The starry sky orientation of nocturnal passerine migrants caged and/or tested in a magnetic field where magnetic N was deflected towards E or W

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(Med et dansk resume´: Nattrækkeres tragt-orientering under en stjernehimmel i magnetfelter, hvor magnetisk nord er eller forudgående har været drejet mod geografisk øst eller vest)

Abstract

Three samples of long-distance passerine juvenile night-migrants were trapped as passage migrants on Christiansø in the Baltic Sea in autumn and transported about 300 km W to Endelave where funnel-experiments under a starry sky were carried out during the next nights or weeks. The birds were all the time caged outdoors with access to view the surroundings (at least partly) down to the horizon and the day- and night-sky. Some of the birds, the experimentals were caged within a magnetic field where resultant magnetic N was deflected towards geographically E or W. The inclination and intensity of the resultant magnetic field mirrored those of the Earth magnetic field. The purpose of the experiments was to find out whether the magnetic compass in the sunset/early night period calibrated the stellar compass for the rest of the night. Such a response/calibration was not found, but sometimes the magnetic compass in the exp.s when tested within the deflected magnetic fields acted as the dominant compass during night. Surprisingly, in those cases the orientation was about reverse compared with the standard direction.

Introduction

According to one or another of the many reviews of the Wiltschkos (e.g. W. Wiltschko et al. 1998) it appears that the role and influence of the magnetic compass is well understood: 1) migrant birds make use of a magnetic **inclination** compass, 2) the magnetic compass is necessary for the development and establishment of a proper **standard direction** (celestial rotation only delivers N/S-information), 3) the magnetic compass **calibrates** the celestial compasses in the sunset/early night phase, and 4) at least after some delay the magnetic compass **dominates** the celestial compasses.

However, when we carried out new and independent experiments for confirmation of these scenarios we found very little support.

Rabøl et al. (2002) could not confirm 1): no indications were found of an inclination compass in action, i.e. the orientation was not reversed when the magnetic field was inverted in four samples of migrant passerines.

Rabøl and Thorup (2006) could not confirm 2): the orientation of first-time migrants raised and tested under a starry sky and in a useless magnetic field deviated significantly from due S.

The present paper reports our experiments concerning whether scenarios 3) and 4) could be generalized. The meaning of the concepts calibration and dominance follows from Figs.1-3.

3): We found no indications of a magnetic calibration of the stellar compass in sunset/early night. The birds were **caged** in the sunset/early night phase in magnetic fields where magnetic N was deflected towards geographical W or E (same intensity and inclination as the Earth`s field). Later on during night they were **tested** in funnels in the natural magnetic field. Both caging and testing were carried out under a clear sunset/starry sky.

4:) We found that in most cases the stellar compass dominated the magnetic compass. However, **sometimes** birds spending the sunset/early night in a **deflected** magnetic field and later on tested in the same **deflected** field under a starry sky displayed **reverse orientation in reference to the magnetic compass** and seemingly celestial information was ignored at least for **establishing** the course. Furthermore, the amount of (reverse) orientation steered by the magnetic compass was not increasing in course of the experimental period; if anything the trend was decreasing.

Clearly, there is much need for further **repetition, outbuilding and reconsideration** of many of those experiments constituting the basis for the generalizations of the Wiltschkos and co-workers. Here we should be aware that a) perhaps it is not possible to generalize too much from experiments carried out under a **stationary "16-star-sky"**, and also b) that the birds when **caged** in most experiments and for extended periods were deprived of celestial but not of magnetic information; the birds only experienced celestial information in the short periods when tested, and probably therefore more or less ignored the celestial cues at least when establishing the course. Furthermore, c) people should seriously consider that in **outdoor sunset/early night** experiments the stellar compass has been poorly matched compared with the magnetic and sunset compasses. In most experiments only few stars were present and only in the very end of the testing period. Finally, d) there is a clear need of more **night/star** experiments to balance the generalizations based in the many sunset/early night experiments (which often are spuriously co-influenced by sunset-taxes), and e) in particular for **long-term, steady (i.e. repeated 24 hours) conflicts** between magnetic and celestial information. This latter procedure should be considered as a logical extension or replacement of the less "natural" standard **short-term, pulse** procedure for answering questions about compass dominance and/or calibration.

Material and methods

If the **magnetic compass** in the sunset/early night **calibrates** the stellar compass for rest of the night Fig.1 by means of three examples depicts how this will be manifested.

Figs.2-3 depict by means of examples how **partial dominance** of the stellar compass (Fig.2) or the magnetic compass (Fig.3) will be manifested. If the dominance of one of the compasses is **total** the outcomes depicted in relation to stellar N and magnetic N will be as in Fig.1, i.e. the compass without influence will reveal itself by a bimodal pattern with 180º between the peaks at right angles to the mean direction of the unimodal distribution depicted in relation to the dominant compass.

Figs.1-3 thus exemplify that **symmetrical deflections towards E and W** (preferably same number of tests/orientations in the two constellations) is a very strong tool for finding calibration and dominance of one or another of the two compasses.

The birds were caged and tested outdoors (in a glade in a forest) exposed (if not overcast) all the time for the sight of the sun or stars. In the light of Muheim et al. (2006a, b) it seems most important that the birds are exposed to the sky down to the horizon. Clearly, in a forest glade this is not possible but the highest horizontal screening towards N was just about 12º-14º. Towards W (and the sunset) there was an almost unobstructed view down to the horizon, and in the other directions the horizontal screening was about 8º-10º.

The **controls** were **caged** in the undisturbed magnetic field whereas the **exp.s** were **caged** in a magnetic field where resultant magnetic N was deflected from geographical N towards geographical W or E, respectively. The resultant inclination and intensity was unchanged compared with the natural values. Ahead of each nightly experiment we controlled for the resultant direction of magnetic N and the resultant magnetic inclination (+70º). The homogeneity of the magnetic intensity was not measured, but as only one single cage or funnel was placed in the centre of each pair of coils the variation was probably even lower than the 0-1% reported by Rabøl et al. (2002) in the same set up with inverted magnetic inclinations.

The deflected magnetic fields were produced by eight Helmholtz coil sets (quadratic 80 times 80 cm. with 45 cm between the two coils). Magnetic N of the coil field was directed towards SW (four sets) or SE (four sets). The applied magnetic vector was horizontal and the intensity $\sqrt{2}$ times the intensity of the horizontal component of the natural magnetic inclination vector. Therefore, resultant magnetic N pointed towards W or E, respectively. Four of the same coil sets were used by Rabøl et al. (2002) when producing the inverted magnetic fields (by adding a vertical, upwards directed magnetic vector twice the intensity of the normal vertical component of the magnetic inclination vector). In 2002 it was not possible – if we had to retain an unchanged magnetic inclination and intensity – to deflect resultant magnetic N of a single coil field towards geographical E. In this single case (resultant) magnetic N was only deflected towards NE. However, the weak asymmetry occurring in the total sample only has a slight influence on the directional patterns resulting.

The birds were tested in plastic funnels; the caging and testing procedure is described in many earlier papers, e.g. Rabøl (1994, 1998a) and Rabøl et al. (2002). In short, the birds were caged two by two in plastic baskets and tested one by one in plastic funnels (upper diameter 30 cm) lined up on the inner slopes with typewriter correction paper.

The orientation and amount of activity of the individual birds were estimated as previously described by e.g. Raboel (1979, 1993). The pattern of scratches was carefully inspected from above to locate the maxima and minima of activity. The mean **direction** was estimated to the nearest 5°. In case of a clear bimodal pattern both peaks were estimated, and the major peak – if there was one – was indicated by an underlining in the tables, and denoted by a large cross on the figures. Sometimes the two peaks in a bimodal distribution were about the same size and then none was underlined in the tables and denoted as two medium sized crosses on the figures. The **concentration** of scratches around the mean direction was estimated as high (3), medium (2), low (1), or disoriented (dis). In the figures a black, dotted and white circle mean high, medium and low concentration, respectively. 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 (Z), very small (VS), small (S), medium (M), large (L), and very large (VL). For an activity lower than S the mean direction is denoted as a small white circle in the figures. The significance of the sample mean vector was found by application of the Rayleigh test. We also used 1) the confidence interval test and the 2) Watson–Williams test for testing the difference between two dependent and independent samples, respectively (Batschelet 1981). Furthermore, 3) the parametric test for the concentration parameter (Batschelet 1981)

The birds were exposed for the sunset and early night stars in their cages (controls in the normal magnetic field, and exp.s in the fields deflected towards W or E) until at least 1½ hour after sunset, i.e. the brighter stars – in case of a clear sky – were visible for at least three quarters. The birds were transferred to the funnels about two hours after sunset – i.e. no trace of the sunset was visible. The birds were now tested in the funnels for about 1½ hour. Sometimes because of a late descending moon the testing was postponed – i.e. all birds were tested on moonless nights.

Normally the controls were **tested** in the normal magnetic fields and the exp.s in the deflected fields (and then always in the very same field and position as when caged), but sometimes the controls were tested in the deflected fields and the exp.s in the normal magnetic field.

The birds always experienced a clear sunset/early night before testing, but in two cases – 16 and 26 Sep. 2001 - the tests during night were carried out with only very few stars on the sky. Very probably, the birds were still able to **maintain** a course selected in the sunset/early night phase in relation to these few stars, but almost certainly they were not able to **establish** a course a relation to stellar rotational N during these nights.

It is important to notice that the experimental birds of ours **spent all** – or almost all (see below) – their **time** within the deflected (or inverted, Rabøl et al. 2002) fields, i.e. the procedure is different from the normal **short–term** treatment (e.g. the Wiltschkos, see, however, Beck 1984 and Beck & Wiltschko 1988), where the birds only for a short time are **tested** within the deflected (or inverted) field but otherwise are **caged** all the time in the normal/undisturbed magnetic field. We return in more length to this point in the "Discussion". Sometimes exp.s were tested in the natural magnetic field, and thus spent 2-3 hours outside the deflected magnetic field. As mentioned the birds were placed two by two in the cages, and only a single bird of each pair was tested (in the natural or in the deflected field) on any single night. The other bird then spent 2-3 hours outside the deflected field, either in a tent or outside but always without access to the sight of the stars.

Three samples of birds were used. All birds were trapped as grounded migrants on Christiansø in the Baltic Sea (55º 19`N, 15º 12`E) and transported about 300 km to another island Endelave in the southern part of Kattegat (55º 45`N, 10º 18`E) where the experiments were carried out.

The **first** group consisted of 40 1Y Pied Flycatchers *Ficedula hypoleuca* trapped 19-20 August 2001. The birds were caged on Christiansø until 29 August, then in Copenhagen until 3 September when transported to Endelave. From the trapping until 6 Sep. when placed outdoors the birds never observed the starry sky but sometimes the sun. Until the first experiments were carried out on the night of 11 Sep. the birds were freely exposed under the day and night sky, but only a single night (8 Sep.) was starry. From now on the birds often experienced the stars, and between 11 and 26 Sep. tests were carried out on seven moonless and starry nights. 12 and 16 birds constituted the controls and exp.s, respectively.

The **second** group consisted of 14 Pied Flycatchers and 9 Redstarts *Phoenicurus phoenicurus* (all 1Y). The birds were trapped between 28 Aug. and 5 Sep. 2002, and transported to Endelave on 6 Sep. On Christiansø the birds never experienced the sunset or the starry sky. The birds were placed outdoors in the sunset/early night phase on Endelave on 6 Sep. and as the sunset and night was overcast on 6 and 7 Sep. the experiments were postponed until 8 and 9 Sep. The sky was clear both day and night on both dates. The birds were divided in 7 controls and 16 exp.s as equal as possible according to species and trapping date.

The **third** group consisted of 15 Pied Flycatchers and 15 Redstarts. All birds were 1Y except three 2Y+ Redstarts. The birds were trapped between 6 and 9 Sep. 2002, and transported from Christiansø on 11 Sep. Before the transport all birds were exposed for the clear sunset and first part of the starry night on 10 Sep. on Christiansø. The birds arrived to Endelave on 12 Sep. in the morning and were immediately placed outdoors experiencing a clear day, sunset and night and were subsequently tested on the clear starry nights of 12, 13 and 14 Sep. The birds were divided in 14 controls and 16 exp.s as equal as possible according to species, age and trapping date.

Results

The results are depicted on Figs.4-5 and in Tables 1-4, where the first three tables enumerate all nightly individual orientations.

A: **Controls** were tested in the **natural** magnetic field on eight nights.

As a sample the controls were more or less disoriented on the first three nights in 2001 (whereas both concentration and activity of the single bird/nights were mostly rather high). For the three nights lumped together a bimodal pattern (peaks E-ESE and SSW-SW) is rather obvious whereas the total sample mean vector is statistically insignificant (148º - 0.286, n = 34, $0.05 < P < 0.10$).

On 26 September 2001 the same controls were clearly oriented in about the standard direction (206º - 0.864***, n = 12). On 8 and 9 September 2002 the mean vectors of the second control sample were 171º - 0.540 (n = 12), and 203º - 0.935* (n = 5), respectively, whereas the mean vectors of the third control sample on 12 and 13 September 2002 were 151º - 0.657* (n = 10), and 129º - 0.631** (n = 14), respectively.

The total of all controls in the natural field is depicted in the upper distribution of Fig.4, and though the mean **sample** vector is highly significant (166º - 0.463***, n = 81) the distribution certainly looks bimodal with peaks in about the standard direction (215º) and a slightly larger peak in about 120º-125º.

Fig.5A depicts the nightly mean directions of the controls tested in the natural magnetic field. The **grand** mean vector is 164º - 0.893** (n = 8).

B: **Exp.s** were tested in the **deflected** magnetic fields on nine nights, and the results are much varying and surprising.

On the first three nights in 2001 the sample mean vector in relation to magnetic N was 19º - 0.564*** (n = 24), and in relation to geographical (stellar) N 214º - 0.241 (n = 24), i.e. the orientation was about reverse the standard direction in reference to the dominating magnetic compass (cf. Table 4).

However, on the fourth night (15 September) the orientation was totally steered by (what probably is) the stellar compass; the sample mean vector in relation to geographical N is 156º - 0.854** (n = 8), whereas the pattern in relation to magnetic N is bimodal with the two peaks in 61º (the E-birds) and 251º (the W-birds), and an insignificant sample mean vector of 300º - 0.090 (n = 12).

On the remaining five nights – and compared with the corresponding orientations of the controls (see above) and exp.s (see below) in the natural magnetic field – the orientation is clearly reverse in reference to magnetic N on 12 September 2002, but standard/"SE" in relation to geographical N on 23 September 2001, 8 September 2002, and 13 September 2002 (the abrupt shift in the significant compass reference from 12 to 13 Sep. 2002 is noteworthy, Tab.4). On 9 September 2002 the orientation is reverse (36º - 0.621, n = 5) in reference to magnetic N and standard (237º - 0.562, n = 5) in relation to geographical N, i.e. the two tendencies are more or less opposite and obscure each other.

The total of all exp.s in the deflected fields is depicted in the second row of Fig.4. The sample mean vector in relation to magnetic N is 20º - 0.324*** (n = 68), and in relation to geographical N 196º - 0.431*** (n = 68), i.e. on the average (compare Table 4) the "influence" of magnetic N to geographical N is –1 to 1.34.
Fig.5B depicts the nightly mean directions of the exp.s in the deflected magnetic fields. The grand mean vector in relation to **geographical N** is 207º - 0.797** (n = 9).

C: **Controls** were tested in the **deflected** magnetic fields on three nights, and in particular on the first two nights the orientation was clearly in reference to geographical N and directed standard or "SE" – just as in the contemporary experiments carried out with the exp.s in the natural magnetic field (see below).

The total of all controls in the deflected fields is depicted in the third row of Fig.4. The sample mean vector in relation to magnetic N is 92º - 0.255 (n = 21), and in relation to geographical N 222º - 0.508** (n = 21), i.e. the "influence" of magnetic N to geographical N is –1 to 1.99 (compare with Table 4).

Fig.5C depicts the nightly mean directions of the controls in the deflected magnetic fields. The grand mean vector in relation to **geographical N** is 220º - 0.805 (n = 3).

D: **Exp.s** were tested in the **natural** magnetic field on five nights, and the orientation is close to standard, except on 26 September 2001 when significantly bimodal 200º(main peak)/20º - 0.509* (n = 16), and 14 September 2002 when very significantly "SSE" (163º - 0.871***, n = 16).

The total of all exp.s in the natural field is depicted on the lower figure of Fig.4. The sample mean vectors of the birds **caged (but not tested)** under condition of a magnetic field deflected towards W or E, respectively, are 205º - 0.589*** (n = 30), and 197º - 0.567*** (n = 28), respectively. There is no significant difference between these two mean vectors (Watson-Williams test), i.e. there is no after-effects of a previous influence (in the sunset/early night phase) of the magnetic compass.

Fig.5B depict the nightly mean directions of the exp.s in the natural magnetic field. The grand mean vector is 203º - 0.930**.

We tested the difference between a) **controls** in **natural** magnetic fields and b) **exp.s** in **natural** magnetic fields. First, the grand mean vectors for the whole material (Fig.5) were considered. The angular difference between the two mean directions is 37º and according to the Watson-Williams two-sample test statistically significant ($0.02 < P < 0.05$). Considering the sample mean vectors based on all nightly individual mean directions (Fig.4); 166º - 0.463***, n = 81 (controls) and 201º - 0.577***, n = 58 (exp.s) the difference is highly significant (Watson-Williams two-sample test, $P < 0.001$). However, restricting to the two nights (8 and 9 September 2002) with contemporary experiments the sample mean vectors based on the nightly individual mean directions; 190º - 0.692**, n = 11, (controls) and 211º - 0.666**, n = 13 (exp.s) the difference was not significant (Watson-Williams two-sample test, $0.30 < P < 0.40$).

We also tested the homogeneity (Watson-Williams multi-sample test) between all four sample mean vectors in Fig.4, and the four grand mean vectors of Fig.5 (in both geographical N was used as the compass reference in the deflected magnetic fields). In both $P < 001$, and the heterogeneity was clearly caused by the more "South-easterly" orientation of the controls in the natural magnetic field. This is also indicated when the remaining three samples are tested for homogeneity. Both when considering the sample mean vectors based on all nights (Fig.5) and the grand mean vectors (Fig.4) $P > 0.05$.

Tab.4 displays the sample mean vectors in reference to geographical (stellar) N and magnetic N, respectively, on the twelve single nights where birds were tested in the deflected fields. The last column signals the influence of the magnetic compass in relation to the stellar compass. The influence is based on the sample concentrations. A negative sign signals a sample mean direction more or less reverse in comparison with the standard direction (SSW–SW).

Discussion

In short, and in perspective

The inspiration of the 2001- and 2002-experiments was Sandberg et al. (2000) where the nightly departure directions of birds spending the sunset/early sunset in a deflected magnetic field were influenced in a way leading the authors to conclude that the magnetic compass in the sunset/early night phase calibrated the stellar compass for (rest of) the night.

However, when we (roughly) repeated the procedure of Sandberg et al. (2000) the magnetic compass during the sunset/early night phase was **not** calibrating the stellar compass for (rest of) the night. 1) In all cases of **exp.s** tested in the **natural** magnetic field (Figs.4-5) the orientation was in about the standard direction. If the magnetic compass in the sunset/early night phase calibrated the stellar compass the orientation when tested in the funnels during night should be bimodal with the two peaks in about right angles to the standard/reverse axis (Fig.1). 2) Also, in the **exp.s** tested in the **deflected** magnetic fields (Figs.4-5) the prediction of a magnetic calibration in the sunset/early night phase (Fig.1) was not fulfilled. 3) Only the controls tested in the deflected magnetic fields (Figs.4-5) were compatible with the sunset/early night magnetic calibration hypothesis. However, an alternative explanation here is that the birds – during night – make use of the stellar sky as the dominating **establishing** compass reference. Considered in concert with 1) and 2) above this alternative explanation seems to be the best one.

However, certainly in one out of four constellations there was an (after)effect of something going on in the sunset/early night phase: In the **exp.s** tested in the **deflected** fields there was a clear dominance of the magnetic compass in four nights (Tab.4). However, this magnetic influence manifested itself as **reverse** orientation whereas a stellar influence – leading to **standard** or South-easterly right angle orientation - dominated in four other series. It therefore seems as if extended exposure to a deflected magnetic field well into the night sometimes leads to dominance of the magnetic compass. However, in all significant cases the orientation was then **reversed**..

Clearly, the interplay between the stellar and magnetic compasses is not well understood and in this connection one has to consider **the possibility that the magnetic compass is not of the inclination type**. We will return to this discussion later.

Very often the orientation of the controls under the starry sky in the natural magnetic field is E of S, i.e. indicative of a prominent influence of **right angle** more than standard orientation (SSW-SW). Such a reaction may be considered as compensatory orientation for the western displacement (the same pattern was observed in two further samples displaced in autumn 2004, Rabøl pers.obs.). Perhaps the "SE" orientation could also be considered as some sort of basic reaction or "nonsense" orientation – i.e. some sort of forerunner to standard orientation (cf. Rabøl 1997).

Sandberg et al. (2000)

Sandberg et al. (2000) first **funnel**-tested their birds in the twilight (sunset/early night) period. In these experiments magnetic N was deflected towards W (1992) or E (1997, 1998). Then about one hour later the same birds were **released** with a light-stick in the tail and the departure directions recorded. All birds were released in the undisturbed magnetic field of the Earth. Here we only consider the clear sky orientation in autumn.

The **sunset/early night orientation (funnel tests)** was much influenced by a positive sunset-taxis in particular in the Catbirds *Dumetella carolinensis* and Indigo Buntings *Passerina cyanea* (both controls and deflected birds). In the two other species, Red-eyed Vireo *Vireo olivaceus* and Northern Watertrush *Seiurus noveboracensis* - and in particular in the former - there was a clear influence of the magnetic compass on the orientation: in 1992 the deflected birds were oriented 50° counterclockwise compared with the controls, and in 1997-98 80° clockwise the controls.

When the birds - both controls and deflected birds - were **released in the undisturbed magnetic field** under a starry sky the formerly deflected vireos and watertrushes in 1997-98 were 104° and 113° clockwise oriented compared with the release orientation of the controls. Seemingly, in 1992 there was no difference in the release orientation of controls and deflected vireos - at least such a difference was not reported and discussed by the Sandbergs.

Summing up, there is a clear and significant co-influence and after-effect of the magnetic compass. However, the early night starry phase in the cages should have been longer - say at least about one hour. Then the interplay between the magnetic compass and one or both of the two stellar compasses, i.e. celestial rotation/rotational-N and stellar-S in the terminology of Rabøl (1998a) probably had sufficient time for a natural and unbiased development. In the cage-tests and releases of Sandberg & Moore (1996) and Sandberg et al. (2000) rotational-N based on the stars probably had too bad and too short opportunities, respectively, for acting as an establishing compass.

The Wiltschkos - and Bingman

According to one or another of the many surveys of the Wiltschkos (e.g. Wiltschko & Wiltschko 1999, 2003) the magnetic compass is dominating and/or calibrates the sunset and stellar (pattern) compasses at least after some days and nights of delay. This statement refers to birds **grown up in the wild under natural conditions and captured on migration**.

For **hand-raised** migrants celestial rotation in the pre-migratory period sets and calibrates all other compasses - including the magnetic compass. However, according to recent scenarios of the Wiltschkos and co-workers celestial rotation only yields N/S-information whereas the magnetic compass in some way (not explained in operational terms) provides additional E/W-information. As an example the initial SW standard direction of German Garden Warblers is supposedly established by a pre-migratory interplay (setting) between celestial rotation and the magnetic field (Weindler et al. 1996, Weindler et al 1998). The evidence for this hypothesis is at best marginal.

In recent years the Wiltschkos have been concerned mostly with Australian migrants, notably Silvereyes where the magnetic compass dominates the **sunset** compass. However, it is a long time ago the Wiltschkos and co-workers performed cue conflict experiments involving the magnetic compass and the **natural starry sky** and in fact only rather few such experiments have been carried out in European chats and warblers. Among these in particular the results and interpretations of Wiltschko & Wiltschko (1975a, b) and Bingman (1987) are generalized and constitute the hard core of the indication and claim that the magnetic compass is the superior one.

Now, the Garden Warbler- and Robin experiments of Wiltschko & Wiltschko (1975a, b) were carried out using the octagonal Frankfurt-cage and with a view of the starry sky much restricted and in all probability not including the rotational point (Polaris).

Furthermore, the birds were only allowed to see the stellar sky during the tests and not in the much longer intervening periods of caging.

The Robin experiments of Bingman (1987) were carried out with the proclaimed intention to improve the possibilities for the stars acting as a directional cue. The changes and improvements of Bingman were use of Emlen-funnels, and low shielding allowing an almost unrestricted view of the stellar sky. However, **again** the birds were caged indoors and only exposed for the starry sky when tested in the funnels. One may wonder why the birds of Bingman were not caged outdoors with more or less unrestricted access to the sun, sunset and starry sky.

In conclusion, the results of Wiltschko & Wiltschko (1975a, b) and Bingman (1987) cannot be generalized and their argumentations how and why a magnetic compass should take over in course of the autumn are not convincing.

Prinz & Wiltschko (1992) produced results resembling the reverse magnetic orientation reported in the present paper. Pied Flycatchers grew up outdoors with access to the day and night sky. Magnetic N was deflected towards 120° in one group and towards 240° in another. Later the birds were tested in the natural magnetic field without access to celestial cues. The sample mean vector of the latter group was 356° - 0.57*** (n = 110) compared with the controls 237° - 0.51*** (n = 41), i.e. it certainly looks like the magnetic compass was calibrated by celestial rotation. However, the orientation of the first group (magnetic N in 120°) was not about 120° - as expected if the magnetic compass was calibrated by celestial rotation. The sample mean vector was 12° - 0.19* (n = 87), and "It is unclear whether the barely significant mean really represents a diffuse directional tendency or whether the distribution should rather be looked upon as random behaviour". Prinz & Wiltschko (1992) end up with an "explanation" of a true asymmetry of behaviour concerning clockwise and counter-clockwise shifts of magnetic N, but miss the more parsimonious explanation, that the **birds in both groups orient in about due N (reverse) in reference to magnetic N as an after-effect of the conflict between celestial N and magnetic N.** Such an interpretation becomes more obvious if the **grand** mean vectors instead of the sample mean vectors are considered. The grand mean vectors of the 240° group and the 120° group are calculated as 358° - 0.86** (n = 8), and 9° - 0.69* (n = 0.70), respectively

The Ables

In US the Ables continued the Savannah Sparrow experiments initiated by Frank Moore (Able & Able 1996). The Ables performed many ingenious experiments with both hand-raised birds and migrants trapped in the wild.

According to the Ables **celestial rotation** is **THE compass** calibrating all the other compasses and not just in the pre-migratory period but also later and frequently under the migratory progress and in both juvenile and adults birds (Able & Able 1995).

According to the Ables a **stellar pattern compass** ranks low in the hierarchy and may be dominated and calibrated by the magnetic compass (and the sunset compasses). The Ables consider stellar patterns just like landmarks as references for the maintenance of migratory orientation established on the basis of other cues.

Now, clearly in the terminology of the Ables **celestial (including stellar) rotation** (i.e. rotational-N in the terminology of mine) **is something different from and superior to a stellar (pattern) compass** so in this elegant way the scenario of the Ables thrives peacefully together with the claim of the Wiltschkos that the magnetic compass dominates/calibrates/sets the stellar compass. Keine Hexerei, nur Behendigkeit.

Åkesson et al. (2002)

Åkesson et al. (2001, 2002) and Muheim & Åkesson 2002) present funnel experiments from Arctic Canada carried out during **sunset/early night** close to the magnetic North Pole under circumstances of very steep magnetic inclinations. The results are indicative that the two species of sparrows investigated made use of both a magnetic compass and a sun(set) compass, whereas there was no indication for use of a stellar compass – and no one should wonder because only very few stars were present late in the test phase.

The magnetic compass was in the role as the establishing compass whereas the sun(set) compass probably was used only for maintaining the course established in reference to the magnetic compass. Thus the results support the findings and conclusion of Sandberg et al. (2000) and may lead to the **general conclusion that the magnetic compass is dominating and calibrating the celestial compasses.**

However, there are some problems with the findings and conclusions of Åkesson et al. (2002).

The orientation (in reference to geographical N; the declination is +33º) of the juvenile **control** birds during sunset was E (86º), which is a significant deviation from both the expected rhumbline (SSE-SE) and the great-circle (SE) standard directions.

A group of sparrows experienced a 90° counter-clockwise outdoor **deflection** of magnetic N for **one hour in the afternoon starting somewhere 2-4 hours before sunset**. Later on, during sunset the birds were tested in the **natural** magnetic field. These birds – as another group of birds deflected 90º counter-clockwise in the test-phase - changed their orientation about 90° counter-clockwise compared with the controls. Certainly it appears that the magnetic compass in the afternoon-phase **calibrated** the sunset compass used in the sunset/early night phase, where the magnetic compass reference was ignored. This result is really outstanding and its deeper significance was not appreciated by the authors, because there is no "conventional" logic in the observation: The afternoon calibration-phase was well ahead of the sunset/early night phase until now considered and argued for should be the sensitive/important calibration period**.** Furthermore, supposedly the birds were not motivated for take off/migration during afternoon. Perhaps the reaction is a spurious outcome of the treatment and cannot be translated in simple terms to normal orientation.

Cochran et al. (2004)

Cochran et al. (2004) investigated the orientation of released, radio-equipped trushes in Illinois (US), spring. Birds were tracked on their nightly migration under a starry sky and in the natural magnetic field after spending the sunset/early night phase in a cage where magnetic N was deflected towards about geographical E. Controls were heading about N (Gray-cheeked Trush *Catharus minimus*) or NW-NNW (Swainson´s Trush *Catharus ustulatus*), whereas “magnetic” birds on the first night following the just preceding treatment were significantly deflected about 80º - 90º counter-clockwise (i.e. about towards WNW and WSW, respectively). Certainly, it looks like the deflected magnetic compass in the sunset/early night phase is involved in some way, and the interpretation of the authors is that the twilight (i.e. sunset) compass calibrated the magnetic compass which thereafter during the night acted as the compass in relation to which the (standard) orientation was maintained. The duration of this calibration was the whole first night, whereas the migratory orientation on the next nights was as in the controls (according to the authors; however, at least the Swainson´s Trushes compensated significantly to a little E of N ($P < 0.05$, Watson-Williams test) compared with the controls).

Muheim et al. (2006a, b)

Muheim et al. (2006a) reviewed "cue-conflict experiments where **the magnetic field was shifted in alignment relative to natural celestial cues**".

Muheim et al. (2006a) concluded that if not full view of the sunset/sunrise sky down to the horizon then as an after-effect the magnetic compass was not the calibrating compass but quite on the contrary (in almost all cases) the calibrated compass.

The main conclusion of Muheim et al. (2006a, p.13) is "we envision a cue hierarchy in which celestial cues available at sunset/sunrise (presumably polarized patterns from the region of sky near the horizon) provide the primary reference system for calibration of the magnetic compass, while the magnetic compass in turn is used to calibrate the star compasses, as well as zenith polarized light patterns".

Muheim et al. (2006b) exposed Song Sparrows at sunset and/or sunrise for "an artificial polarized light pattern rotated +/-90º relative to the natural polarization pattern at that time of day. During exposure, the birds had a full view of the surroundings, including the horizon, through the polarization filters that produced the artificial pattern". The birds were subsequently tested indoors in the natural magnetic field, i.e. the magnetic compass was (very probably) the only compass available. Following the cue conflict the birds were bimodally oriented at an about right angle to the initial orientation, i.e. Muheim et al. (2006b) demonstrated rather convincingly that a sunset compass calibrated the magnetic compass. However, the data treatment of Muheim et al. (2006b) was rather remarkable and dubious, and their exposure/treatment of the birds in quadratic cages perhaps introduced some spurious and enforced orientation. So their conclusions about a general, primary sunset/sunrise averaging compass calibrating the magnetic and stellar compasses in all migrant bird species were all too far fetched.

Considered in concert with the experiments of Sandberg et al. (2000), Åkesson et al. (2002), Cochran et al. (2004), and ours, the scene is confusing: Sandberg et al. (2000) conclude that the magnetic compass in the sunset/early night phase calibrates the stellar compass. Aakesson et al. (2002) that the magnetic compass in the afternoon calibrates the sunset compass, and Cochran et al. and Muheim et al. that a sunset/sunrise based compass calibrates the magnetic compass (which perhaps later on calibrates the stellar compass). Finally, in our investigation it appears that there is no (long-lasting) calibration between the celestial- and magnetic compasses, but that the stellar compass normally dominates the magnetic compass, and if the latter sometimes dominates the orientation is reversed. At least part of our findings come close to the perception of the Ables.

Some of the reasons for these discrepancies are discussed in the next section.

The compasses at sunset/early night

When people carry out sunset/early night **conflict** experiments the magnetic-, the sunset- and the stellar compasses are implicitly considered **competitively matched**. However, if the birds display directed activity before the stars appears on the sky the stellar compass is clearly disadvantaged. The same holds true for the sunset compass if the experiments are carried farther into the night than the sunset is visible.

In September 2002 we noticed at what time after sunset the stars appeared on the night sky. The first bright stars (Vega, Altair and Deneb high in the sky and Arcturus lower in the W) became visible 40 to 45 minutes after sunset. The next about six or seven stars then appeared 20 minutes later, and Polaris and the patterns of the Big Dipper and Cassiopeia were first prominent about 80 minutes after sunset.

80 minutes after sunset is about the time where most people finish their sunset/early night tests.

Very clearly, under such circumstances the stars are given only low possibilities for manifesting themselves as independent compass references and probably no chance at all acting as a base for stellar navigation.

In clear sky experiments of ours all three compasses were available in the sunset/early night exposure, whereas only the stellar and magnetic compasses were available during the testing phase in the funnels. As already mentioned the sunset/early night phase of ours was generally about a half or one hour longer than normally executed. Clearly, the stellar compass was here given a fair chance in the “competition” with the magnetic compass.

Most people consider the twilight period (= the sunset/early night phase) a most important and significant stage where the three “kinds” of compasses couple together and where a stellar pattern compass is calibrated by the magnetic and/or the sunset compasses. The **hypothetical scenario** is one of 1) a narrow calibration stage closely associated to 2) the simple clock-&-compass hypothesis and the perception of 3) a single directional establishment per migratory step.

The **perception of ours** is somewhat different: When the twilight activity starts in the cages or funnels - or when real departures are initiated - the stars are not yet visible on the sky nor to a sufficient degree available for stellar compass orientation nor (in particular) for stellar navigation (Rabøl 1997, 1998a). To a start only the magnetic compass and the sun/sunset compasses are available for use. Then gradually the stellar compasses come into function and compass calibrations and in all probability also navigatory checks (based on the stellar sky and/or the Earth´s magnetic field?) are carried out several times in course of the night.

Reverse orientation

The sometimes very prominent component of **reverse orientation** in reference to magnetic N of the **exp.s tested in the E or W deflected fields** is an outstanding new result, which both calls for an explanation and is a potential bomb under the magnetic inclination compass hypothesis.

But let us start in more general terms.

Reverse orientation, i.e. orientation in about the reverse/opposite direction compared with the standard direction, is a common phenomenon. Reverse orientation is found in connection with low fat reserves, low plasma corticosterone level, an overcast (and/or rainy) sky, overshoot in migratory progress, headwind migration, lack of food - and **inversion of the magnetic inclination** (e.g. Sandberg 2003, Martin & Maier 1973, Åkesson et al. 1996, Lindström & Alerstam 1986, Rabøl 1967, 1983, 1985, 1994, 1995, Geil et al. 1974, Giunchi & Baldaccini 2004, and Wiltschko & Wiltschko 1996).

Rabøl (1998b) distinguished between **receptor**– and **motivation**–mediated orientation, and when the Wiltschkos in one or another of their many experiments inverted the magnetic field and the orientation of the birds shifted (about) 180º this was clearly considered as a **receptor**-mediated response: the receptor **registered** the inversion as a 180º shift in the compass reference. Therefore, the birds were (said to be) endowed with an **inclination** compass. Now, another partly overlapping distinction could be between a **rigid** and a **flexible** response. In the present context the first means that the (intended) orientation is always in the standard direction, whereas the outcome of a flexible system depends on the circumstances and may be standard, reverse, or right angle orientation, or a combination. In the scenario of the Wiltschkos the reaction to an inversion of the inclination is a rigid response; the bird still performs standard orientation (or believes it does). However, in the natural world the compass reference shifted 180º. Apparently, it never occurred to the Wiltschkos – or others - that the **inverted birds perhaps performed a motivation–mediated reverse response in reference to a magnetic polarity compass** – but clearly this scenario should not be dismissed as a serious alternative.

The outcome of the experiments of Wiltschko & Wiltschko (1992) and Beason (1992) is interpreted as a mixed rigid and flexible response where the change from one rigid (standard) orientation to the next rigid (reverse) orientation is mediated through a transitory state of horizontal magnetic inclination supposed to signal a magnetic equator crossing. In this way the scenario of a steady magnetic inclination compass in charge is "preserved", but in particular in the experiments by Beason (1992) the results are more simply interpreted in terms of a magnetic polarity compass. Also the interpretation of the Wiltschkos could be challenged, and certainly the experiments should be repeated in species like the Robin wintering North of the magnetic equator, and also in trans-equatorial migrants following another treatment than an intermediary stage of horizontal inclination. Perhaps an intermediary stage of vertical inclination, strongly increased or decreased magnetic intensity or one or another kind of significant stress also leads to reverse orientation.

Magnetic short–term contra long-term magnetic deflections

An important scenario of the Wiltschkos is that if the magnetic compass is not dominating at first we just have to wait for some more nights and days and then in the long run the magnetic compass will dominate the celestial compasses (e.g. Wiltschko & Wiltschko 1975a, 1975b, Bingman 1987, Wiltschko & Wiltschko 1999, Wiltschko et al. 1998).

Now in almost all experiments the magnetic deflection was added as an about one-hour (short–term) ″pulse″ in a presumed sensitive period or when tested during night or sunset/early night (Fig.6, type 2). After the funnel-testing the birds returned to their cages in the natural magnetic field, i.e. magnetic N = geographical N. However, as far as we can see this is not an optimal procedure; the optimal procedure in compass conflict experiments should be a more nuanced procedure as the one presented here (Fig.6, type 4) and Rabøl et al. (2002).

In our own magnetic pulse experiments (controls tested in deflected magnetic fields, and exp.s tested in the natural magnetic field) no influence of the magnetic compass was observed. We need more repetitions and the types 3, 6 and 7 (Fig.6). In fact, the most dramatic results – varying from time to time – were in type 4 (Fig.6). So perhaps the strong effects of the pulse experiments by other people has something to do with their standard procedure; the birds are caged inside without exposure for celestial cues except when tested or in a short time ahead of the tests. In the experiments of ours the birds are caged outdoors all the time and (more or less) freely exposed for the sun and stars.

Resume´

Nattrækkeres tragt-orientering under en stjernehimmel indenfor magnetfelter, hvor magnetisk nord er eller forudgående har været drejet mod geografisk øst eller vest

Nogle fundamentale betragtninger og spørgsmål

Trækfugle-forskerne tror på, at unge trækfugle har en normal-trækretning nedlagt i generne. Det må i så fald være i forhold til en ydre kompas-reference, for en retning er ikke noget, der svæver frit i luften.

Hvilke kompas-referencer står til rådighed? Ja – her er magnet-kompasset en oplagt mulighed. Vi bruger det selv.

Et stjerne-kompas forekommer også oplagt: Stjerne-himlens rotations-punkt, tæt ved Nordstjernen, står hele tiden i N og er dermed en simpel kompas-reference.

En tredje mulighed er Solen, der dog er en noget kompliceret kompas-reference, da den bevæger sig i sin bane med 15º i timen, men i forhold til horisonten er bevægelsen mere kompliceret og tids- og breddegrads-afhængig. Dag-dyr bruger dog i stor udstrækning Solen som kompas. Solen indgår således som er en vigtig kompas-reference i Brevduens navigations-system. Solnedgangen og solopgangen er også mulige kompas-referencer – og især et gennemsnit af dem, fordi et saadant altid uanset tid på året og breddegrad udstikker den geografiske N/S-akse.

Ved at udelukke muligheden for at bruge en eller flere kompas-referencer, har man fundet ud af, at trækfugle kan bruge dem alle tre i fravaer af de to andre. Fugle, der vokser op uden at se Solen og stjernerne, er således orienterede i normal-trækretningen, og denne kurs kan vises at være fastlagt i forhold til et magnet-kompas. Nyere forsøg foretaget med Tornsangere på Endelave, tyder også på, at fugle der vokser op i et ubrugeligt magnetfelt har genetisk fastlagt deres trækretning i forhold til Solen og/eller stjernerne.

Man kan nu spørge, hvilket kompas, der er det primære i udviklingsforløbet og/eller det dominerende i den aktuelle situation. I mange år mente man – og især de tyske orienterings-forskere Roswitha og Wolfgang Wiltschko - at magnet-kompasset var det primære, medfødte kompas, der så senere **kalibrerede** de andre kompasser (se Fig.1).

Så kom der resultater frem, der klart tydede på, at stjernehimlens rotationspunkt var en mere primær kompas-reference end magnet-kompasset. Wiltschkøerne har siden arbejdet hårdt på, at få "sidestillet" deres kære magnet-kompas med stjerne-rotations-kompasset, som de hævder kun giver N/S-information, medens magnet-kompasset er nødvendigt for at kunne skabe en trækkurs såsom SV afvigende fra stik S. Ovennævnte Tornsanger-forsøg (Rabøl & Thorup 2006) tyder dog ikke på, at deres (bort)forklaring er frugtbar.

Vi ved endnu ikke, hvordan fugle sanser magnetismen i forbindelse med deres brug af et magnetisk kompas, men meget tyder på, at sansningen sker gennem øjet.

Med hensyn til solnedgangen (og solopgangen) er det det tilsyneladende ikke den lysende V- eller Ø-himmel i sig selv, der virker som kompas-reference. Men især omkring solopgang og solnedgang er himlens lys polariseret, og for dem der kan se det (og det kan fuglene), strækker der sig på disse tidspunkter et lys-bånd mellem N og S, der gaar gennem himlens midtpunkt, zenith. Dette bånd kan bruges som kompas-reference, selv om det ikke i sig selv skelner mellem geografisk N og S.

Konflikt-forsøg

For at forstå hvilket kompas der er det kalibrerende og/eller dominerende er det oplagt at lave konflikt-forsøg. Disse kan laves på mange måder. Det er især nemt gennem kunstige magnetfelter at ændre på det magnetfelt som fuglene sanser, og f.eks. dreje magnetisk N om i geografisk V. I planetarier har man mulighed for at dreje "stjerne-himlens" rotationspunkt i forhold til magnetisk N, og gennem polarisations-filtre kan man dreje solnedgang-himlens bånd af polariseret lys, så det ændrer retning i forhold til geografisk og magnetisk N/S.

Spørgsmålet er så, hvordan fuglene opfatter og reagerer på sådanne **konflikter**, der saedvanligvis er unaturligt store (90º til 120º). I naturen skal vi til områder med kraftige magnetiske anomalier, eller til det nordlige Nordamerika/Grønland tæt ved den magnetiske nordpol. Måske reagerer fuglene på unaturligt store kompas-konflikter ved ikke at følge det ene eller andet kompas, eller lave et simpelt kompromis, men ved at der sker noget helt tredje eller fjerde så som omvendt orientering i forhold til det ene af kompasserne.

Mine – og Sandbergernes - forsøg

I efterårene 2001 og 2002 lavede jeg tragt-orienterings-forsøg med unge Brogede Fluesnappere og Rødstjerte. Fuglene var fanget som trækgæster på Christiansø, og derfra transporteret til Endelave. Fuglene blev anbragt i bure og tragt-testede udendørs i en skovlysning. **Kontrol**-fuglene stod i det uforstyrrede, naturlige magnetfelt, medens **forsøgs**-fuglene var anbragt i bure indenfor nogle kunstige magnetfelter, hvor den resulterende magnetiske vektor havde samme styrke og inklination (+70º) som i det naturlige jordfelt, men **hvor magnetisk N vendte mod Ø (fire felter) eller V (andre fire felter)**. Fuglene havde normalt adgang til at se sol- og stjernehimlen både i burene og i tragtene, hvor de blev testet een ad gangen.

Formålet med forsøgene var især at eftergøre et forsøg af Sandberg et al. (2000), der hos amerikanske nattrækkere, især Red-eyed Vireo *Vireo olivaceus* fandt og konkluderede, at magnet-kompasset i solnedgang/tidlig nat fasen **kalibrerede** stjerne-kompasset, der så var det kompas, som fuglene tog kursen efter i det senere nattræk. Sandbergerne tragt-testede først fuglene solnedgang/tidlig nat indenfor de drejede magnetfelter, og senere samme nat slap de fuglene løs med et lys-mærke i halen og noterede sig bortflyvnings-retningerne. Hvis magnet-kompasset indenfor de opsatte magnetfelter var drejet Ø eller V solnedgang/tidlig nat viste disse fugle i tragtene en henholdsvis højre- eller venstre-drejet orientering i forhold til kontrollerne, der blev testet i det naturlige magnetfelt. Denne drejede orientering blev så opretholdt i bortflyvnings-retningerne om natten i det naturlige magnetfelt, d.v.s. den rimelige konklusion var, at stjerne-kompasset i tragtene i solnedgang/tidlig nat fasen var blevet kalibreret af det drejede magnet-kompas, og at den drejede orientering senere på natten blev fastholdt i forhold til stjerne-kompasset, medens informationerne fra magnet-kompasset nu blev ignoreret.

Jeg gentog disse forsøg af Sandberg et al. (2000) dog således, at **fuglene blev tragt-testede om natten efter at have tilbragt solnedgang/tidlig nat i deres bure**; så jeg kender faktisk ikke deres orientering i denne første fase. **Kontrol**-fuglene blev normalt (8 gange) tragt-testede i det naturlige magnetfelt, men jeg undersøgte også 3 gange deres orientering i de Ø- eller V-drejede magnetfelter. **Forsøgs**-fuglene blev normalt (9 gange) tragt-testede i de Ø- eller V-drejede felter, men også (5 gange) i det naturlige magnetfelt. Specielt den sidste konstellation er interessant, fordi den i princippet svarer til, hvad Sandbergerne gjorde, og på Fig.1 i er vist (tredje raekke), hvordan nat orienteringen i mine forsoeg burde falde ud efter en magnetisk kalibrering solnedgang/tidlig nat. Jeg fandt dog **ingen spor af en sådan kalibrering** (Fig.4).

Som det i øvrigt fremgår af resultaterne på Figs.4-5 – sammenlignet med modellerne på Figs.1-3 – er orienteringen normalt ikke domineret af et magnet-kompas. Det er klart nok, at den **dominerende retningsgiver** mestendels er relateret til **geografisk N**, og derfor med meget stor sandsynlighed er et **stjerne-kompas.**

I forsøgene ses dog **dominans af et magnet-kompas** i fire nætter ud af de ni, hvor **forsøgs-fuglene blev tragt-testede i de Ø- eller V-drejede magnetfelter** (se Tabel 4). I alle disse tilfælde – og i øvrigt generelt for testene i et Ø- eller V-drejet magnetfelt – er orienteringen imidlertid **omvendt** (reverse) i sammenligning med normal-trækretningen. Dette resultat var højst uventet; det er ikke erkendt før, men bortset fra det optræder omvendt træk/orientering ganske ofte især under bestemte omstændigheder såsom ved lavt eller manglende fedtindhold, under en overskyet himmel, efter forlænget forårstræk, og i forbindelse med modvindstræk. Desuden efter invertering af magnetfeltets hældning (inklination). Bortset fra det sidste formenes et omvendt træk at have overlevelsesværdi i den pågældende situation, medens omvendt orientering i forbindelse med en invertering af inklinationen er blevet tolket som normal orientering som opfattet af fuglens magnetiske sanse-mekanisme.

Forskellige stjerne-kompasser

En nøjere granskning af resultaterne tyder på, at et eller flere stjerne-kompasser bruges til at **fastlægge** (establish) og/eller **fastholde** (maintain) kursen efter.

Der er nemlig tilsyneladende mere end eet stjerne-kompas.

Det vigtigste – og det der formentlig fastlægger kursen – er stjernehimlens rotationspunkt. Det kaldes også rotational N, celestial(stellar) rotation eller Nordstjernen (Polaris). Et andet er det man kan kalde et syd–himmel kompas: Stjernerne på sydhimlen bevæger sig som Solen i en bue fra øst over syd mod vest, og de er derfor velegnede til at fastholde en kurs efter. Fuglene skal blot huske at korrigere med ca. 15º i timen for bevægelsen hen over himlen for at kunne bruge stjernene på sydhimlen som et kompas. Jeg har kaldt et sådan kompas for et "time-compensated stellar S compass" og det bruges formentlig meget af trækfuglene om efteråret, når fuglene skal mere eller mindre syd på og derfor har kursen rettet mere eller mindre mod stjernen på sydhimlen. En gang i mellem bliver det så formentlig kalibreret af Nordstjerne-kompasset, der jo konstant står i stik N.

Det kalibrerende solnedgangs-kompas

Efter en del aar med Wiltschkoeerne som de toneangivende skete der noget nyt på kalibrerings-fronten: Cochran et al. (2004) publicerede nogle forsøg med amerikanske *Catharus*-drosler, der udstyret med radio-sendere blev sluppet fri om natten efter at have tilbragt solnedgang/tidlig nat i et bur, der befandt sig i et magnetfelt, der var drejet 90º. Dette forsøg lignede altså meget Sandberg et al. (2000), men resultatet var ganske anderledes: Der var klare tendenser til, at nattrækket blev styret af et magnet-kompas, der forudgående var blevet kalibreret af et solnedgangs-kompas.

Sidste nyt er to artikler af Muheim et al. (2006a og b), der på linie med Cochran et al (2004) finder, at det ikke er magnet-kompasset, der i solnedgang/tidlig nat fasen kalibrerer solnedgangs- og eller stjerne-kompasset, men tværtom et gennemsnit mellem solopgangs- og solnedgangs-kompasset, der kalibrerer magnet-kompasset (og stjerne-kompasset). Muheim et al. (2006a og b) hævder, at det er essentielt for den styrende kalibrering fra solned/opgangs-kompasset, at der har været frit syn fra bure/tragte ned til horisonten. Den af Wiltschkøerne m.fl. (herunder Muheim og Åkesson i andre artikler) fundne styrende kalibrering fra magnet-kompasset er altså – i følge denne opfattelse – et forsøgs-artefakt forårsaget af horisont-afskærming af bure eller tragte i solnedgang/tidlig nat fasen.

Sidste nyt fra Christiansø og konklusion

Sidste nyt er forsøg af mig på Christiansø i efteråret 2006, hvor der i lighed med 2001 og 2002 forsøgene på Endelave ikke kunne påvises kalibrering fra hverken magnet- eller solnedgangs-kompasset. Heller ikke efter uindskrænket syn ned til horisonten solnedgang/tidlig nat. Ganske øjensynligt tog fuglene, der alle var fanget samme eller foregående dag, mestendels kurs efter stjernerne uden forudgående kalibrering fra andre kompasser.

Man skulle tro, at det var nemt at finde ud af, hvilke kompasser der dominerer og/eller kalibrerer de andre kompasser. Men det er det ikke; forskellige forskere får forskellige resultater, og det er derfor umuligt at generalisere og sige, at nattrækkende småfugle gør sådan og sådan. Problemet er endvidere, at fuglene ofte laver noget andet og mere end det rene og simple kompas–orientering. De forsøger efter min bedømmelse også at **navigere**, d.v.s. at mål–rette deres kurs. Endelig behandler og tester forskerne deres fugle forskelligt og ofte – givetvis mestendels ubevidst – på en måde så deres forventninger til, hvad der skal ske, opfyldes i størst mulig grad.

Hvad der kan siges med sikkerhed, er, at de ledende kompas-konflikt forskere som Wiltschkøerne, Muheim og Åkesson har været for tidligt ude med deres generaliseringer, samt at både magnetfeltets og solnedgangens indflydelse er overvurderet. Men det er jo sådan set bare den sædvanlige historie indenfor forskningsverdenen beskrevet så udmærket af Platt (1964): Paradigme–holderne bliver så forelskede (det skriver han faktisk) i deres yndlings–hypoteser, at de er blinde og døve overfor alternative og mere nuancerede (fortolknings)muligheder.

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16B: 70, 120, 240, - , - , 180, W 80, **16**: 30, 260, 120, - , W 20, 195, W 330, **18B**: 220, 150, 20, - , - , 180, - , **18**: 160, 190, 215, - , W 15, 230, - , **19B**: 60, 315, 200, - , W 75, 250, W 60, **19**: 245/(45), 90, 100, - , W 50, 165, W 300/105, **2B**: 250, 220, 205, - , E 75, 230, - , **2**: 240, 120, 75, - , E 50/(250), 240, - , **5B**: 105, 60, 85, - , E 70, 165, E 75/260, **5**: 225, 290, DIS, - , - , 240, E 100, **15B**: DIS, 120, 150, - , - , 180, E 80, **15**: 125, 340, 105, - , E 95, 220, E 105.
3B: W 40, - , W 30, - , 290/(70)/(185), W 360, 190, **3**: - , W 50, - , W 310, 215, - , 185, **6B**: W 120, - , W 265, - , 190/(55), W 165, 250, **6**: - , W 70, - , W 320/(35), DIS, - , 15, **11B**: W 75, - , W 50, - , 300, W 10, 350, **11**: - , W 85, - , W 255, 230, - , 195, **7B**: W 30, - , W 355, - , 240, W 335, 175, **7**: - , W 340, - , W 295, 220, - , 190, **12B**: E 270/(345), - , E 330, - , 275/(100)/(180), E 35, 180/320, **12**: - , E 70, - , E 315, 185, - , 225/10, **10B**: E 280, - , E 275, - , 260, E 95, 30, **10**: - , E 40, - , E 40, 235, - , 210, **1B**: E 15/(280), - , E 5, - , 140, E 25, 250, **1**: - , E 305, - , E 10, 200, - , 250, **14B**: E 60, - , E 60, - , 230, E 90, 60, **14**: - , E 30, - , E 50, 205, - , 330.

Table 1: The **2001**-experiments. The birds from **16B** until **15** are **controls**, and from **3B** until **14 exp.s.** Experiments were carried out on the seven nights 11, 13, 14, 15, 16, 23 and 26 September. 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)).
Forsøgene i 2001. 16B til 15 er kontroller, og 3B til 15 forsøgsfugle (d.v.s. fugle der står i bure inden i magnetfelterne).

FB15: 200, 235, **F15**: 210, 170, **FB16**: 140, 200, **F16**: 360/190, 210, **RB20**: 105, DIS, **R20**: 135, DIS, **R19**: 290, 200.
RB3: W 285, 100, **R3**: 170/(360), W 60, **FB12**: W 75, 255, **F12**: 250, W 10, **FB14**: W 50, 270, **F14**: 280, W 60, **F11**: W 330, 200, **R11**: DIS, W DIS, **RB10**: E 50, zero, **R10**: zero, E DIS, **F17**: E 60, 220, **R17**: 120, E 5, **FB8**: E 70, 200, **F8**: 215, E 70, **FB18**: E 70, 205, **F18**: 195, E DIS.

Table 2: The **first 2002** experiments, 8 and 9 September. **F** and **R** mean Pied Flycatcher and Redstart, respectively. The first seven birds from **FB15** until **R19** are controls, whereas the rest from **RB3** until **F18** area exp.s. zero means zero activity. Otherwise text as Table 1. However, in birds F17 and R17 120° has to be added instead of 135°, and 75° instead of 45° (because within this coil field "paper N" was directed towards 120º and resultant magnetic N was only deflected towards geographical NE).
De første 2002 forsøg. FB15 indtil R19 er kontroller, medens resten er forsøgsfugle.

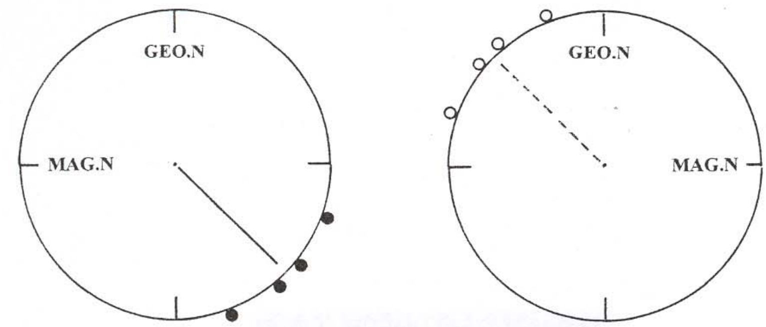
FB1: 120, 45, W 120, **F1**: 190, 105, W 215, **FB2**: 85, 85, E 290, **F2**: 130, 180, E 65, **FB7**: 230, 210, W 280, **F7**: 240, 110, W 285, **RB11**: 135, 90, - , **R11**: 170, 140, - , **RB12**: - , 100, - , **R12**: - , 100, - , **RRG**: 90, 225/(60), E 50, **RG**: 150, 220, E 50, **R18**: - , 125, - , **F18**: - , 140, - .
FB19: W 45, - , 195, **F19**: - , W 315, 190, **FB6**: W 15, - , 145, **F6**: - , W 310, 150, **RB13**: W 10, - , 185, **R13**: - , W 285, 145, **RR15**: W 80, - , 160, **R15**: - , W 330, 155, **RB20**: E 260, - , 110, **R20**: - , E 240, 105, **FB5**: E 350, - , 130, **F5**: - , E 40, 185, **FB4**: E 360, - , 170, **F4**: - , E 360, 175, **RB8**: DIS, - , 200/(35), **R8**: - , E 90, 205.

Table 3: The **second 2002** experiments, 12, 13, and 14 September. The first birds from **FB1** until **F18** were controls, the rest from **FB19** until **R8** exp.s. **RB11**, **R11**, and **R12** were adults, the rest juveniles. Text otherwise as Tabs.1-2. In birds B5 and 5 120º has to be added instead of 135º, and 75º instead of 45º.
De næste 2002 forsøg. FB1 til F18 er kontroller, og resten er forsøgsfugle.

Date	Magn.N	Geogr. N	n	ratio Magn.N/geogr. N
11 Sep. 01	19º - 0.642	293º - 0.180	8	–3.57/1
13 Sep. 01	36º - 0.621	222º - 0.410	8	-1.51/1
14 Sep. 01	357º - 0.495	175º - 0.368	8	-1.35/1
15 Sep. 01	300º - 0.090	156º - 0.854	8	-1/9.49
23 Sep. 01	78º - 0.245	207º - 0.648	8	-1/2.64
8 Sep. 02	90º - 0.284	207º - 0.708	8	-1/2.49
9 Sep. 02	36º - 0.621	237º - 0.562	5	-1.10/1
12 Sep. 02	3º - 0.745	240º - 0.211	7	-3.53/1
13 Sep. 02	259º - 0.315	170º - 0.662	8	1/2.10
16 Sep. 01	47º - 0.407	243º - 0.856	8	-1/2.10
26 Sep. 01	97º - 0.295	245º - 0.793	6	-1/2.69
14 Sep. 02	137º - 0.308	142º - 0.495	8	1/1.61

Table 4: Exp.s and controls tested in the deflected field first nine rows, and last three rows, respectively. The mean vectors denoted originate in the sum of the orientations of the birds tested in the fields deflected towards W and E. The last column denotes the influence of the magnetic compass in relation to the geographical (stellar) compass. A negative sign in the concentration-ratios signals a reverse sample mean vector, i.e. a sample mean direction more or less reverse in comparison with the standard direction (SSW-SW).

Forsøgsfugle (de første ni rækker) og kontroller (de sidste tre rækker) testet i de mod E eller W afbøjede magnetfelter. Der er vist gennemsnitsvektorerne i forhold til geografisk N og magnetisk N (se Fig.2-3). n betyder antal fugle i forsøg pr. nat. Den sidste søjle angiver forholdet mellem den magnetiske og geografiske vektor–koncentration. 3.57 er således 0.642 divideret med 0.180, og det negative fortegn betyder, at vektor–retningen af den magnetiske gennemsnitsvektor peger mere væk fra end i normaltrækretningen (SSW-SW, se Fig.3).


GEO.N
MAG.N
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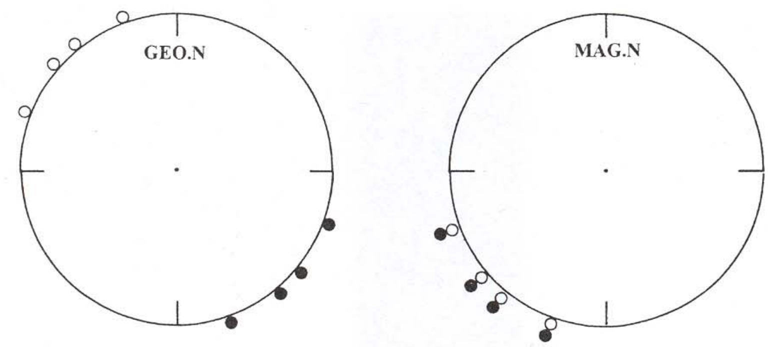
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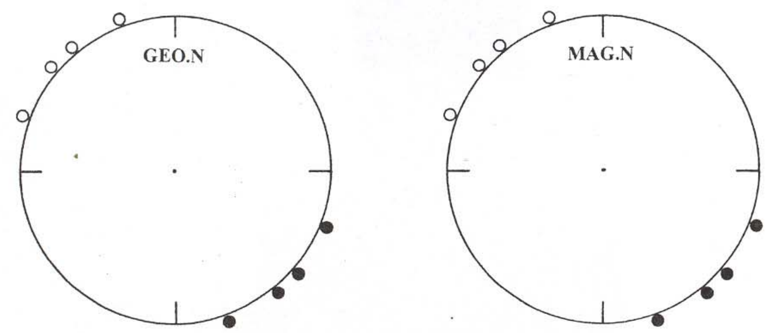
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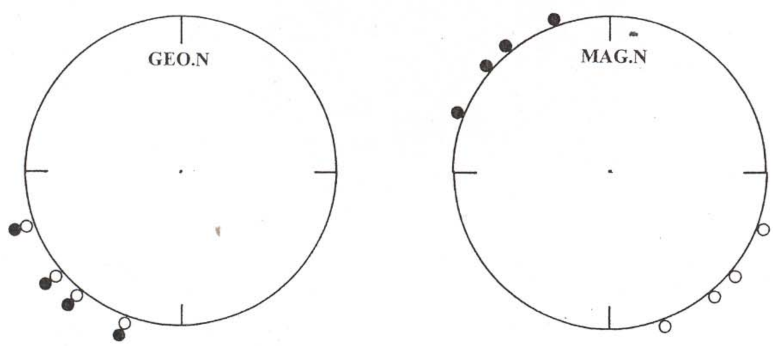

GEO.N
MAG.N

Fig.1. Constructed examples devoted to test the **hypothesis that the magnetic compass calibrates the stellar compass in the sunset/early night phase**.

The two **upper** figures depict the orientation of four and four birds (the dots), respectively, in a magnetic field where magnetic N is deflected towards geographical W and E, respectively. The standard direction is SW (225°) in reference to magnetic N and for the sake of reality some directional variation is introduced, 200˚, 220˚, 230˚ and 250˚, sample mean vector 225˚ - 0.951 (n = 8).

The **second row** figures depict the night orientation in relation to geographical (stellar) N and magnetic N for the **exp.s** spending the sunset/early night in magnetic fields **deflected** towards W
(black dots) or towards E (white dots). The birds were tested in the **deflected** fields.

The **third row** figures depict the night orientation for the **exp.s** spending the sunset/early night in the **deflected** fields but tested in the **normal** magnetic field (i.e. magnetic N = geographical N).

The **lower** figures depict the night orientation for the **controls** spending the sunset/early night in the **normal** magnetic field but later on tested in the fields **deflected** towards W or E.

Konstruerede eksempler og udfald, der skal vise om magnet–kompasset i solnedgang/tidlig nat fasen kalibrerer stjerne–kompasset til brug for resten af natten. Man forestiller sig en normaltrækretning mod SW i forhold til magnetisk N, og som vist i øverste raekke en vis variation (fra 200° til 250°) symmetrisk omkring normaltrækretningen. I dette eks. betyder en kalibrering, at magnet-kompasset bestemmer fuldstaendigt over stjerne-kompasset, der retter sig helt ind efter magnet-kompasset for den foelgende periode (timer eller doegn indtil der kalibreres igen). I denne periode bruger fuglene ikke magnet-kompasset, og de tager saaledes ikke notits af hvis der som i disse forsoeg skiftes mellem afboejede magnetfelter og det naturlige magnetfelt.

*Den **anden række** viser den efterfølgende nat orientering i det afbøjede magnetfelt i forhold til geografisk(stjerne) N og magnetisk N – **hvis der har fundet en kalibrering sted**. De sorte prikker/retninger henviser til forsøgsfugle, der tilbragt solnedgang/tidlig nat fasen i et af W-afbøjede felter og senere samme nat er tragt-testede indenfor de samme felter. De hvide prikker henviser tilsvarende til forsøgsfugle i de E-afbøjede felter.*

*Den **tredie række** viser nat orienteringen af forsøgsfuglene i det normale magnetfelt.*

*Den **nederste række** viser nat orienteringen af kontrollerne i de mod W (sorte prikker) eller E (hvide prikker) afbøjede magnetfelter.*

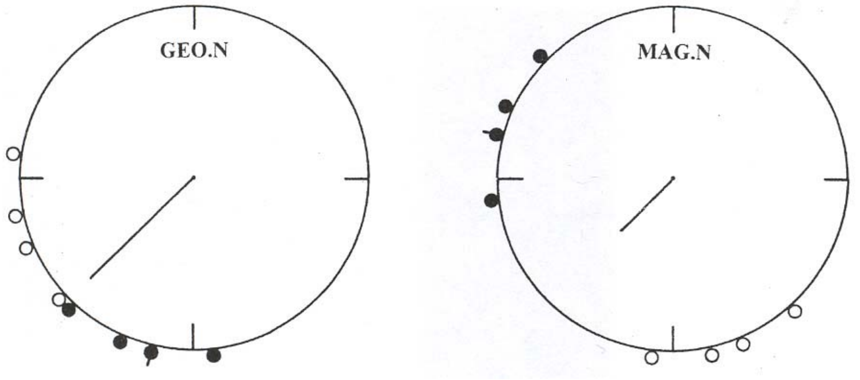


Fig.2. Constructed example depicting the influence of a **dominating stellar** compass. The vectorial influence of stellar N is twice the influence of magnetic N. The birds – which could be controls or exp.s – are **tested in a deflected field** during night and there was no calibration in the sunset/early night phase (or such a calibration was later on subdued). As an example, the black dots with a mark show the orientation of a bird with resultant directions between a vector pointing towards 220˚ in relation to stellar N and a half-sized vector pointing 220˚ in relation to magnetic N (directed towards geographical W). The resultant directions are 194.43º in reference to stellar N and –76.57º (283.43º) in reference to magnetic N. The sample mean vector of the eight birds in relation to stellar N is 225˚ - 0.851, and in relation to magnetic N 225˚ - 0.426. The latter concentration is half the size of the former, and in general a vectorial influence ratio of x/1 produces a sample concentration ratio of x/1. If the stellar compass is totally dominating the W-birds (black dots) are orienting around NW, and the E-birds (white dots) around SE when depicted in reference to magnetic N (as in Fig.1 lower right).

Man forestiller sig her, at fuglene – når de testes under stjernehimlen i et mod W eller E afbøjet magnetfelt – kompromisser med at orientere sig i forhold til både magnet–kompasset og stjerne–kompasset og at den sidste tilbøjelighed er dobbelt så stærk. Den sorte plet med streg på viser således en fugl, der kompromisser ved at orientere sig mod 220 ° i forhold til begge kompasser. Da magnetisk N i dette tilfælde vender mod geografisk W bliver kompromis–vektorens retning 194.43 ° i forhold til geografisk(stjerne) N og 283.43 ° i forhold til magnetisk N). Ser vi på de otte kompromis–retninger under eet bliver gennemsnitsvektoren rettet mod SW (225 °) i begge tilfælde, medens koncentrationen kun bliver halvt så stor ved afbildning i forhold til magnetisk N.

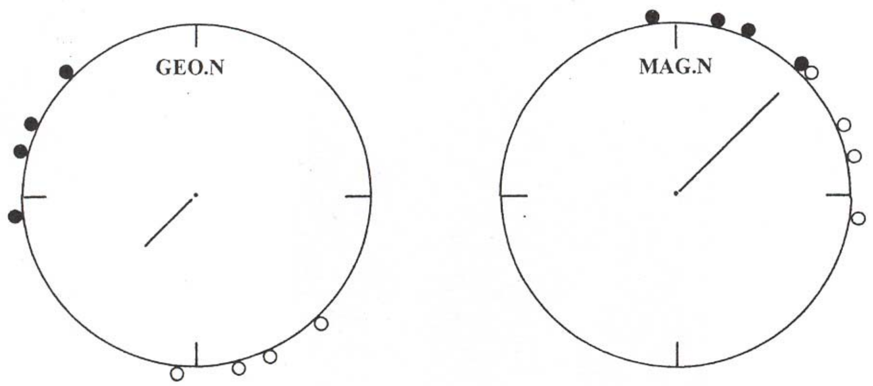
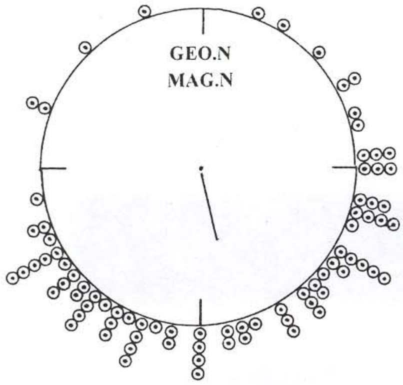
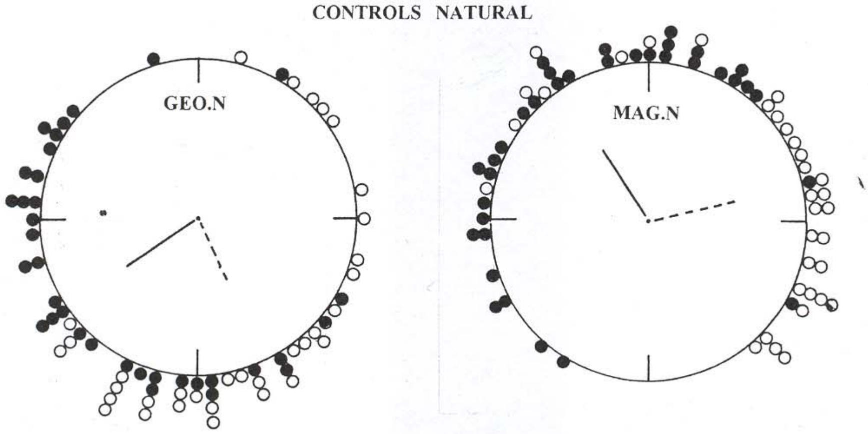


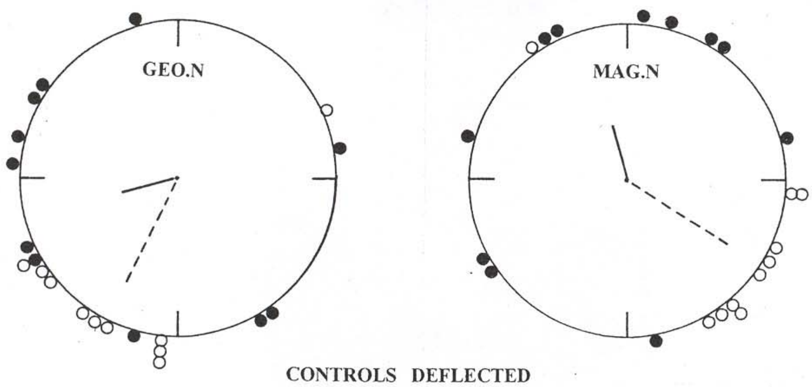
Fig.3. Constructed example depicting the influence of a **dominating magnetic** compass in the **reverse** (NE) direction. The birds are tested in a deflected field. The vectorial influence (standard, SW) of the stellar compass is half. The two mean vectors are 225º - 0.426 and 45º - 0.851, i.e. the ratio between the two concentrations is 1/2 (compare Fig.2).
Svarer principielt til Fig.2, men nu er det tilbøjeligheden til orientering i forhold til magnetisk N, der er dobbelt så stærk, og fuglene viser omvendt orientering i forhold til magnet–kompasset.



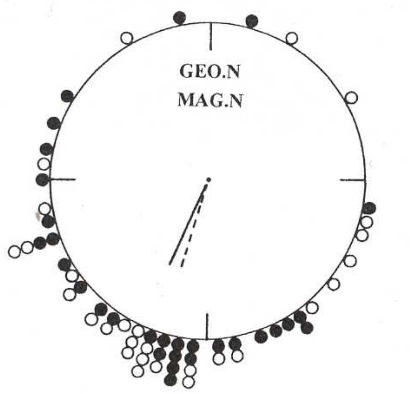
CONTROLS NATURAL



EXP.S DEFLECTED



CONTROLS DEFLECTED



EXP.S NATURAL

Fig.4: The **upper** figure depicts the orientation of the **controls** tested in the **natural** magnetic field, i.e. magnetic N = geographical (stellar) N. The sample mean vector is 166º - 0.463*** (n = 81).

The two distributions in the **second row** depict the orientation of the **exp.s** tested in **deflected** magnetic fields. The black and white dots refer to birds caged and tested in a magnetic field deflected towards W or E, respectively. In reference to **magnetic N** (right figure) the mean vector of the W-birds is 326º - 0.542*** (n = 35), and of the E-birds 75º - 0.572*** (n = 33). The combined mean vector (not depicted) is 20º - 0.324*** (n = 68). In reference to **geographical N** (left figure) the mean vector of the W-birds is 236º - 0.542*** (n = 35), and of the E-birds 156º - 0.582*** (n = 33). The combined mean vector is 196º - 0.431*** (n = 68).

The two distributions in the **third row** depict the orientation of the **controls** tested in **deflected** magnetic fields. The black and white dots refer to birds tested in a magnetic field deflected towards W or E, respectively. In reference to **magnetic N** the mean vector of the W-birds is 345º - 0.364 (n = 11), and of the E-birds 123º - 0.756** (n = 10). The combined mean vector is 92º - 0.255 (n = 21). In reference to **geographical N** the mean vector of the W-birds is 255º - 0.364 (n = 11), and of the E-birds 206º - 0.762** (n = 10). The combined mean vector is 222º - 0.508** (n = 21).

The **lower** figure depicts the orientation of the **exp.s** in the **natural** magnetic field, i.e. magnetic N = geographical (stellar) N. The black and white dots refer to birds caged (but not tested) under condition of a magnetic field deflected towards W or E, respectively. The mean vector of the W-birds is 205º - 0.589*** (n = 30), and of E-birds 197º - 0.567*** (n = 28). The combined mean vector is 201º - 0.577*** (n = 58).

*Vi ser de fire kombinationer af kontroller (controls) og forsøgsfugle (exp.s) tragt–testede i henholdsvis det naturlige (natural) og de afbøjede (deflected) magnetfelter. Nederst og øverst ses forsøgsfugle og kontroller testede i det naturlige magnetfelt, hvor der jo er sammenfald mellem geografisk og magnetisk N. De to midterste rækker viser orienteringen af kontroller og forsøgsfugle i de afbøjede felter. De sorte og prikkede streger, der udgår fra cirklernes centrum, viser gennemsnitsvektorerne af henholdsvis de W og E afbøjede fugle. Bemærk hvordan orienteringen er omtrent modsat rettet normaltrækretningen for de to afbildninger i forhold til magnetisk N. Hvis vi ser paa de fire totale gennemsnitsvektorer i forhold til geografisk N er der ikke den store forskel (fra oven og nedad: 166° – 0.463***, 196° – 0.431***, 222° – 0.508**, og 201° – 0.577***).*

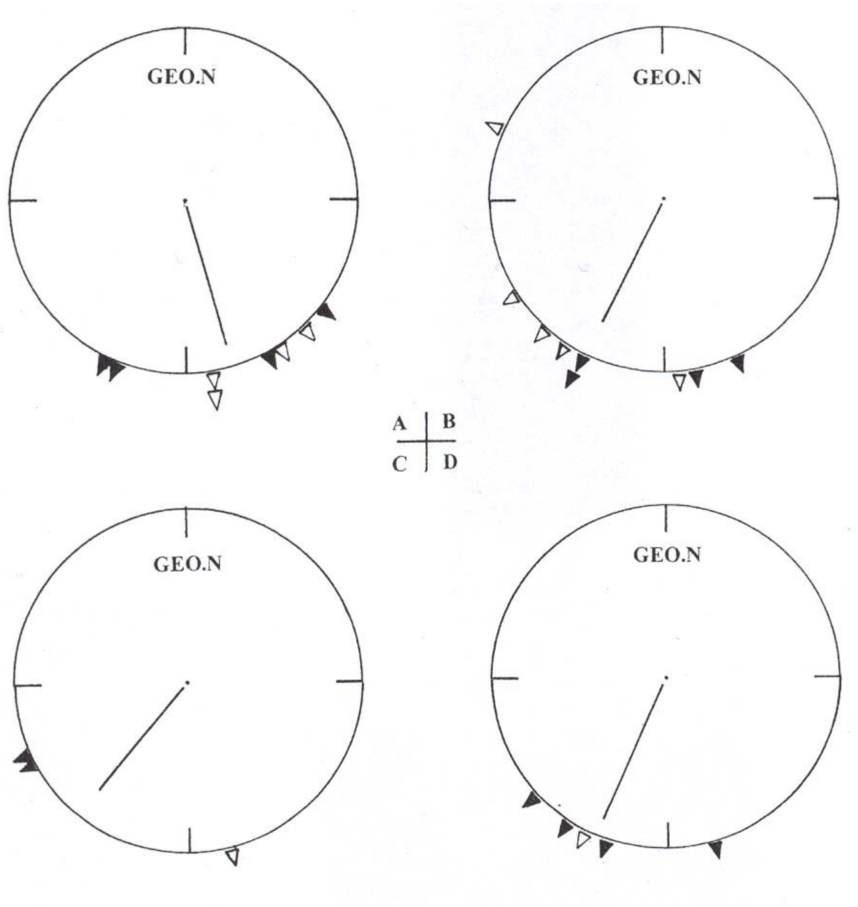


Fig.5: Grand mean vectors. **A** depicts **controls** tested in the **natural** magnetic field, **B exp.s** in **deflected** fields, **C controls** in **deflected** magnetic fields, and **D exp.s** in the **natural** field. In A and D the compass reference is magnetic N = geographical (stellar) N. In B and C the compass reference is geographical (stellar) N. The black triangles refer to directions of significant nightly mean vectors ($P < 0.05$, Rayleigh test). The white triangles refer to directions of insignificant nightly mean vectors ($P > 0.05$). The four grand mean vectors are 164º - 0.893** (A), 207º - 0.797** (B), 220º - 0.805 (C), and 203º - 0.930** (D).

Denne figur viser i princippet det samme som foregående i relation til geografisk N, men hvor Fig.4 viser fuglenes enkeltretninger, er der her set på retningerne (trekanterne) af de natlige gennemsnitvektorer. A ogD er henholdsvis kontroller og forsøgsfugle i det naturlige magnetfelt, medens B og C er henholdsvis kontroller og forsøgsfugle i de afbøjede magnetfelter. Igen er der ikke den store forskel på retningerne, medens koncentrationerne som forventet bliver noget større i forhold til Fig.4.

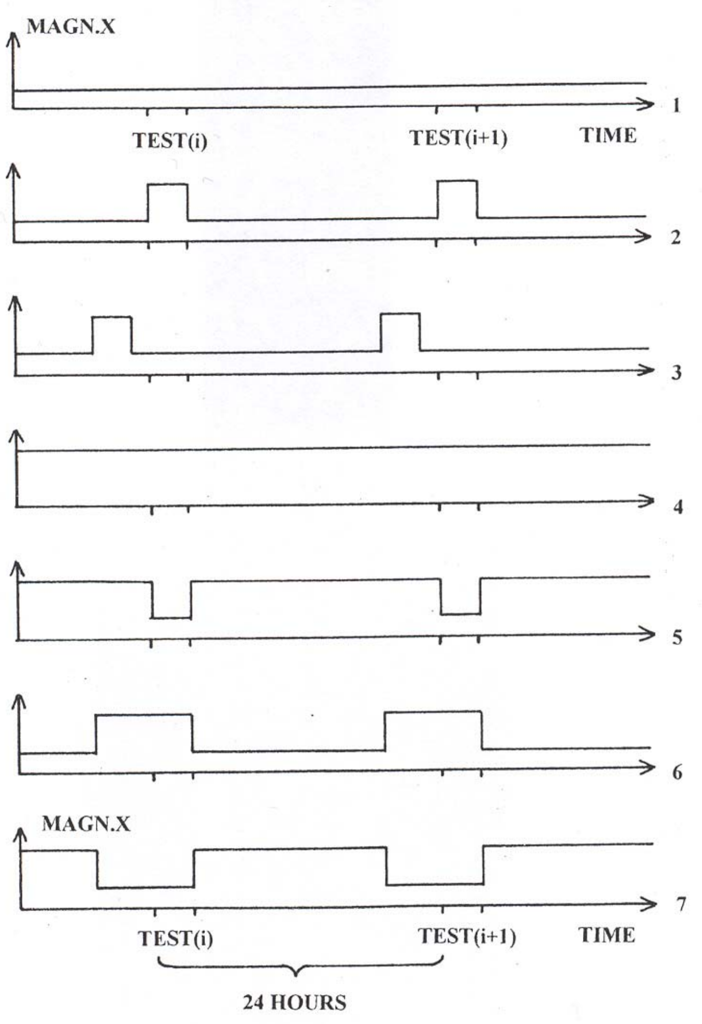


Fig.6: Different types of pulse and constant state of experiments. Magnetic X could be a) the direction of magnetic N, b) the inclination, c) the intensity or d) a mixture. Before the first test(i) the birds spent at least some days and nights under constant magnetic conditions. After another 24 hours a new test(i+1) was carried out, and so on. **1** is the control situation where magnetic X is the natural one for the site. **2** is the classical pulse experiment where the bird is exposed for a new value of magnetic X in the test-period only. The test-period is normally short; no longer than 1-2 hours per 24 hours. In **3** the birds are exposed for another value of magnetic X in a short (about one-hour) period in the afternoon and then tested in the sunset/early night phase in the natural magnetic field (Åkesson et al. 2002). Another variant of 3 is Sandberg & Moore (1996) and Sandberg et al. (2000): Here the birds were exposed and funnel/cage-tested in the deflected magnetic field in the sunset/early night phase and then later on in the night released with a light-stick in the tail. **4** is the procedure of mine: the exp.s were caged and tested all the time outdoors in the deflected (or otherwise changed) magnetic field. **5** is as 4 but the exp.s were tested in the natural magnetic field. **6** is a variant of 2 where the birds were exposed in their cages for some time (e.g. in the sunset/early night phase) before tested in the funnels (e.g. during night) under the changed magnetic conditions. **7** is a variant of 5. 1, 2, 4 and 5 were carried out in 2001 or 2002, and 6 and 7 on a single occasion by Rabøl et al. (2002).

X–aksen er en tidsakse, hvor 24 hours angiver 24 timer (1 døgn). Y–aksen viser en eller anden magnetisk faktor, f.eks. og i relation til denne artikel retningen af magnetisk N i forhold til geografisk N. ***1*** *viser situationen for kontrollerne, der er holdt og testet i det naturlige magnetfelt, medens* ***4*** *er forsøgsfuglene holdt og testet i et afbøjet magnetfelt.* ***2*** *er det jeg kalder det klassiske ″puls″ forsøg, hvor forsøgsfuglene kun udsættes for det afbøjede magnetfelt i test fasen.* ***3*** *svarer en situation, hvor forsøgsfuglene i solnedgang/tidlig nat fasen udsættes for et afbøjet magnetfelt, medens de senere testes i det normale magnetfelt.*