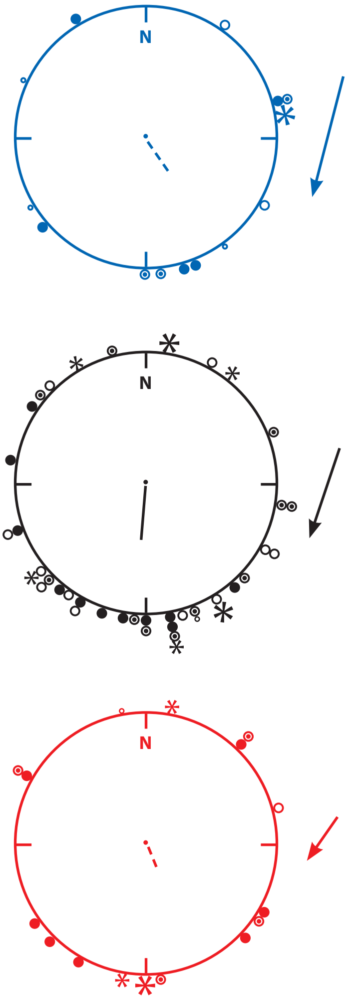

Fig. 4. Orientation of adult long-distance migrants 30 August - 4 September 2005. The upper figure shows the orientations of the N experimentals under the N condition with a sample mean vector of 144° – 0.314 (n = 14). The middle figure shows the control condition with a sample mean vector of 185° – 0.448*** (N = 36). The lower figure shows the orientations of the S experimentals under the S condition giving a sample mean vector of 158° – 0.175 (n = 14). In fact, the orientation of the S experimentals was very different between 30-31 August and 3-4 September (118°/298° – 0.464, n = 8 and 17°/197° – 0.927**, n = 7, respectively). See Fig. 2 for further explanation. *Orienteringen af adulte langdistancetrækkere 30. august - 4. september 2005. Se Fig. 2 for yderligere forklaring.*

Juvenile European Robins (2004)

The orientation of each individual is presented in Appendix 1. Fig. 3 shows the orientation on the four starry nights of 8, 9, 10 and 11 October 2004, where most birds were tested twice, but a few either one or three times. There is no apparent difference between the southerly orientation of the three groups of birds, but the concentration of the sample mean vector of the S experimentals is the smallest and not statistically significant.

Adult Common Redstarts, Garden Warblers, Pied Flycatchers and Spotted Flycatchers (2005)

All orientation and activities by each individual are presented in Appendix 1. The circular distributions and sample mean vectors of the controls and the two experimental groups on 30 August – 4 September, on 6 and 8 September and on 10 and 12 September, are shown in Figs 4, 5 and 6, respectively.

There were no significant differences between the juvenile and adult Pied Flycatchers, or between the species.

All three samples were badly oriented on 30-31 August (not shown), and only the controls displayed standard orientation (although not significantly). During 3 and 4 September, the orientation of the S experimentals was significantly bimodal with the peaks in the standard and the reverse directions. The orientation of the N experimentals and the controls were unimodal and in about the standard direction ($P < 0.05$ for the controls).

I compared the orientation of the individual experimental birds on 3 or 4 September with their previous orientation on 30 or 31 August. In the N experimentals, the sample mean vector was -64° – 0.339 (n = 6) and in the S experimentals -102° – 0.691 (n = 5), i.e. there

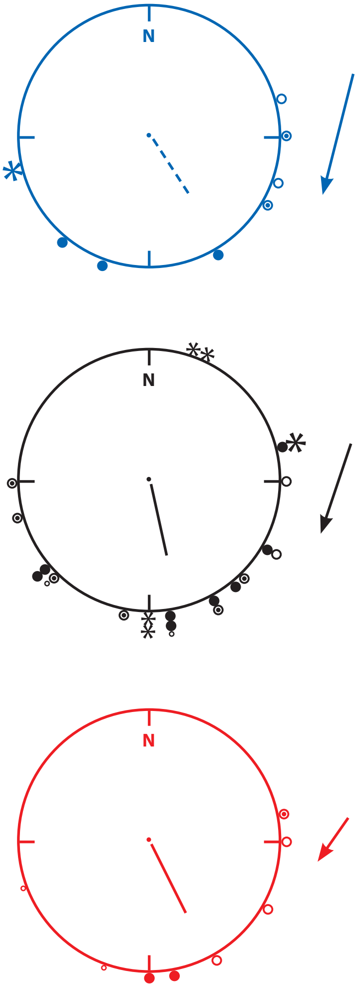

Fig. 5. Orientation of adult long-distance migrants 6 and 8 September 2005. The upper figure shows the orientation of the S experimentals tested on the N condition with a sample mean vector of 146° – 0.516 (n = 8). The middle figure shows the controls with a sample mean vector of 167° – 0.572* (n = 19), and the lower figure the N experimentals tested under the S condition giving a sample mean vector of 153° – 0.624* (n = 8). See Fig. 2 for further explanation. *Orienteringen af adulte langdistance-trækkere 6. og 8. september 2005, hvor S 'ekperimentfuglene' er testet under N betingelsen (øverst) og omvendt (nederst). Se Fig. 2 for yderligere forklaring. Behandlingen synes uden effekt.*

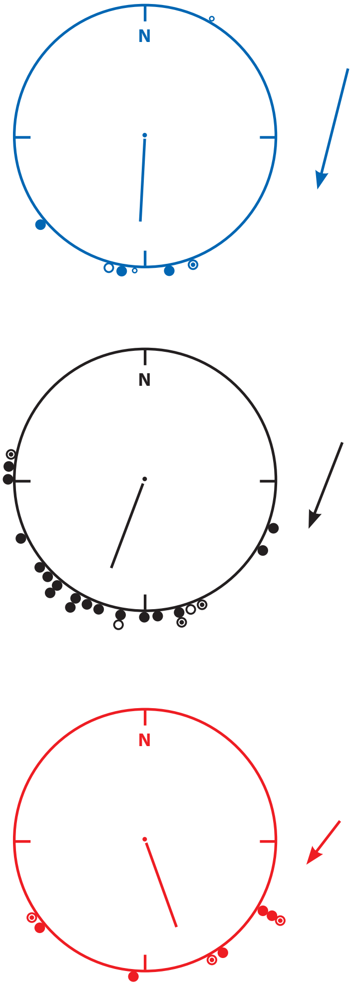

Fig. 6. Orientation of adult long-distance migrants 10 and 12 September 2005. The upper figure shows the orientation of the former controls tested on the N condition giving a sample mean vector of 183° – 0.665* (n = 7). The middle figure denotes former experimentals now tested in the local magnetic field giving a sample mean vector of 200° – 0.736*** (n = 22), and the lower figure former controls tested on the S condition giving a sample mean vector of 160° – 0.720* (n = 8). See Fig. 2 for further explanation. *Orienteringen af adulte langdistance-trækkere 10. og 12. september 2005. Her er der byttet rundt på kontroller og 'eksperimentfugle' tilsyneladende uden nogen effekt. Se Fig. 2 for yderligere forklaring.*

was no clear relation between the orientation on the first and second night. Analyzed in the same way, the controls – including the four juvenile Pied Flycatchers – displayed more or less the same orientation on first and second (later) nights, as the sample mean vector was -17° – 0.544* (n = 11). In five controls, we here used the means of 30 and 31 August, and 3 and 4 September, respectively.

There seems to be no effect of the shift of the N and S experimentals into the S and N magnetic conditions, respectively, during sunset/early night and testing during the first part of the night. Furthermore, if the orientations of the individual experimental birds on 3 or 4 September are compared with orientations on 6 or 8 September, there seems to be no significant shifts in orientation especially considering the N experimentals. The sample mean vector of these birds is -3° – 0.690* (n = 8), or 9° – 0.732* (n = 6). In the first case, two birds tested in August but not 3 or 4 September are included. In the S experimentals the sample mean vector is 46° – 0.538 (n = 6).

Finally, there was no significant difference between the orientation of the three groups in the last period 10 and 12 September (Fig. 6). The former experimentals now caged and tested in the natural magnetic field displayed a rather westerly orientation (sample mean vector 200° – 0.736*** (n = 22), whereas the combined sample mean vector of the former controls now caged and tested under the N or S magnetic condition was 170° – 0.682*** (n = 15). I tested the difference between the two sample mean vectors using the Watson-Williams test, but found no significant difference (0.05 < P < 0.10).

The former experimentals shifted significantly clockwise, when their orientation on 6 or 8 September was compared with the orientation on 10 and/or 12 September. The 12 birds were tested once 6 or 8 September and all except a single bird twice 10 and 12 September. Using the mean of the two directions 10 and 12 Sep-

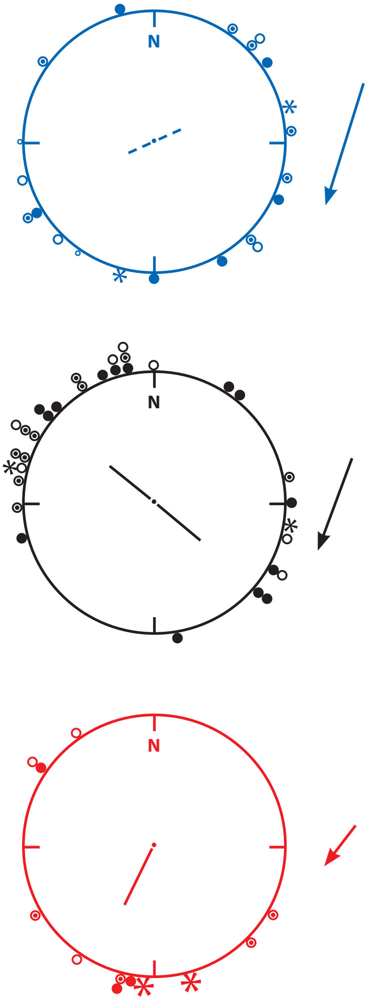

Fig. 7. Orientation of juvenile long-distance migrants 9-14 August 2007. The controls in the middle were significantly axially oriented: 308°/(128°) – 0.459***, n = 32 (considered as unimodal the sample mean vector was smaller: 334° – 0.399**, n = 31). Also the N experimentals (upper figure) were insignificantly axially oriented: 67°/247° – 0.210, n = 20. The S experimentals (lower figure) showed 206° – 0.502*, n = 12. See Fig. 2 for further explanation. *Orienteringen af unge langdistance-trækkere 9.-14. august 2007. Se Fig. 2 for yderligere forklaring.*

tember, the sample mean vector of the deviations was 58° – 0.618** (n = 12). Applying the confidence interval test, the directional shift is significant (0.01 < P < 0.05). Considering the two samples separately, 6 and 8 September was 136° – 0.699** (n = 12), and 10 and 12 September 201° – 0.743** (n = 12). The difference (65°) is close to the deviation of 58° mentioned above. Applying the Watson-Williams two-sample test – not quite legal as the samples are related – the difference is significant (P < 0.01).

There was, however, no significant shift in the former controls (4 or 6 September) now tested under the magnetic N or S condition (10 and 12 September). The two sample mean vectors were 176° – 0.722* (n = 8), and 167° – 0.622* (n = 8), respectively. The sample mean vector of the directional changes was -6° – 0.523 (n = 8).

On the whole, the sample orientation of the adult birds in 2005 was more concentrated in the control condition than in the two experimental conditions. The mean vector of all control conditions was 186° – 0.547*** (n = 77), of all N conditions 159° – 0.431** (n = 29) and of all S conditions 157° – 0.425** (n = 30). There is no difference between the two experimental groups, and considered together and compared with the controls, the difference is significant (0.001 < P < 0.01, Watson–Williams two-sample test).

Experiments 2007

During the first five nights of 9 through 14 August, the orientation of the controls was far from the standard direction at about SSW-SW. Therefore, these nights are considered separately (Fig. 7). The controls were significantly axially oriented: 308°/(128°) – 0.459***, n = 32 (considered as a unimodal distribution the sample mean vector was smaller: 334° – 0.399** (n = 31). The N experimentals were also axially oriented: 67°/(247°) – 0.210 (n = 20), whereas the sample mean vector of the S experimentals was 206° – 0.502* (n = 12).

The orientations on the three overcast nights (9, 10 and 12 August) were: controls 307°/(127°) – 0.446* (n = 20), N condition 206° – 0.236 (n = 11) and S condition 226° – 0.526 (n = 7). The orientations on the two starry nights (13 and 14 August) were: controls 310°/(130°) – 0.480 (n = 12), N condition 67°/(247°) – 0.422 (n = 8) and S condition 179° – 0.575 (n = 5).

In the next period of 17 through 22 August (Fig. 8), the controls was significantly oriented in about the standard direction (SSW): 168° – 0.396** (n = 33). The N experimentals were axially though insignificantly oriented: 172°/352° – 0.206 (n = 23), whereas the S experimentals were significantly oriented at about a right angle to the standard direction: 123° – 0.643** (n = 12).

The night sky was cloudy on the three nights of 20, 21 and 22 August, where the sample orientation of the controls was 174° – 0.408* (N = 18), N condition 177° – 0.273 (n = 13) but looks bimodal, and doubling the angles leads to 177°/(357°) – 0.254, and S condition 139° – 0.734* (n = 7). On the two starry nights 17 and 18 August, the sample mean vector of the controls was 160° – 0.389 (n = 15) or, if doubling the angles, 180°/(360°) – 0.345, N condition 163°/(343°) – 0.156, and S condition 95° – 0.629 (n = 5). Again – as during 9 through 14 August – there seems to be no significant differences between the orientation on overcast and clear nights. The same was concluded for juvenile Redstarts and Robins on Endelave in 2004.

In the last period of 4 and 5 September, the orientation (not shown) was insignificant: The controls showed 112° – 0.394 (n = 9). The orientation of the N experimentals was northerly: 350° – 0.447 (n = 7), and the S experimentals showed about standard orientation: 227° – 0.459 (n = 8).

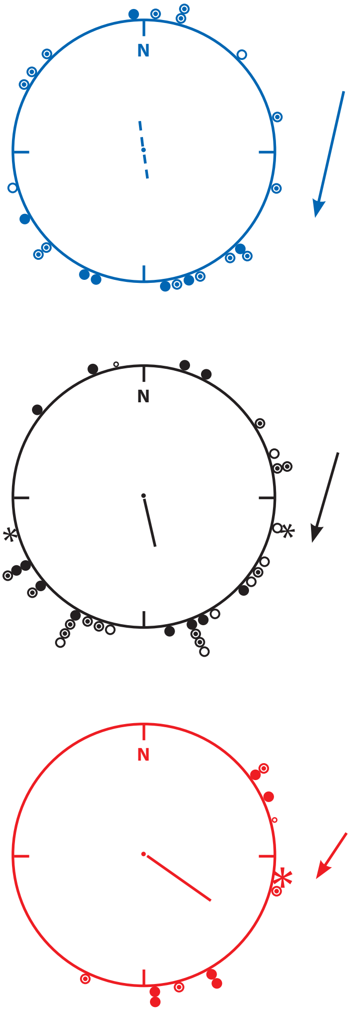

Fig. 8. Juvenile long-distance migrants 17 through 22 August 2007. The controls shown in the middle figure were significantly oriented: 168° – 0.396** (n = 33). The N experimentals (upper figure) were insignificantly oriented: 172°/352° – 0.206 (n = 23). The S experimentals (lower figure) were significantly oriented: 123° – 0.643** (n = 12). See Fig. 2 for further explanation. *Orienteringen af unge langdistance-trækkere 17.-22. august 2007. Se Fig. 2 for yderligere forklaring.*

Summing up

In order to investigate a navigatory effect of the magnetic treatment, the ideal scenario is a control group displaying clear orientation in about the standard direction and the sample concentration should be high and significant.

Considering all periods where the orientation under the control condition was close to the standard direction (i.e. omitting 9 through 14 August and 4-5 September 2007), the total sample mean vector of the controls was 182° – 0.537*** (n = 169), N condition 174° – 0.354*** (n = 83) and S condition 168° – 0.483*** (n = 75). Applying the Watson-Williams test, the difference between the sample mean directions of the three samples were tested two by two. None of the constellations came close to a significant difference (i.e. P > 0.05). However, use of this test is not optimal when the mean vector concentrations is less than 0.75 (Batschelet 1981). I also tested for differences in sample concentrations using the test for the concentration parameter. Here, the difference between the controls and N condition was statistically significant (P < 0.05).

I also investigated whether any differences existed between the three groups concerning the individual concentrations, i.e. our classification of low (1), medium (2) and high (3) for birds showing unimodal orientation on an activity level of at least 'small'. Under the N condition, the ratios came out as 0.13, 0.39, 0.48 (mean 2.35, n = 69), under the control condition 0.21, 0.33, 0.46 (mean 2.25, n = 156), and under the S condition 0.12, 0.36, 0.52 (mean 2.41, n = 69), so obviously there were no significant differences between the groups. Of course, these sample means have limited meaning and should only be taken as a short-cut for comparisons. The differences between the ratio-distributions may be tested two by two by means of e.g. the Kolmogorov-Smirnov two-sample test (Siegel 1956), but none of the three comes close to significance at the 0.05 level (as an example, the accumulated maximum difference between the N condition and controls is 0.08 and the corresponding P = 0.05 is calculated as 0.20).

Discussion

The present results and in general

Rabøl (1998) is a logical entrance to the present paper and discussion. The paper is about orientation following simulated geographical displacements under a planetarium 'starry' sky: Apparently, the birds compensated for the 'displacements', indicating some sort of stellar navigation. Could this experience be extended to include magnetic navigation?

In the planetarium, the magnetic field was the unchanged ambient field inside the building, and the displacements were simulated only by changing the stellar position, i.e. the latitude and/or longitude of the rotating 'stellar' sky. The compass-direction towards stellar N = geographical N was not changed.

In the present outdoor experiments, I simulated a geographical displacement towards N or S by changing the magnetic field. Some of the experiments were carried out under an overcast or close to overcast night sky, and so eliminated the possible co-influence of the stellar sky.

As envisioned in the Introduction (Fig. 1), the research hypothesis considered was a significant change in orientation to about the reverse (on a N/S-axis) under the S condition compared with the control orientation (supposed to be in the standard direction). However, other scenarios were envisioned too, in particular the possibility that a significantly altered magnetic field elicited a reverse orientation in a vector orientation system under both the N and S condition. In that case, magnetic gradient navigation is not involved at all.

Thinking in terms of navigational markers (see below), another pattern may emerge in the long-distance migrants tested: Perhaps the magnetic field of the S condition acts as a sign for shifting the standard compass-course from SSW-SW to SSE (following the shift in the migratory route in southern Spain).

If no reactions were observed when changing the magnetic field, the reason might be that the influence of the magnetic field could not manifest itself under the experimental conditions, or – if the sky was not covered – that celestial compass orientation or navigation dominated and suppressed magnetic navigation. Furthermore, the used magnetic shifts were perhaps too large because we could expect several kinds of relationship (linear, logarithmic, exponential, hump-backed) between magnetic intensity or inclination and the amount of reaction as the dependent variable. If hump-backed, the relationship may be zero or close to zero for large shifts.

An important question is whether the discrepancy in match between the resultant magnetic intensities and inclinations – compared with naturally occurring relationships – had any effect. In particular, whether a navigational response was suppressed. We do not know, and cannot in fact make any qualified guess. Smaller mis-matches between intensity and inclination also occurred in the magnetic 'displacements' of e.g. Fischer *et al.* (2001) and Deutschlander *et al.* (2012). One may guess about the possible presence of forbidden combinations concerning the match between intensity and inclination. However, in the present investigations both were changed up/up or down/down as naturally occurring pairwise values on the Earth.

The magnetic fields of mine were restricted to only two different fields: 1) a vector $\sqrt{2}$ times the size of the horizontal component of the magnetic field in Denmark, or 2) a vector two times the size of the vertical component of the magnetic field in Denmark. Therefore, I had restricted possibilities simulating a geographical displacement based in a resultant magnetic field – in fact I had no choice; 1) was the only possibility.

Further possible reasons for the apparent absence of magnetic gradient navigation may be listed: Magnetic navigation is non-existent; free flying migrants navigate using the geomagnetic field, whereas caged birds cannot detect it or use it for navigation; the experiments were finished too soon (Fischer *et al.* 2003 in their silvereye experiments used a much longer period of adaptation to the Armidale magnetic field); the experiments (in 2004 and 2005) were carried out too late – instead the birds should have been tested shortly after the displacement on the very first night after the transference to the changed magnetic fields.

As the great majority of birds in these experiments were juveniles most people may still consider magnetic gradient navigation a serious possibility in adult birds, and in reference to the wintering area as in the silvereyes (Fischer *et al.* 2003, Deutschlander *et al.* 2012), or the breeding area as in the Baltic Reed Warblers (Kishkinev *et al*. 2013). Furthermore, most people do not believe in gradient navigation in juvenile birds, and the hypothesis of a(n intermediary) moving goal area (Rabøl 1969, 1985) is controversial and not generally accepted (Åkesson 2003). For these people, the lack of magnetic navigation in the juvenile birds will be no surprise.

If the reactions were based only in compass orientation one may wonder about the (insignificant) tendency of higher sample concentrations of the controls compared with in particular N conditions as there were no changes in the direction of neither magnetic N nor stellar N in course of the experimental period. A possible explanation could be that if the magnetic intensities are increased or decreased more than about 20-30%, then magnetically based orientation is not possible until after some days and nights of adaptations (as claimed by e.g. Wiltschko & Wiltschko 1995, see however Wiltschko *et al.* 2006 and Winklhofer *et al.* 2013 for much shorter periods of adaptation). This may explain the lower concentrations on the first nights of 30 and 31 August 2005 (Controls 199° – 0.305, n = 19), N experimentals 101° – 0.042, n = 8) and S experimentals 159° – 0.281, n = 8). However, later on the birds and samples were well oriented when shifted between magnetic intensities far exceeding 20-30%: The relative magnetic intensities under the N, normal and S condition was 1.46, 1 and 0.57, respectively. Thus, the results are indicative that large shifts in total (and/or vertical) intensity has 1) no influence on magnetic compass orientation, 2) the magnetic compass was not used, or 3) magnetic navigation was not carried out or needs more time for manifesting itself.

The reason for exposing the birds to the sunset and stars was to increase the possibilities for maintaining a direction otherwise established by means of the magnetic navigation. Anyway, the experimental procedure should be repeated under indoor or overcast conditions. Clearly, the generalizations of the Wiltschkos building on old experiments with European Robins in Frankfurt-cages is – and has to be – challenged, and systematic experiments with other species in Emlen-funnels should be carried out. The problem is that such experiments – though time-consuming – are not very rewarding and may be difficult to publish in the significant scientific journals.

It could be maintained that the simulated displacement towards S was not sufficient – especially in case of the species wintering in sub-Saharan Africa. As mentioned, the simulated inclination corresponded to the latitude of Sicily, and for a person with a belief in goal area navigation towards an intermediary goal between the breeding area and wintering ground (say France for the present cases) this may be a sufficient displacement – considering the inclination in isolation. Even more convincing, the same holds true in the European Robins where the centre of gravity for the Christiansø ringing recoveries during winter is about Barcelona (Rabøl l981).

The problem is if the important magnetic parameter is the intensity and the birds are navigating towards their wintering area and not an intermediary goal area. Then the simulated displacement (to about Magnetic Equator) must be considered insufficient for producing clear northerly orientation in the Africa migrants. However, in case of the 'displacements' under the planetarium 'starry sky' the birds (in this case Africa migrants) behaved as if they navigated towards an intermediate goal area (Rabøl 1998).

As an important note, I am convinced that caging and handling of the birds are not causing reverse or right angle compass orientations. These reactions are elicited/coupled to lack of food (low weight), bad weather, overcast or conflicting information (personal experience).

Taking all possibilities and experimental results into consideration, the conclusion is that the results are not indicative of a navigation system where (one of) the gradient(s) is based on magnetic intensity and/or inclination:

1) In the juvenile European Robins, the lower concentration in the S experimentals may be a weak sign of such a system, but in the juvenile Common Redstarts and Pied Flycatchers the initial north-easterly (bimodal) orientation in the N experimentals is more indicative of a simple compass system which at least sometimes is influenced by the stronger and steeper magnetic field producing a kind of stress condition leading to reverse compass orientation.

2) In the adult long-distance migrants sometimes (in the first two periods) there was a lower concentration under the N or S condition, or some change in the mean orientation, which, however, is not easily interpreted in terms of a navigational process.

3) In the early August 2007 experiments on Christiansø (where the juvenile birds as mentioned were tested only once and very soon after the trapping and the arrival to the island) the control orientation was bimodal with the prominent main peak in NW. However, both the insignificant ENE/(WSW) orientation of the birds tested under the N condition and the mostly southerly orientation of the birds tested under the S condition are not indicative of navigation towards a goal area NW of Christiansø. According to personal experience, it often happens that the orientation in the early part of the season of the Africa-migrants is bimodally SSW/NNE, but clearly the NW/(SE) orientation of the controls resembles more a right angle response in a simple compass system. However, why a right angle response was only seen in the controls remains unclear.

4) In the late August 2007 experiments on Christiansø, the controls were oriented SSE-S, and if steered by a magnetic navigation system one should expect 'NE' orientation in the experimentals tested under the S condition. However, the ESE-SE orientation observed is explained in a more parsimonious way as unchanged orientation compared with the controls.

Before discussing the results and conclusions of other scientists dealing with magnetic navigation I want to say the following. First, I am not at all against magnetic orientation or navigation. In fact, I am convinced that the magnetic field of the Earth very often has significant and important influences on the compass orientation of migrant birds, pigeons and other animals. Second, this is not a crusade against persons like John Phillips, Kenneth Lohmann, nor the Wiltschkos. However, I has a strong feeling (and I think also a lot of documentation) that magnetic gradient navigation is an overrated and misunderstood phenomenon. Furthermore, the nature of the magnetic compass seems uncertain and needs reconsideration (Rabøl *et al.* 2002, Rabøl unpubl.).

During recent years, the significance and importance of magnetic orientation and navigation has developed in scientific journals and public media to be an almost magic concept. Even the weakest possible signal of magnetic navigation (e.g. Wiltschko & Wiltschko 2003 and Mora *et al.* 2004) is now published in the leading and distinguished scientific journals. One can fear that this allows less critically tested and evaluated results to take advantage (cf. the consideration of Treiber *et al.* 2012 contra e.g. Fleissner *et al.* 2008 and the following discussion in RIN-forum and Mouritsen 2012). Very often, the conclusions appear not to be fully supported by the experimental results, with the risk of bias towards the positive side of magnetic importance and significance (e.g. Beason *et al.* 1997 and Walker 1998). It appears to me that some researchers are not following common rules for logical treatment, and models are proposed which first describe and then later on are used to explain a certain system or mechanism (e.g. Phillips *et al.* 2002b, Fig. 2).

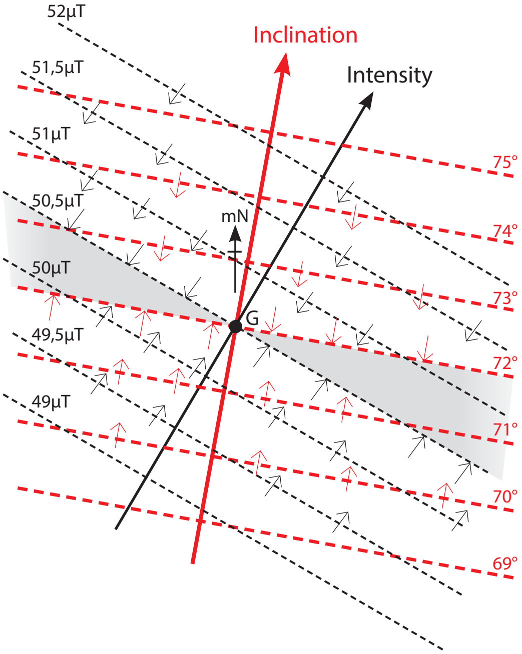

Fig. 9. Approximate isoclines for magnetic inclinations (red dotted) and intensities (black dotted) in the Baltic area, Europe. In reference to geographic N the isoclines of inclination are oriented about 280°/100° and the isoclines of intensity about 300°/120°. The two gradient axes are directed towards 10° (red, inclination) and 30° (black, intensity). The direction towards magnetic N is about 0°. The goal is denoted by a G. *Omtrentlige isolinjer for den magnetiske inklination (prikket rød, 280° /100°) og intensitet (prikket sort, 300° /120°) i det baltiske område. Isolinjerne for inklination og intensitet er tæt på at være parallelle og udgør derfor ikke et velegnet navigations-system. Hvis målet som vist er G (72°, 50,5 µT), bliver orienteringen efter en stedbestemmelse i forhold til målet (følgende de to gradient-akser 190° /10° (rød, inklination) og 210° /30° (sort, intensitet) i den store kvadrant 'NNØ' for målet 190° og/eller 210° (vist med de mange små røde og sorte pile), eller i den store kvadrant 'SSV' for målet 10° og/eller 30°. De fleste steder i disse kvadranter bliver orienteringen derfor ikke rettet direkte mod målet, men skråt til højre eller skråt til venstre for målet. I den lille grå kvadrant 'ØSØ' for målet bliver orienteringen enten mod 10° eller mod 210° afhængigt af om inklinationen eller intensiteten er bestemmende. I den lille grå kvadrant 'VNV' for målet bliver orienteringen tilsvarende enten mod 190° eller mod 30°. Et yderligere problem for et sådant magnetisk navigations-system er, at retningen mod magnetisk N (her ca. 0°) ikke forløber i hverken den ene eller anden gradient-akse. Disse gradientakser skal derfor kendes i forvejen eller findes gennem scanning af et større område og så fastlægges i relation til magnetisk N og/eller stjerne-N. Det er en adfærd, der kræver både tid og en fritflyvende fugl, og den kan derfor vanskeligt realiseres i forbindelse med (simulerede) geografiske forflytninger med efterfølgende tragt-forsøg. Her kan forsøgsfuglen i praksis kun bruge et fælles-estimat (N/S) for de to gradient-akser, hvilket betyder, at et unøjagtigt bi-koordinat-navigationssystem reduceres yderligere til et mono-koordinat-navigationssystem.*

Gradient/coordinate navigation contra navigational markers

Traditionally – when trying to explain the process behind an observed orientation – we have two major concepts: compass orientation and gradient/coordinate navigation. Compass orientation means to keep a course in reference to a compass. Such a compass reference could magnetic N, a star(pattern) or the sun. Normally, in case of gradient navigation two gradients are envisioned. A possible example is shown in Fig. 9 where the gradients considered are the magnetic inclination (axis 10°/190°) and magnetic intensity (axis 30°/210°). The goal is situated in 72°, 50.5 µT. Because the angle between the axes is only 20° – far from the optimal 90° – the navigation process is normally not very precise. For a bird displaced to 75°, 51.5 µT, the course selected on basis of a navigator process is about SSW, whereas the goal direction is about SE. Within the two grey quadrants, the deviation can grow even bigger, up to about 90°.

In recent years, a third concept (though on a different level), navigational marker (alias sign post navigation or position marker) has been added. The major problem with this new concept – it may also be considered as an advantage – is the vagueness. Should the resulting orientation be considered as a compass reaction or a navigational response?

First, compass orientation and gradient navigation are firmly anchored in observations. They are documented processes – or at least people feel they are. A navigatory marker as proposed in the field of hatchling turtles (Lohmann *et al.* 2001) or Pied Flycatchers (Freake *et al.* 2006) is still on the theoretical or explanatory level.

When the juvenile Garden Warblers of Gwinner & Wiltschko (1978) shifted their migratory orientation from SW to SSE, time of the year – in the present case 1 October – supposedly acted as a signal for carrying out the shift.

When the juvenile Pied Flycatchers in the second group of Beck & Wiltschko (1988) experienced the magnetic shift from 0.42G and 52° towards 0.39G and 35°, the shift supposedly was taken as a signal for altering the compass orientation from SW to SSE.

When the juvenile Eleonora's Falcons *Falco eleonorae* of Gschweng *et al.* (2008) crossed magnetic equator, this could be the signal, which forced the birds to change the migratory direction from S to due E (later on in the autumn another sign may shift the E- to a SE-direction).

When the orientation under the S condition (the present experiments) is a little east of the orientation of the controls (sample mean vectors 168° – 0.483*** (n = 75) contra 182° – 0.537*** (n = 169) the S condition could be a marker for changing the magnetic compass from S towards SSE. However, we are guessing as the difference between the sample mean vectors is far from being statistically significant.

In these four cases, one may imagine a system/process connecting to the concepts of sign post navigation/navigational markers/position markers. However, as there is no need for invoking anything else than simple compass orientation this 'something' may better be termed an orientational marker.

Turning to the third group of Pied Flycatchers (Beck & Wiltschko 1988), the compensatory orientation towards the migratory route in western Europe must involve either some kind of gradient navigation towards NW, or the magnetic intensity/inclination acted as a orientational marker and the following orientation was a right angle reaction in a simple compass system.

In case of the famous Lesser Whitethroat *Sylvia curruca* of Sauer (1957), stellar latitude acted as an orientational marker for the shift in orientation from SE to S – at least according to Sauer's interpretation. According to Wallraff (1960), there was no significant directional shift with latitude. However, Rabøl (1988) found a significant correlation between latitude and direction, which – when the partial correlation coefficient between latitude and direction was calculated – disappeared if a third variable, date was included. So probably Wallraff was 'right'.

A turtle moving around in the Atlantic gyre for a year or more has much – at least superficial – resemblance to a migrant bird moving around its migratory route from the breeding ground towards the one or more (Tøttrup *et al.* 2012) wintering areas and back again to the breeding ground. According to most people, the juvenile migrant bird 'follows' a vector orientation programme whereas according to Rabøl (1985), it navigates towards a moving goal area, the 'position' of which is a function of season/time of year.

It is important for the turtle to stay within the gyre where transported (mostly) passively around and back again to the breeding area. If straying too much outside (or inside) the gyre, the turtle needs some responses bringing it back again on the right course.

However, the navigational marker system of the Lohmanns in essence explains little, because it may be handled to explain most directional responses: The problem following Lohmann is that he – initially – has too many degrees of freedom in interpreting his data when shifting only the magnetic intensity or inclination. When shifting both, the degrees of freedom are much more restricted, and finally if introducing the time of year, we are 'down' in the moving goal area scenario. The Lohmanns (for a recent extension see, however, Putman *et al.* 2011) only shifted magnetic intensity and inclination in symphony three times, and perhaps these cases were selected just like the Lohmanns for future presentations selected the most promising orientations in their first paper (1994).

Experiments indicating or claiming magnetic navigation

Since I rejected the claimed magnetic navigation in the investigations considered below, I have explained my reservations in some length in Appendix 2. The most important points follow here.

Perhaps Tasmanian silvereyes are endowed with a magnetic navigation system. The combination of Fischer *et al.* (2003), Deutschlander *et al.* (2012) and the pulse magnetization experiments by the Wiltschkos and co-workers give a slight indication. However, the results could also be interpreted differently. Pulse magnetization experiments with other passerines and pigeons show no indications of a magnetic navigation system.

Perhaps German Pied Flycatchers (Beck & Wiltschko 1988) navigate or display development in orientation indicative of magnetic navigational markers.

Procellariformes (e.g. Benhamou *et al.* 2003) and alligators (Rodda 1984) show no clear signs – in fact no real signs at all – of a magnetic homing mechanism.

There are no signs of magnetic navigation in the old experiments of W. Wiltschko (e.g. 1968) with European Robins, and the indications in White-crowned Sparrows *Zonotrichia leucophrys* (Åkesson *et al.* 2005) are at best marginal. The most parsimonious explanation is that only compass orientation is involved.

The indirect indications of magnetic navigation in Swedish chats (e.g. Fransson *et al.* 2001) are based on unrealistic and/or too speculative interpretations, whereas the Lesser Whitethroat (Henshaw *et al.* 2010) shows some direct indication. However, the results could more parsimoniously be interpreted in other ways.

Danish chats and warblers (this paper) show no signs on magnetic navigation.

Reed Warblers in spring possibly compensate for an eastern displacement by means of some kind of magnetic navigation (Kiskkinev *et al.* 2013).

In pigeons (e.g. Beason *et al.* 1997, Dennis *et al.* 2007) there is no unambiguous evidence of magnetic navigation. In fact, there are a lot of observations and experiments which indicate that magnetic navigation is a 'phantom'. However, the recent findings of Wu & Dickman (2012) once more bring the possibility of magnetic navigation in circulation.

The experiments on juvenile turtles (Lohmann *et al.* 2004), newts (e.g. Phillips *et al.* 2002a) and spiny lobsters (Boles & Lohmann 2003), where the magnetic inclination was changed simulating geographical displacements, are clearly indicative of something like a magnetic navigation system in work. However, at least in the

The many experiments failed to show signs of magnetic gradient navigation. *De mange forsøg kunne ikke påvise navigation efter Jordens magnetfelt.* Photo: Erik Biering, Spotted Flycatcher/*Grå Fluesnapper*.

newts and lobsters the magnetic changes were so large that their relevance for what is going on under natural conditions in the home area remains obscure. Furthermore, several other experiments with adult turtles (e.g. Luschi *et al.* 2007) show no clear sign – or no signs at all – on magnetic navigation. At the very best, hatchling turtles (Lohmann & Lohmann 1994, 1996, 1998) make use of magnetic navigational markers.

Conclusions

Summing up, there are many investigations where (some of) the results are indicative of 'something else' (magnetic) than simple magnetic compass orientation. Indeed, the sum/product of many small, insignificant indications could be considered as a rather strong 'proof' of a magnetic navigation system in operation, if the results presented were not positively selected interpretations in favour of magnetic navigation – which I fear.

Thus, the overall indication of the presence and importance of magnetic navigation in birds and other animals is at best weak and probably not present in the normal strict sense of our conception of gradient/coordinate navigation. Magnetic navigation seems close to deserve the designation an 'evergreen phantom' (Wallraff 1999).

A possible way to resurrection of magnetic navigation could be (1) publication of all results attempting to demonstrate magnetic navigation, i.e. also 'negative' results not pointing towards a magnetic navigation system; (2) avoidance of data filtrations and too much blind hypothesis fidelity, and 3) reconsideration and integration of the two concepts compass orientation and gradient/coordinate navigation.

Resumé

Navigerer trækfugle ved hjælp af Jordens magnetfelt?
I løbet af den sidste snes år er det blevet populært at betragte Jordens magnetfelt som den vigtigste kilde til dyrs navigation.

At navigere vil sige at finde frem til et mål, som dyret ikke sanser direkte, men som det kan beregne eller bedømme den omtrentlige retning imod ud fra observationer af nogle gradient/koordinat-værdier på det sted, hvor det befinder sig. Disse observerede værdier sammenlignes så med et (andet) sæt værdier, der ligger lagret i dyrets hukommelse. Det er nemt at forestille sig navigation i forhold til bredde- og længde-graderne. En brevdue flyttes fx fra sit dueslag i 56° N/12° Ø til et sted på 54° N/13° Ø. Det er to breddegrader mod S og én længdegrad mod Ø. Kursen hjem er således ca. NNV. Bredde- og længde-grader er såkaldte isolinier defineret og bestemt i forhold til sol- og stjernehimlen, og da gradient-retningerne N/S (breddegrad) og Ø/V (længdegrad) står vinkelret på hinanden, er det et ideelt navigations-system med mulighed for en præcis retningsfastlæggelse mod målet.

En trækfugls efterårs-trækrute kan være resultatet af navigation direkte mod vinterkvarteret, eller mod et målområde, der i efterårets løb vandrer ned gennem trækruten og ender i vinterkvarteret. Målområde-navigationshypotesen blev fremsat af Rabøl (1969). Efter mange år i ubemærkethed står den nu til at vinde øget opmærksomhed og anerkendelse. Problemet for hypotesen er en udtalt skepsis med hensyn til ungfugles brug af navigation mod et mål, hvor de ikke fysisk har været til stede før. Det kan ikke lade sig gøre, siger man, men det er en fordom mere end en underbygget antagelse. Unge trækfugle kan alene kompas- eller retnings-orientere, siger man. Det vil sige holde en kurs i forhold til en retnings-reference såsom magnetisk N, stjerne N (retningen mod Nordstjernen) eller Solen. Der er masser af forsøgsevidens for, at trækfugle kan retnings-orientere i forhold til magnetfelt og stjerner, og brevduer i forhold til Solen og magnetfeltet.

Det er muligt at navigere efter Jordens magnetfelt ved at måle/observere to eller flere af følgende gradient/koordinatværdier: 1) Inklinationen (hældningen af de magnetiske kraftlinier, der varierer fra -90° ved den magnetiske sydpol, over 0° ved magnetisk ækvator til +90° ved den magnetiske nordpol), 2) total-intensiteten af magnetfeltet (der stiger fra magnetisk ækvator mod de magnetiske poler), 3) den vandrette komposant af feltet, 4) den lodrette komposant af feltet, samt 5) deklinationen, også kaldet misvisningen (vinkelforskellen mellem retningen mod magnetisk N og geografisk N).

Problemet med at forestille sig brugen af magnetnavigation er det uensartede magnetfelt og især, at isolinjerne for 1) og 2) – de to traditionelt mest oplagte parametre – over store dele af Jorden forløber stort set parallelt – og derfor udgør et par dårligt definerede sæt positions-markører (isolinjerne står vinkelret på gradient-retningerne; se evt. Fig. 9). Desuden er Jordens magnetfelt ikke stabilt. Feltstyrken har i lang tid været svagt men jævnt aftagende, og de magnetiske poler flytter sig lidt fra år til år. Disse ændringer er dog formentlig uden praktisk betydning, fordi de nødvendige genetiske justeringer kan følge med.

Fordelen ved magnetfeltet er, at det altid er for hånden. Det er 'på' hele tiden i modsætning til Solen og stjernerne, der kun er synlige henholdsvis dag og nat og i øvrigt ikke, hvis det er alt for overskyet. Som nævnt ovenfor kan man også navigere efter Solen og stjernehimlen, og især stjerne-navigation forekommer let at programmere og udføre: Højden af stjernehimlens rotationspunkt (meget tæt ved og i praksis lig Nordstjernen) angiver breddegraden, og stjerne-himlens omdrejningsfase definerer længdegraden.

Jeg har altid været skeptisk over for trækfugles (og andre dyrs) brug af navigation efter Jordens magnetfelt, men min holdning bunder alene i manglende eller svag forsøgs-evidens. Jeg kasserer ikke tanken om magnetisk navigation, fordi jeg har sandsynliggjort brugen af navigation efter stjernehimlen (Rabøl 1998). Det ene system udelukker ikke det andet, og både i forskning og i det virkelige liv er det som oftest ikke et spørgsmål om enten/eller men om både/og.

Jeg har i årenes løb læst mange artikler om magnetisk navigation hos fugle og andre dyr, men meget få virker bare marginalt troværdige. I 2004, 2005 og 2007 gik jeg selv i gang med at undersøge sagen ved hjælp af orienterings-forsøg med nattrækkende småfugle. Jeg brugte tragtmetoden, og 'logikken' var den samme som i mine forsøg i stjerne-planetarierne Tycho og Steno (Rabøl 1998), nemlig simulerede geografiske forflytninger. I planetariet viste jeg fuglene en 'stjernehimmel' svarende til en længde- og/eller breddegrad forskellig fra den samtidige stjernehimmel i Danmark. På Christiansø viser den naturlige stjernehimmel således en position på 55° N og 15° Ø. En Rødstjert fanget på træk om efteråret på Christiansø og testet her orienterer sig normalt mod SSV-SV. Hvis fuglen nu eksponeres under en 'stjernehimmel' i et planetarium – eller under den naturlige stjernehimmel – på en position svarende til Kap Farvel (60° N og 45° V), Napoli (40° N og 15° Ø) eller Madrid (40° N og 5° V), forventer jeg en orientering mod henholdsvis ØSØ, NV eller NØ, hvis fuglen stjerne-navigerer mod – hvad jeg skønner – er det i øjeblikket gældende målområde i Nordfrankrig (49° N og 5° Ø). Målområdet gennemvandrer i efterårets løb trækruten fra yngleområdet og ned gennem Vesteuropa og Vestafrika for at ende i vinterkvarteret i det nordlige Ghana (10° N og 0° Ø).

Simulerede forflytninger i et planetarium er at foretrække frem for rigtige, geografiske forflytninger: I et planetarium ændres kun på 'stjernehimlen'. Når fuglen flyttes til en anden position på Jorden ændres ikke bare stjernehimlen, men også andre omverdens-faktorer, såsom magnetfeltet. Hvis der kommer en kompensatorisk reaktion på forflytningen, er det derfor umuligt at vide, hvad der bliver reageret på. Det behøver jo ikke at være ændringen af stjernehimlen.

Det er nemt at simulere en forflytning på 'stjernehimlen' i et planetarium. Det er sværere at simulere en geografisk forflytning ved at ændre på magnetfeltet, især fordi (som nævnt ovenfor) de to mest oplagte gradient-felter (inklinationen og intensiteten) som oftest ændrer sig næsten parallelt og derfor i samspil giver nogle mægtige usikkerheder på fastlæggelsen af en bestemt position og kursen mod målet (Fig. 9).

Jeg råder over otte kunstige magnetfelter, der kan indstilles til at skabe en magnetisk vektor på 1) to gange styrken af den lodrette komposant af Jordens magnetfelt i Danmark eller 2) $\sqrt{2}$ gange styrken af den vandrette komposant af Jordens magnetfelt i Danmark. 1) har været brugt som et opadvendt lodret felt til at skabe et inverteret resulterende magnetfelt med en inklination på -70° (i Danmark er inklinationen af Jordens magnetfelt +70°; se Rabøl *et al.* 2002). 2) er blevet brugt som et vandret felt til at skabe et resulterende magnetfelt, hvor magnetisk N peger mod enten geografisk Ø eller geografisk V (Rabøl 2010).

I forsøgene 2004, 2005 og 2007 blev 2) tilføjet som et lodret felt. Hvis dette bliver vendt 1) nedad, kommer der et resulterende magnetfelt ud med inklinationen +76,5° og feltstyrken 70 µN (hvor det naturlige magnetfelt i Danmark er +70° og 48 µT). Hvis det kunstige felt vendes 2) opad, bliver inklinationen og feltstyrken af det resulterende felt henholdsvis +53° og 27 µT. På Fig. 2-8 er de resulterende felter vist med pile, der afspejler inklinationen og feltstyrken.

For den, der kan magnet-navigere, signalerer 1) en geografisk forflytning til en breddegrad gennem Nordnorge (inklinationen) eller nordligere (intensiteten), medens 2) signalerer en breddegrad gennem Sicilien (inklinationen) eller sydligere svarende til ækvator (intensiteten).

For en magnet-navigerende trækfugl anbragt i en tragt under 1)-betingelsen, forventer jeg derfor en lidt sydligere orientering end i et magnetfelt svarende til Danmark. Under 2)-betingelsen forventer jeg en orientering med en nordlig komponent – i hvert fald hvis fuglen (efterår) navigerer mod et målområde, der p.t. er i Nordfrankrig (se Fig. 1).

Mine forsøg foregik i 29 forsøgsnætter, hvor normalt 16 fugle blev testet pr. nat. Ialt 478 fugle blev undersøgt.

Hvad skete der så? Kort fortalt: Der var intet, der indikerede, at mine fugle navigerede efter magnetfeltet. Det kan man så prøve at forklare – eller bortforklare. 1) De anvendte magnetfelter duede ikke; men det viste jævnlige kontrol-målinger, at de gjorde, og fuglene kan ikke skelne mellem det naturlige magnetfelt og de tilførte, kunstige felter. Hvad de kan sanse (hvis de kan sanse noget) er alene blandingen, det resulterende magnetfelt. 2) I de fleste forsøg blev fuglene testet under den naturlige stjernehimmel, så magnetisk navigation kan have været undertrykt af kompas-orientering eller navigation efter stjernerne. Men det var overskyet nogle nætter, og orienteringen disse nætter lignede orienteringen på de stjerneklare nætter. 3) Fuglene kan ikke magnet-orientere/navigere under de givne betingelser indespærret i en lille tragt. 4) Fuglene kan ikke magnet-navigere selv under naturlige, frit flyvende forhold. Det sidste virker som den mest sandsynlige forklaring, for med hensyn til 3), så er der masser af forsøg, der viser, at trækfugle magnet-kompas-orienterer i tragte.

Hvor står vi så efter mine forsøg? Det kan vi ikke svare på endnu. Men en ting er sikkert, 'magnet-forskerne' vil fortsætte med deres forsøg; de er mange, og de har investeret meget tid, penge og prestige i deres magnet-forsøg. De vil blive ved med i årevis at præsentere resultater, som de vil hævde, er udslag af navigation efter magnetfeltet. Der vil fortsat være mange, der tror på disse resultater, og måske viser det sig til sidst, at det i nogen udstrækning er en strid om ord, et definitionsspørgsmål, om magnetisk navigation eksisterer.

Til slut. Disse undersøgelser handler om, hvorvidt trækfugle navigerer efter magnetfeltet, dvs. bestemmer deres (magnetiske) position i forhold til positionen af et mål beskrevet i magnetiske koordinat-værdier og efterfølgende kompenserer for forskellen. Trækfugle har også en anden orienterings-form kaldet kompas- eller retnings-orientering. De kan fx holde en kurs mod SV ved at orientere sig skråt væk til venstre for magnetisk N eller stjerne N, eller skråt til højre for retningen mod Solen kl. 12 midt på dagen. Alle – inklusive mig – er enige om, at fugle kan kompas-orientere i forhold til magnetfeltet. Mellem de to begreber (gradient/koordinat)navigation og kompas-orientering har der for nylig skudt sig et tredje system ind, der kaldes "sign post navigation" eller orientering på baggrund af "navigatory markers". I princippet er der tale om en reaktion baseret i kompas-orientering, der udløses af overskridelsen af en bestemt omverdens-værdi, såsom en magnetisk inklination på +60° eller en breddegrad på 40° N. Fuglene kompas-orienterer fx mod SV, indtil de når og sanser overskridelsen af en magnetisk inklination på +60°. Så skifter de kurs til SSE. Allerede for mange år siden – i fx Rabøl (1969) – luftede jeg en idé om, at tiden/datoen er inde, som det man nu kalder en navigatory marker. Et sådant tredje orienterings-system vinder tiltagende opmærksomhed og popularitet blandt orienterings-forskerne, fordi det kan forklare (eller tilsløre) en del reaktioner, der ikke kan tilskrives koordinat/gradient navigation i egentlig/snæver forstand.

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Appendix 1: http://www.dof.dk/doft/2014/4.appendix1
Appendix 2: http://www.dof.dk/doft/2014/4.appendix2

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