

Conflict between celestial and magnetic compasses. Orientation experiments with migrant passerine birds from Denmark

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Introduction

For a long time it was almost a law of nature that in migrant birds trapped en route and tested in funnels during autumn migration that the magnetic compass calibrated the celestial and in particular the stellar compass(es), e.g. Wiltschko et al. (1998). This generalization was confirmed by the studies of e.g. Bingman (1987), Sandberg et al. (2000) and Åkesson et al. (2002), however see Able & Able (1995).

Then Cochran et al. (2004) found evidence that in radio-tracked *Catharus*-trushes it was quite on the contrary the sunset compass which calibrated the magnetic compass (and perhaps also and/or through the magnetic compass the stellar compass).

Recently, it then turned into a pushing possibility that access to view of the lower horizontal part of the sky in the sunset/early night phase is of significant importance for the interaction between the celestial and magnetic compasses (Muheim et al. 2006a, b): If the lower part of the sky is screened away the magnetic compass will dominate and calibrate the celestial compass(es) in the subsequent nightly test-phase. If the birds have access to the lower part of the sky the sunset compass will dominate and calibrate the magnetic compass. Implicitly it is clear from Muheim et al. (2006a, b) that the stellar compass(es) is considered secondary and calibrated by one or both of the other two compasses.

Next, Wiltschko et al. (2006) released another important finding. Robins just after one hour of habituation/adjustment to the double magnetic intensity of the normal one would orient properly in this stronger magnetic field. According to earlier expectations (e.g. Wiltschko & Wiltschko 1995) an adjustment period of several days was considered necessary for total magnetic intensities exceeding 20-30% increases or decreases.

Furthermore, for a long time it has been a more or less well known secret/suspicion that prolonged exclusion of celestial cues in caged migrants will favour the influence/dominance of the magnetic compass at the expense of the celestial compasses.

Summing up, the time is ripe for a reconsideration of many of the older conflict experiments and for new carefully described standards in the experiments to come.

In the following is reported four series of conflict (and/or "overcast") experiments three of which were never previously published. It is also important that all results are reported whether or not in accordance with the latest popular hypothesis and thus easily published.

Experiments on Endelave, August-September 1999

Material and methods

During 22-29 Aug. 1999 8 juvenile Pied Flycatchers and 12 juvenile Garden Warblers *Sylvia borin* were trapped as grounded migrants at Blåvand, westernmost point in Denmark. On 30 Aug. the birds were transported to Endelave (about 140 km a little N of E). On 1 Sep. the birds were placed outside two by two in plastic baskets (top and bottom diameter 40 cm and 30 cm, respectively, and height 40 cm) with a free view to the sky and to all sides down to the horizon, except towards W-NW and E-SE where the lower part of the horizon were screened away, 5° and 5° to 10°, respectively.

From 3 Sep. through 16 Sep. most birds were tested every night 1 to 1.5 hour (starting 2 hours after sunset) in funnels (for a description see e.g. Rabøl et al. 2002).

The first three nights (3 through 5 Sep.) all birds were tested in the natural, undisturbed magnetic field. On all occasions the birds experienced a clear (0/8) sunset/early night in the baskets, and a clear starry night in the funnels.

In the period 6 through 12 Sep. (except 7 Sep., see below), the birds experienced a clear sunset/early night in the baskets whereas the tests were carried out in "overcast", i.e. the funnels were covered above with non-transparent but translucent plastic leaving no sight of the stars but reducing the light intensity only to a small degree. 4 flycatchers and 4 Garden Warblers were all the time caged and tested in a magnetic field, where magnetic N was turned about 250° (WSW).

We used four magnetic coil fields as described by Rabøl (2003). In short, each field consisted of two wired quadratic frames (80 times 80 cm) separated by 45 cm, where magnetic N was turned SW (225°). The horizontal strength of the coil field was the square root of 2 times the strength of the horizontal component of the earth magnetic field. The resultant magnetic vector then has the same strength and inclination as the natural magnetic vector but is turned W instead of N.

Unfortunately, in the set up during Sep. 1999 (but not during Oct. 1999, see the next section) we had to place all four coil fields on the same table, and as the distance between the fields were rather small there was some interference/reinforcement between the fields and resultant magnetic N was directed about 250°, whereas the inclination was about 59° (and not 70°), and the total intensity about 1.1 times the normal intensity. There were only small differences between the four resultant fields, and the single birds were always caged and tested with the same coil field. The homogeneity of the magnetic field was probably more 99% within the baskets/funnels, which were placed in the very middle of the coils. According to the expectations of Wiltschko & Wiltschko (1995) there should be no problems for the birds habituated to these magnetic fields to orient properly in the normal way. Furthermore, there should be no problems to carry out proper orientation if transferred from these fields to the about 10% weaker natural magnetic field or vice versa. As only 4 birds could be tested per night the other 4 birds during testing were placed in a tent without sight of the surroundings nor the sky.

On 13 and 14 Sep. the 8 experimental birds were **tested** in the natural magnetic field, and 5 controls were tested one or two times within the coils in the resultant magnetic field with magnetic N turned 250°. Outside the short testing period the birds were placed in their normal baskets under their

normal magnetic conditions, i.e. the controls in the natural field, and the exp.s in the changed field. The sky was clear during sunset/early night, and also at night but the birds were tested under "overcast" conditions.

On 15 and 16 Sep. both controls and experimentals were again tested under their normal magnetic conditions. Again the sunset/early night was clear, and the night was also clear and starry. This time – and for the first time since 5 Sep. - the birds were tested with full access to view the starry sky.

Results

The results are shown in Tab.1, and also some of the results on Figs.1-3.

In the following we have not distinguished between the species as there seemed to be no significant differences.

The orientation on the first night (3 Sep., Fig.1) was clearly bimodal, and the sample mean vector was $115^\circ - 0.121$ ($n = 18$). Doubling the angles leads to $96^\circ/276^\circ - 0.368$ ($n = 18$), or if the bimodal orientation $30^\circ/270^\circ$ is included $94^\circ/274^\circ - 0.358$ ($n = 19$). The easterly peak was a little larger than the westerly.

On 4 Sep. the birds were rather scattered but a peak was found in SE-SSE. The sample mean vector was $180^\circ - 0.310$ ($n = 14$).

On 5 Sep. the orientation was significantly towards the S, but several birds were still rather much E or W oriented (Fig.1, sample mean vector $180^\circ - 0.645^{**}$, $n = 18$).

On 6 Sep. four birds were tested under "overcast" conditions in a magnetic field where magnetic N was directed towards WSW. The orientation of these birds (the exp.s) was $198^\circ - 0.449$, whereas the orientation of six controls tested in the normal/natural magnetic field was $177^\circ - 0.309$. There seems to be no significant difference between the two groups and the combined sample mean vector is $187^\circ - 0.359$ ($n = 10$). Though insignificant this mean direction is close to the mean direction of 5 Sep. However, the orientation seemed somewhat bimodal and doubling the angles the mean vector was $134^\circ/314^\circ - 0.337$ ($n = 10$, five birds between 105° and 155° , mean SE, and five other birds between 230° and 330° , mean W).

On 7 Sep. the birds – as the only exception – experienced an overcast sunset/early night in the baskets, and then when tested in the funnels an overcast sky changing towards a partly clear starry sky for the last hour of the experiment. Because of the initial overcast no plastic sheets were placed above the funnels, and therefore for the last hour the birds were exposed for an at least partly starry sky. Furthermore, for about 15 min.s in the middle of the experiment there was some car-light/horizon glow towards NE, and perhaps this elicited positive photo-taxes in some of the birds and/or in part of the orientation. The orientation of the controls was $75^\circ - 0.568$ ($n = 9$), and of the exp.s $339^\circ - 0.876$ ($n = 3$). Because of the uncertainty of a spurious photo-taxis response towards NE these experiments on 7 Sep. are omitted for further considerations.

As seen at Fig.2 the orientation of the controls during the five nights 8 through 12 Sep. was insignificantly directed towards NE-ENE. The sample mean vector was $53^\circ - 0.290$ ($n = 27$). However, the distribution looks somewhat bimodal and doubling the angles leads to $28^\circ/208^\circ - 0.227$ ($n = 27$), or $25^\circ/205^\circ - 0.230$ ($n = 31$). The orientation of the exp.s was $323^\circ - 0.447$ ($n = 13$).

Also here perhaps the orientation should be considered bimodal and doubling the angles leads to $2^\circ/182^\circ$ 0.305 (n = 13), or $5^\circ/185^\circ$ - 0.348 (n = 14). Applying a M-W-W test on the two distributions – with the means in 53° and 323° , respectively - revealed a significant difference ($P < 0.05$).

On 13 and 14 Sep. the exp.s were **tested** in the natural magnetic field, and the controls in the resultant field where magnetic N is directed towards 250° . The sample mean vector of the exp.s was 338° - 0.316 (n = 12), whereas the sample mean vector of the controls was 104° - 0.521 (n = 5), i.e. the groups acted more or less as in the period 8 through 12 September. We also investigated the change in orientation from 12 Sep to 13 Sep., and from 11 Sep. to 14 Sep., and for 15 possible combinations found a mean vector of 1° - 0.597**. Certainly, for both considerations it looks like nothing changes (significantly) in reference to the preceding orientation on 8 through 12 Sep.

Finally, during 15 and 16 Sep. the controls were again (caged and) tested in the natural magnetic field, and the exp.s in the changed resultant field with magnetic N in 250° (Fig.3). All tests were carried out under a clear starry sky – following a clear sunset/early night. The sample mean vector of the controls is 165° - 0.304 (n = 19), but the distribution looks rather bimodal and doubling the angles leads to $176^\circ/356^\circ$ - 0.340 (n = 20), or $173^\circ/353^\circ$ - 0.346 (n = 19). The orientation of the exp.s does not look bimodal and the sample mean vector is 259° - 0.495 (n = 8). The difference between the two distributions is just significant ($P = 0.05$, M-W-W test). In conclusion, the orientation of the controls looks like standard/(reverse) compared with 5 Sep., whereas the exp.s are oriented reverse in reference to magnetic N or in a right angle to the right of the standard direction in reference to geographical/celestial N.

Discussion

It is important to recall that the birds experienced a clear sunset/early starry night in their baskets ahead of the transfers to and testing in the funnels. On most occasions – except 15-16/9 – the birds were tested during night in "overcast", and on all nights – except 13-14/9 – the birds were tested under the same magnetic conditions as they experienced in the sunset/early night phase.

Considering **3-5/9** we have no possibility to detect whether the orientation was **steered** by the magnetic compass or a stellar compass. Furthermore, we have no possibilities to find out the possible role of the **sunset** compass or whether one of the compasses in the sunset/early night phase **calibrated** the other compasses for the rest of night.

Considering **6/9 and 8-12/9** we expect a southerly standard orientation in both controls and exp.s if the magnetic compass is calibrated in the sunset/early night phase by a sunset/stellar compass.

Such a pattern – though statistically insignificant - was observed on **6/9**. If the magnetic compass in the "overcast" test-phase dominated a possible calibration in the sunset/early night phase the exp.s should orient about opposite to 250° i.e. about ENE. Clearly, this was not the case.

The interpretation of the patterns on 8-12/9 is more difficult – also because the controls were **not** displaying southerly standard orientation. The **controls** showed something like a bimodal **reverse(N)/standard(S)** orientation in reference to both the geographical and magnetic compass (and the magnetic compass could be calibrated by a celestial compass in the sunset/early night phase, or the magnetic compass alone could be the agent in the nightly test-phase; we cannot distinguish between these two possibilities). However, an other interpretation of the orientation of the controls is that they display a unimodal (about) right angle response towards NE-ENE. The

exp.s show a unimodal NW-NNW or a bimodal N/S orientation in reference to geographic N, whereas the orientation in reference to the magnetic N is ENE or ESE/WNW. To us it mostly looks like **reverse**/standard orientation in reference to the magnetic compass calibrated by a sunset/stellar compass in the sunset/early night phase. The dominant reverse component – in both controls and exp.s - perhaps has something to do with the "negative" change from a clear sky in sunset/early night to the more inferior state of an overcast sky in the test-phase (cf. Rabøl 1983, 1985).

Concerning the orientation on **13-14/9** we have to look at the previous period and if the orientation in the period 8-12/9 is considered unimodal and steered by the magnetic compass in the test-phase (53° in the controls and 73° in the exp.s), the exp.s during 13-14/9 tested in the natural magnetic field should orient about ENE whereas the controls tested in the resultant field deflected towards 250° should orient about 63° to the right of magnetic N, i.e. in NW in reference to geographical N.

Clearly, it is not so. The exp.s orient in about NNW and the controls in about ESE in reference to geographical N.

In the other interpretation of the orientation during 8-12/9 the controls orient bimodally NNE/SSW, and the exp.s bimodally N/S. Here the interpretation must be that the magnetic course is calibrated by a celestial compass in sunset/early night. Looking at 13-14/9 we therefore expect the controls tested in the resultant field with magnetic N in 250° that the birds should orient about W in reference to geographical N. On the other hand, the exp.s tested in the natural magnetic field should orient in about ESE.

Clearly, neither this expectation holds true.

What we know (see **Results**) is that the orientation on 13-14/9 in both groups shows the same as in the previous period. This is difficult to explain – except if we follow Bardrum (2001) who suggested that there must be an until now unknown, third kind of compass available on both clear and overcast days and nights.

Finally, we should consider **15-16/9**. Here we should expect a more or less southerly standard orientation in both groups – if a stellar compass dominates (and/or calibrates) the magnetic compass. In fact, it seems to be so – more or less. If the magnetic compass is the dominating and/or calibrating compass we should expect the exps. to orient 110° to the left of the controls. But clearly this is not the case. The orientation is about 90° to the right.

Summing up: In general, the low sample concentrations mostly make clear interpretations difficult or impossible. Anyway, there are some rather obvious tendencies such as northerly/reverse orientation under "overcast" test-conditions. The agent for this reverse orientation seems to be the "deterioration" from a clear sunset/early night to an "overcast" night sky. Finally, calibration of the magnetic compass by a celestial compass in sunset/early night seems to be more important than a separate/independent action of the magnetic compass in the nightly test-phase.

Experiments on Endelave, October 1999

Five Robins *Erithacus rubecula* and ten Blackcaps *Sylvia atricapilla* were trapped at Blåvand during 27 through 30 Sep. and displaced to Endelave the latter date. Because of bad weather – rain and strong winds – the birds were kept indoors until 4 Oct. The birds were then placed outdoors on the tables as described in the previous experiments. The two species are considered together.

Until 6 Oct. incl. all birds were kept two by two in the plastic baskets in the natural magnetic field, and on 5 Oct. tested in funnels during night under the condition of "overcast" after having spend the sunset/early night under natural overcast conditions. On 6 Oct. the cloudiness in sunset/early night was 6/8, whereas the birds when tested during night experienced a partly clear sky with many stars towards the end (6/8 changing towards 2/8). On 5 Oct. ("overcast") the orientation the sample mean vector was $83^\circ - 0.268$ ($n = 7$). However, the distribution looks bimodal and doubling the angles leads to $176^\circ/356^\circ - 0.570$ ($n = 7$), or $172^\circ/352^\circ - 0.418$ ($n = 8$). On 6 Oct. (starry sky) the orientation was more unimodal with a sample mean vector of $187^\circ - 0.399$ ($n = 11$). However, the distribution could also be considered as bimodal, $214^\circ/34^\circ - 0.316$.

From now on the birds were divided in two groups: Controls caged and tested in the natural magnetic field, and exp.s caged and tested in a resultant magnetic field where magnetic N was directed towards 270° (see the previous section). On 8, 9 and 15 Oct. the birds were tested under conditions of a clear starry night, and on 10, 13 and 14 Oct. under conditions of an "overcast" night. During 8, 9 and 15 the sunset/early night was clear. The same was true on 14 Oct., whereas the sky was overcast in sunset/early night on 10 and 13 Oct.

The combined orientation under the clear, starry nights of 8, 9 and 15 Oct. was $221^\circ - 0.736^{***}$ ($n = 14$) in the controls, and $220^\circ - 0.715^*$ ($n = 8$) in exp.s (Figs.4 and 5). On the "overcast" nights of 10, 13 and 14 Oct. the mean vector was $276^\circ - 0.291$ ($n = 8$) in the controls. Or – in fact – the distribution looks bimodal and doubling the angles leads to $220^\circ/40^\circ - 0.310$ ($n = 8$) (Fig.4). In the exp.s the sample mean vector was $238^\circ - 0.382$ ($n = 6$) (Fig.5).

Summing up, the **clear sky orientation** was significant and directed in the standard direction – also in the exp.s, and this points towards a dominance of the stellar compass on the behalf of the magnetic compass.

The **"overcast" orientation** (and in most cases preceded by an overcast sunset/early night) appeared to be scattered SW-WSW or bimodal SSW/NNE. Clearly this orientation – with gN as the compass reference - is in better correspondence with the clear sky orientation of both controls and exp.s. However, no celestial compasses were available for reference nor calibration (and in particular not so on 10 and 13 Sep. with an overcast sunset/early night sky).

Orientation experiments 1974-77

Rabøl (1979) reported on the orientation in a deflected magnetic field (magnetic N = 60°) in seven samples of nocturnal passerines comprising almost 400 single experiments (including the controls). All birds were trapped as migrants – and all except a single sample on Christiansø. Experiments were carried out both spring and autumn (almost all birds juveniles), and most experiments on the same or a few nights after the trapping.

Before the nightly test in the usual plastic funnels the birds were caged indoors in translucent plastic cans, and thus never experienced the sunset or had the possibilities to transform directions from one compass to another.

The exp.s were tested within an artificial magnetic field produced by 2 times 3 bar magnets which where fixed beneath a wood frame mounted on the funnel. The head of the bird standing on the pad in the funnel was approximately level with the magnets. The artificial field was horizontal and magnetic N deflected towards 120° (i.e. between geographic ESE and SE). The distance between

the two rows of each three magnets was calibrated with a compass needle in such a way that magnetic N of the resultant field was directed towards 60° (i.e. between NE and ENE). The total intensity and inclination of the resultant field was thus close to Earth's magnetic field. As the upper diameter of the funnel (30 cm) was less than half the distance between the two rows of magnets, the resultant magnetic field was rather homogeneous and the direction of magnetic N varied less than 10% within the funnel. Probably, the same holds more or less true in case of the magnetic intensity and the inclination.

The orientation of three sub-samples involving 114 single experiments were investigated on **starry** nights (Figs.6, 7, and (10+11+12) in Rabøl 1979) and there was no sign of influence of a magnetic compass, i.e. there were no differences between the orientational patterns of controls and deflected birds. **These experiments are never mentioned in recent surveys of compass conflicts** - probably in particular for the following reason mentioned in the paper: "The resultant magnetic field intensity in the present funnel experiments is too heterogeneous, weak or strong. The birds could interpret this as a severe magnetic storm in which the magnetic information is temporarily unreliable (W. Wiltschko pers.comm.)". Both W. Wiltschko and the author thus felt that the magnetic compass - compared with the stellar compass - was too much disadvantaged by the circumstances; the magnetic compass was not given a fair chance in the competition. Therefore we have to be reluctant concluding too much about a stellar superiority.

Now most experiments reported in Rabøl (1979) were carried out under the condition of **overcast or "overcast"** and it was concluded "- - that in the absence of stellar cues the birds sometimes make use of the earth magnetic field as a directional cue". In two out of seven sub-samples the directional patterns of the controls and the deflected birds were clearly identical, i.e. there were no indications of a significant difference between the patterns (Figs.3 and 9 in Rabøl 1979). Considered in separation the statistical difference between controls and deflected birds was at best marginal in the remaining five sub-samples. However, all differences were to the expected side (supposing an influence of the magnetic compass); comparing the mean vectors the following clockwise deflections were found: 67°, 73°, 86°, 92°, and 123° (which combined to a mean vector yields 88° - 0.943** (n = 5)). In fact, including the two "identical" sub-samples mentioned above (where the deflections were -15° and -19°) the combined mean vector is still significant - and very close to 60° (63° - 0.661*, n = 7).

In conclusion, the magnetic compass probably - at least in most cases - steered the orientation on the overcast/"overcast" nights. This is an important conclusion because as mentioned the heterogeneity of the magnetic field inside the funnel presumably was in the order of 10%. So though perhaps the magnetic compass was somewhat disadvantaged compared with the stellar compass on nights with a starry sky the birds nevertheless were still able to use their magnetic compass within this rather heterogeneous magnetic field produced by six bar-magnets.

Orientation experiments on Endelave, Sep. 2001.

40 juvenile Pied Flycatchers were trapped on Christiansø in the Baltic Sea 19-20 Aug. 2001. On 3 Sep. they were transported to Endelave about 300 km a little N of W.

The starry sky tests of these birds were considered by Rabøl (in print). Here we consider the night tests carried out under condition of an "**overcast**" sky. An "overcast" sky means that the funnel was covered with translucent but not transparent plastic. When tested under "overcast" the birds are not able to see the stars nor the surroundings, including the coils.

In Rabøl (in print) two groups of birds were considered: Outdoor controls and exp.s which spent all their time except for a few times and hours (see below) in the natural, magnetic field (the controls) or in a magnetic field with resultant magnetic N deflected towards E or W (the exp.s).

Here we compare two control groups of birds: 1) **Outdoor controls** (already mentioned, 12 birds), placed outdoors in the natural magnetic field two by two in plastic baskets under the open sky and with an almost full view down to the horizon from 6 Sep. until 28 Sep. These birds often experienced the sunset and the starry night sky. Mostly, the outdoor controls were tested under a starry sky, and then mostly in the natural magnetic field but three times also in a (resultant) magnetic field where magnetic N was deflected E or W. 2) **Indoor controls** (another 12 birds, not considered in Rabøl in print), placed two by two in plastic baskets placed three by three in two tree-boxes measuring 100 times 100 times 80 cm) covered with a translucent (but not transparent) plastic roof. These boxes were placed outdoors in the natural magnetic field and the birds were thus sometimes exposed for a blurred image of the (moving sun) for part of the day. However, the birds had no possibility to see the sunset (at least not the sunset-sky, but perhaps the direction towards the sunset) nor the stars, and were always tested under condition of "overcast". Sometimes the indoor controls were also tested in a magnetic field deflected W or E. These birds were also released on 28 Sep.

We carried out "overcast" experiments with the two control groups on four nights, and the results are presented in Tables 3 and 4. In these tables are also denoted the magnetic conditions during the test.

The results are also depicted in Fig.5, where the contemporary patterns of the outdoor and indoor controls could be compared on the four nights of 19 Sep., 21 Sep., 22 Sep., and 27 Sep. 2001.

The **simple expectation** – following the vector orientation hypothesis - would be that there should be no difference between the two control groups and these should be oriented in about the standard direction (SW) – in reference to magnetic N (supposedly the only compass available during testing). Therefore, when tested in the deflected magnetic field and depicted in reference to geographical N the sample orientation should be bimodal SE/NW with the W-deflected birds in the SE-peak, and the E-deflected birds in the NW-peak.

A more **nuanced expectation** would be that perhaps the indoor controls would be more consistently oriented in the standard direction, whereas the outdoor controls - normally exposed for and relying on the sunset/stars (Wiltschko et al. 1987) - would be more scattered. As the outdoor controls also sometimes in the starry test-phase experienced a deflected magnetic field this could cause further confusion/dispersion.

However, probably no one had forecasted the patterns as depicted on Fig.5. In short, the orientation is mostly in about the standard/reverse axis, but the differences between the two groups striking on most nights.

On **19 Sep.** the **indoors** (in the natural magnetic field) display clear standard orientation, whereas the **outdoors** (in the deflected magnetic fields) are bimodally standard/reverse oriented with the most prominent peak in the reverse direction in reference to magnetic N (mN). The sample mean vector in reference to geographical N (gN) was $110^\circ/290^\circ - 0.620$, but because of the "overcast" condition in connection with the general axis of orientation corresponding to the standard/reverse axis we consider magnetic N as the most obvious compass reference. The sunset/early night as experienced by the outdoors in the baskets was cloudy. On the two preceding sunsets and nights the sky was cloudy and it often rained. On 16 Sep. (Rabøl in print) the outdoor controls experienced a clear sunset/early night in the natural magnetic field but were later on tested during the starry night in the deflected fields. Here the orientation in reference to gN was $235^\circ - 0.823^{**}$ ($n = 8$), and clearly gN was the compass in operation as the orientation in reference to mN was $156^\circ/336^\circ - 0.503$ ($n = 8$), and all four W-deflected birds were in the NW-peak.

After a sunny day on **21 Sep.** the cloudiness increased one hour before sunset, and no clear sunset and only a few stars were experienced by the outdoor controls in the sunset/early night phase. The **indoor** controls spent about 15 minutes in the funnels before a rather heavy rainy shower appeared. The **outdoor** controls were transferred to the funnels immediately ahead of this shower. To the covering of the opaque plastic sheaths producing the "overcast" was now added tree-plates for further protection for the rain, and these tree-plates were on for the next about 35 rainy minutes. No birds – nor papers – became wet but certainly the birds experienced a dark period with the sound of the drumming rain just above their heads. When the rain stopped the tree-plates were removed and the experiment continued (the birds are supposed to be inactive in the dark when covered by the tree-plates) for the next about one and a half hour (except for the first about 10 minutes the sky was clear and starry). The rain – and/or (the darkness under) the tree-plate covering – in the initial phase of testing clearly influenced the both individual activities and orientations; the level of activity was generally low and the patterns more bimodal than normally. Also the concentrations of the individual activities were lower than normal.

A first interpretation would be that the **indoors** – tested in the deflected magnetic fields - displayed a bimodal right angle orientation (ESE/WNW) in reference to magnetic N. The orientation in reference to geographical N was bimodal NNE/SSW, and if we consider a standard/reverse pattern to be more parsimonious than a bimodal right angle response – other things being equal – this pattern should be considered the most "appropriate". However, as far as we know there was no compass available in a straightforward reference to geographical N. The **outdoors** tested in the natural magnetic field displayed a clear bimodal standard/reverse orientation – and perhaps the reverse component was promoted by the rainy shower and temporary covering (and darkening). If so – and the indoors were experiencing about the same situation – it is difficult to consider the two control groups react so differently. So perhaps we have to interpret the reaction of the indoors as standard/reverse in reference to geographical N.

On 20 Sep. the sunset and night was overcast and rainy which perhaps reinforced the reverse component of the orientation.

On **22 Sep.** the sunset for the outdoor controls was rather prominent, but only few stars were visible in the early night phase. We are forced to believe that the **indoors** – tested in deflected magnetic fields – displayed their unimodal standard orientation in reference to geographical N. If depicted in

reference to magnetic N bimodal orientation is displayed, and the four W-birds were oriented around 354°, and the four E-birds around 136° if depicted in reference to magnetic N. This strongly infers that the magnetic compass is without influence on the orientation (see Rabøl in print for an explanation). Clearly, the birds followed a compass in straightforward reference to geographical N. The **outdoors** were badly oriented, but if anything displayed a weak reverse response.

On **27 Sep.** no sunset nor stars were visible in the sunset/early night phase. Most birds were tested in the natural but some in a deflected magnetic field. If the two sub-groups are combined the orientation in reference to magnetic N in both outdoors and indoors displayed the highest sample concentration. The **indoors** were reversely oriented whereas the **outdoors** displayed (close to) standard orientation.

On 26 Sep. the sunset/early night was clear whereas only few stars were visible when the birds were tested during night. The outdoor controls were tested in the deflected magnetic fields and clearly gN was the compass in charge (the sample mean vector in reference to gN was 245° - 0.793* (n = 6), and 97° - 0.295 in reference to mN).

The differences in the orientation between the outdoor and indoor controls is signal that the orientation programme is more complicated than just simple vector orientation: Birds experiencing different environments often behave very differently.

According to Sandberg (2003) lean/fat-free migrants often orient in the reverse direction compared with the standard direction. But the birds in both control groups were not lean but in a well fed physiological state (through the fat-classes were estimated).

Clearly, the results depicted in Fig.5 do not make interpretations of what is going on easier.

A third kind of compass not yet recognized?

In order to describe some of his results Bardtrum (2001) hypothesed about an unknown compass, a "third" compass besides the well known magnetic and celestial compasses.

Sometimes standard orientation (or orientation in the same direction as in the controls) appears in a deflected (or not usable) magnetic field **under conditions (overcast/"overcast") where orientation in reference to a celestial compass is considered to be impossible.**

In the present paper such a pattern was observed on 21 Sep. and in particular on 22 Sep. in the Endelave 2001 experiments (Fig.5), and also in the Endelave 1999 experiments (Fig.4). Furthermore, the phenomenon is observed in Figs. 3 and 9 in Rabøl (1979).

Rabøl (1975) also reported on several cases of Robins tested in "overcast" and under disturbed/deflected magnetic conditions where the orientation was as in the controls (starry sky, natural magnetic field)..

Sometimes, such orientation could be explained as a photo-taxis against the sunset, city-light or the light from a lighthouse. Certainly, we must take much care not to carry out the night experiments too early after the sunset under "overcast" conditions. In principle, it may also be caused by a calibration of the magnetic compass by the stellar compass in the sunset/early night phase on the same or a previous day.

However, in some cases it may perhaps be caused by the mysterious third compass (in a straightforward relation to gN) not yet recognized, and we have to look for under which circumstances such a possible compass is occurring.

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Ind.	Orientation
P1	110, 300, 230, 230, 345 , -, 230/(45) , -, 225 , -, 300, 250/(80), 210
P2	170, 0, 165, -, -, 300 , -, 20/190 , -, 300 , 285/(60), 75, 280 , -
P3	105, 75, 150, -, 0 , -, 355/(250) , -, 20/(150) , -, 20, 15, -, 200
P4	235, 195, 170, 150 , -, 315 , -, dis , -, dis , dis, 40, -, 225
P5	120, 280/(140), 90, 330, 165, 80, 115, 60, 30, 30, -, 60/150 , 170, 30
P6	60, 0, 0, 0, 10, 30, 120, dis, 0, 0, 0, 0 , 130, 165
P7	75, 300, 250, 140, 40, 255, dis, 15/(180), 120/270, 190, -, -, 180, 130
P8	250, 285, 190/(10), 135, 70, 360/230, 310/(150), 330/(15), 45/(255), 30, 35, 60 , 10/(190), 315
G1	25, dis, 240, -, -, dis , -, dis , -, 145/(270) , 140, dis, -, 20
G2	30/270, 135, 220, 315, 10 , -, 0 , -, dis , -, 0, 0, -, 345
G3	105, 120, 105, 155 , -, 230 , -, 10 , -, 360 , 140, 345, 215 , -
G4	290, dis, 195, -, 300 , -, 340 , -, 30 , -, 300, 285, 300 ,
G5	285, 150, 220, 250/(60), 45, 55, dis, 120, 0, 195, 190, 165 , 210, 90
G6	135, 230, 255, dis, 170, 240, 235, 360, 0, 360/160, -, -, 195, 210
G7	255, dis, 190/330, 0, 90, 0, dis, dis, 10, 0, -, -, 200, 55/180
G8	20, 180, 150, 230, 120/(340), 0, dis, dis, 170, dis, -, -, 165, 140
G9	120, 60, 190, -, dis, -, 0, -, 35/185, -, -, -, 340
G9.5	dis, 50/215, 80, -, 10, -, 30, -, 0, -, -, -, 240, 330
G10	330, 150, 150, 105, -. 0, -, 75, -, 120, 90 , -, -,
G10.5	255/(75), 170, 140, dis, -, 330, -, 170, -, 0, -, -, -, 80

Table 1. P and G mean Pied Flycatcher and Garden Warbler, respectively. The symbols denote the orientation in degrees on the fourteen dates in September 1999, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16. Unimodal orientation is denoted as e.g. 170, and bimodal orientation as e.g. 255/(75) or 50/215. In the first case there is a dominant peak (255). In the latter the two peaks are about the same size. Dis-orientation is marked with dis, and no activity with 0. – means no experiment. Bold typing means testing within a coil field with resultant magnetic N in about 250° (WSW).

Ind.	Orientation
B1	350, 285, 250 , -, 305 , -, -, 230/(60)
B2	180, 200, 200 , -, -, -, 190, 140
B3	300/90, 210, 240 , -, 225 , -, -, -
B4	-, -, 225 , -, 270 , -, 30 , -
B4.5	150, -, -, 170 , -, -, -, -
B5	-, -, -, 160, -, -, -, -
B6	-, 240, 240, 165, -, -, -, -
B7	30, 180, -, -, -, 290, 165, -
B7.5	170, 15, 270, 220, 240, -, -, 270
B8	75, 195, 230, 180, 240, -, -, 240
R2	350/(140), 135, -, 300 , -, 165/(20) , -, -
R5	-, 210, -, 250, 230, 360/(180), -, 150/(30)
R6	-, 75, 255, 170, -, 360, 60, 225/75
R8:	-, 90, -, -, -, -, -, 270

Table 2. B and R mean Blackcap and Robin, respectively. The symbols denote the orientation on the eight dates in Oct. 1999, 5, 6, 8, 9, 10, 13, 14, 15. The symbols mean the same as in Table 1, with the exception that – covers dis, zero activity and no experiment.

Ind.	Orientation
P8R	180, 120W , 20W , 255W
P8	185, 20W , 50W , (60)W
PGR	230, 150W , 40/(200)W , (345)E
PG	190, 15/135W , 45W , 45/(145)E
P13R	200, 15E , (100)E , 85/250E
P13	320, 50/220E , 60E , 40
P20R	240, -, -, 30
P20:	285, -, -, 15
P4R	230, 250E , 135E , 50
P4	235, 105E , 80E , (345)
P17R	220, -, -, 355
P17	150/(325), -, -, 150/300

Table 3: Orientation experiments with Indoor exp.s. Endelave 19, 21, 22 and 27 Sep. 2001. All tests were carried out in "overcast". The numbers refer to mean orientation in angular degrees (N = 360°). Most orientations were unimodal, but sometimes a major peak in bi- or tri-modal patterns were found, e.g. 245°/(45°), and sometimes two about equal sized peaks were apparent, e.g. 180°/320°. DIS means dis-orientation, and – means no experiment. W and E mean magnetic N deflected towards W and E, respectively, during the funnel-testing. Here the angel denoted ("paper N") has to be transformed when depicted in relation to magnetic N (by adding 45° (E) or subtracting 45° (W)), or geographical (stellar) N (by adding 135° (E) or subtracting 135° (W)). Bold types mean tested in a magnetic field where magnetic N was turned towards W or E.

Ind.	Orientation
P16B	-, 45/225, 240, 140
P16	250W , 165/360, 20/210, 30/(250)
P18B	-, (60), (110), dis
P18	30W , 210/360, 30/(150), 150
P19B	20W , 70, 30/(225), 180/(65)
P19	70W , 180/(20), 55/(245), 225
P2B	165/(240)E , 60/(240), 300, 195/(45)
P2	185E , 220, dis, 175/(20)
P5B	340E , dis, dis, 210/(20)W
P5	-, 20, dis, disW
P15B	-, 165, dis, disE
P15	10E , 220, 165, 80E

Table 4. Outdoor controls on the "overcast" nights 19, 21, 22 and 27 Sep. 2001.

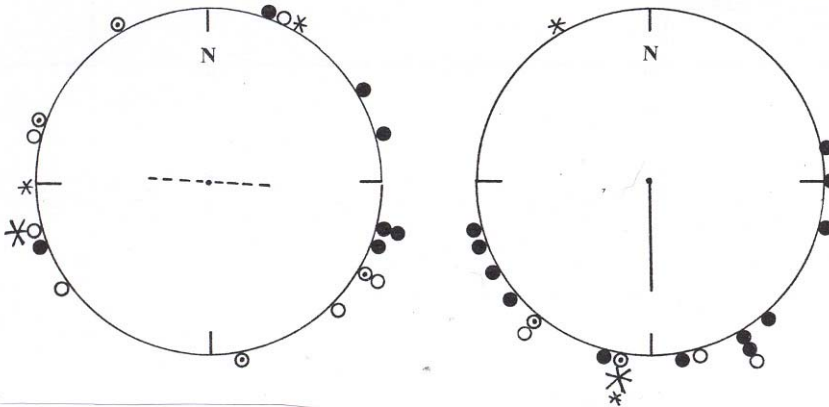


Fig.1. The clear starry sky orientation 3 Sep. (left) and 5 Oct. (right) 1999. On 3 Sep. the orientation is bimodal $94^\circ/274^\circ - 0.358$ ($n = 19$), and on 5 Sep. unimodal $180^\circ - 0.645^{***}$ ($n = 18$). In Figs.1 through 5 black dots signal oriented activity highly concentrated, whereas a dotted and a white refer to medium and low concentrations, respectively. Large crosses signal major peaks in bimodal activity patterns (minor peaks are not depicted). A small cross signals on in a pair of about equal sized bimodal activity.

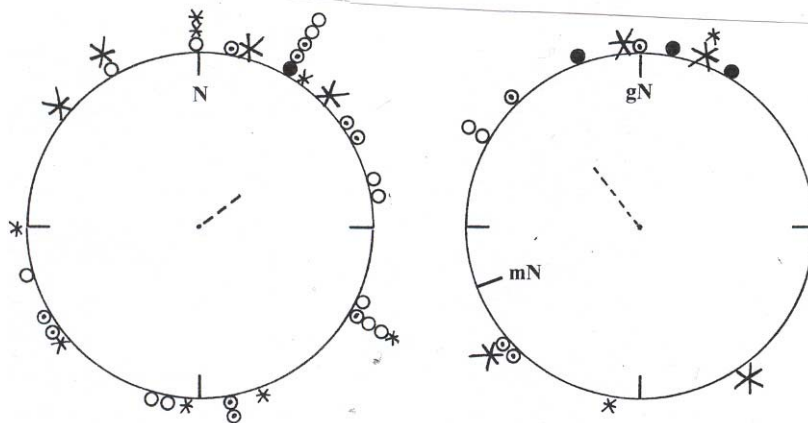


Fig.2. The "overcast" night orientation (following a clear sunset/early night) on 8 through 12 Sep. 1999, controls to the left and exp.s (magnetic N in 250°) to the right. The sample mean vector of the controls is $53^\circ - 0.290$ ($n = 27$). The distribution perhaps looks bimodal. However, doubling the angles leads to a smaller sample concentration ($25^\circ/205^\circ - 0.230$, $n = 31$). The sample mean vector of the exp.s is $323^\circ - 0.447$ ($n = 13$). Also here the distribution perhaps looks bimodal. However doubling the angles leads to smaller sample concentration ($5^\circ/185^\circ - 0.348$, $n = 14$).

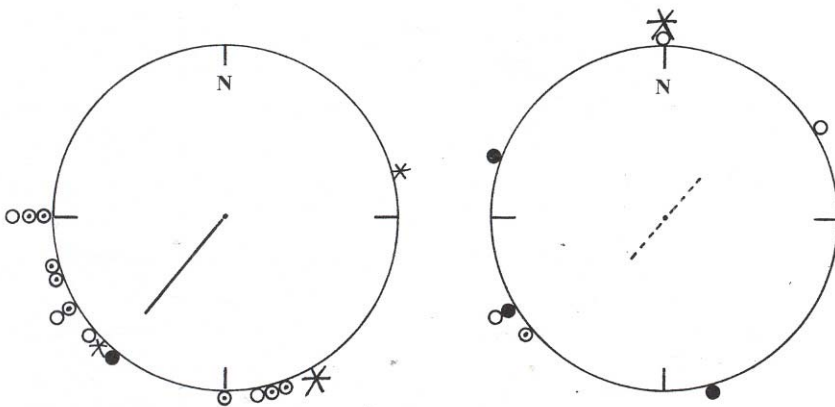


Fig.3. The clear starry night orientation of the controls on 8, 9 and 15 Oct. 1999 (left), and on the "overcast" nights 10, 13 and 14 Oct. 1999 (right). The sample mean vector to the right is $221^\circ - 0.736^{***}$ ($n = 14$), and to the right $40^\circ/220^\circ - 0.310$ ($n = 8$). Concerning the left distribution the three Robins are between 0° and 60° , and five Blackcaps between 165° and 290° .

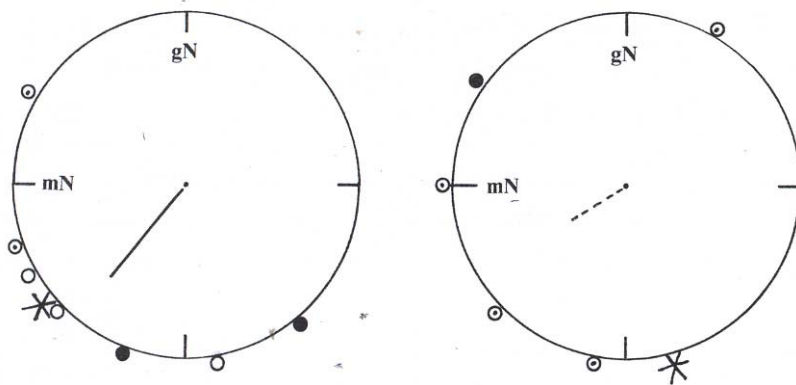


Fig.4. The clear starry night orientation of the exp.s (magnetic N in 270°) on 8, 9 and 15 Oct. 1999 (left), and on the "overcast" nights 10, 13 and 14 Oct. 1999 (right). The sample mean vector to the left is $220^\circ - 0.715^*$ ($n = 8$), and to the right $238^\circ - 0.382$ ($n = 6$).

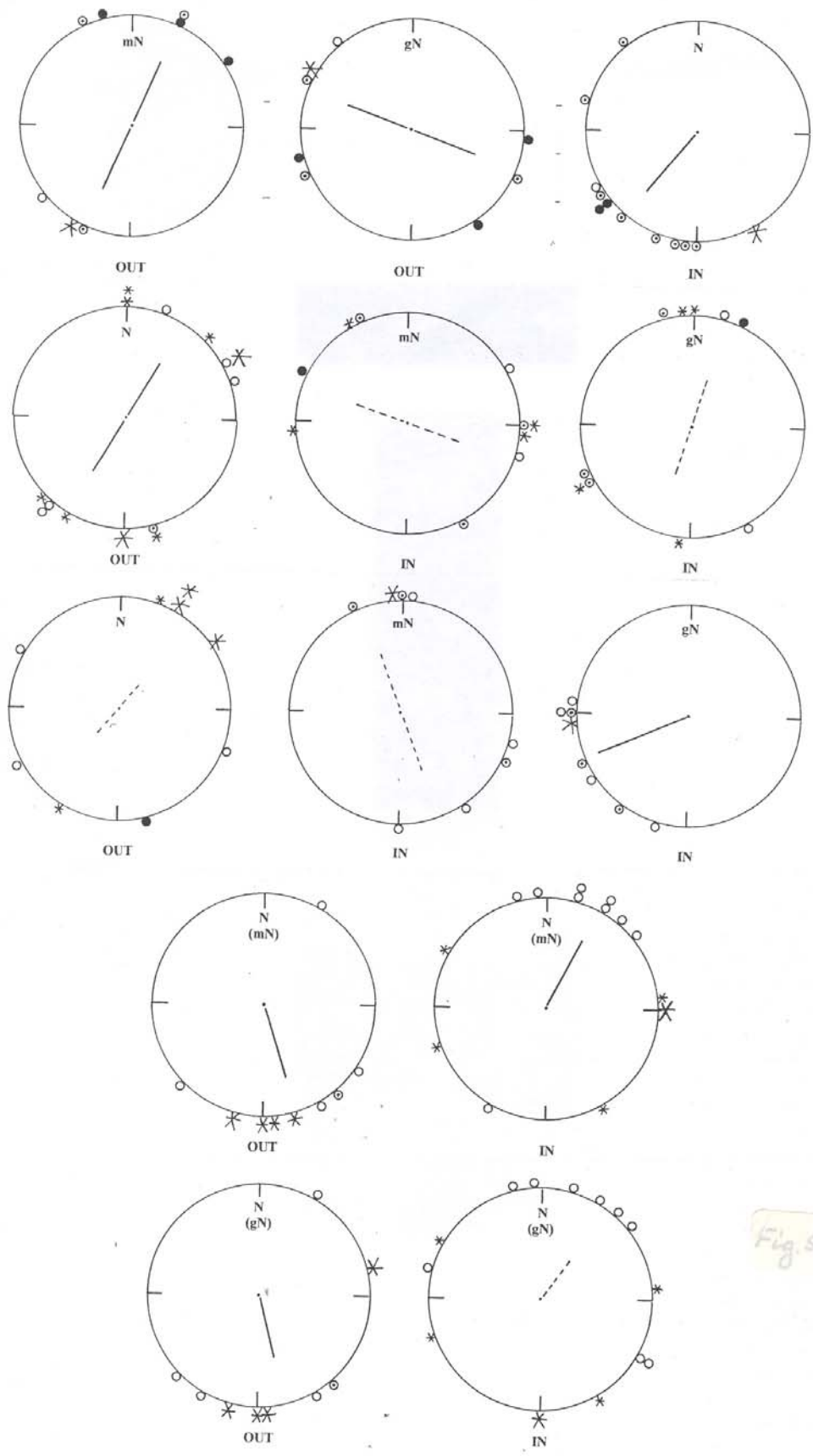


Fig.5. The "overcast" night orientation of the Outdoor controls (OUT) and the Indoor controls (IN) on 19, 21, 22 and 27 Sep. 2001 in reference to $N = 0^\circ = 360^\circ$ (geographical N = magnetic N), or mN = magnetic N, or gN = geographical N.

On 19 Sep. (first row) the sample mean vector of OUT, mN is $24^\circ/204^\circ - 0.641^*$ (n = 8), and of OUT, gN $110^\circ/290^\circ - 0.620^*$ (n = 8), and of IN, N $219^\circ - 738^{***}$ (n = 12).

On 21 Sep. (second row) the sample mean vector of OUT, N is $31^\circ/211^\circ - 0.580^*$ (n = 11), and of IN, mN $109^\circ/289^\circ - 0.495$ (n = 8), and of IN, gN $17^\circ/197^\circ - 0.445$ (n = 8).

On 22 Sep. (third row) the sample mean vector of OUT, N is $40^\circ/220^\circ - 0.290$ (n = 8), and of IN, mN $160^\circ/340^\circ - 0.569$ (n = 8), and of IN, gN $247^\circ - 0.890^{***}$ (n = 8).

On 27 Sep. the sample mean vector of OUT, N/(mN) is $163^\circ - 0.695^{**}$ (n = 9). The two birds in reference to mN are in 125° and 165° . The sample mean vector of IN, N/(mN) is $27^\circ - 0.690$ (n = 10). The four birds in reference to mN are in 15° , 30° , 90° and 210° (fourth row). The sample mean vector of OUT, N/(gN) is $166^\circ - 0.577^*$ (n = 9). The two birds in reference to gN are in 75° and 210° . The sample mean vector of IN, N/(gN) is $37^\circ - 0.432$ (n = 10). The four birds in reference to gN are 120° (two), 180° , and 285° (fifth row)10.