

## Compass calibration in migratory passerine birds

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This doc. constituted part of the draft to “Discussion” in the paper Rabøl, J. & K. Thorup 2006: *Migratory direction established in inexperienced bird migrants in the absence of magnetic field references in their pre-migratory period and during testing*. – Ethol. Ecol. & Evol. 18: 42-51. It was written in 2003 and only minor corrections were carried out.

### *Due S orientation*

Considering the question “*How to decide when the orientation is due S*” an appropriate procedure – and the one used by the Wiltschkos and co-workers - could be to investigate whether due S, i.e.  $180^\circ$  is encompassed within the 95% confidence limits of a) the sample mean vector of all bird/nights or – what would be a more modern approach – b) the grand mean vector. If so, the orientation of the birds is considered to be in correspondence with due S.

However, there may be problems with such a test-procedure.

Let us consider the constructed example in Fig.5 depicting the mean directions of eight birds each tested between 8 and 14 times. The grand mean vector is  $183^\circ - 0.764^{**}$  ( $n = 8$ ), and the 95%- and 99% confidence intervals are about  $\pm 35^\circ$  and  $53^\circ$ , respectively. Clearly due S, i.e.  $180^\circ$  is within  $183^\circ \pm 35^\circ$ , so the first obvious conclusion should be that the observed orientation – expressed by the grand mean vector (direction) - is not deviating from and in fact is in very good correspondence with due S. Furthermore, if the standard direction is – say – SW then a confidence interval test on basis of the grand mean vector above will reveal that SW, i.e.  $225^\circ$  is outside the 95% confidence limits ( $183^\circ \pm 35^\circ$ ). If the eight birds was a sample from a species/population with a SW standard direction which never experienced a proper magnetic field in the pre-migratory state then the outcome of such a two-step testing as mentioned above seemingly constitute a convincing base for a judgement that the presence and interaction of the magnetic field is a necessary demand for the development of proper (standard) migratory orientation. Of course such a judgement is further strengthened if the grand mean vector of a control sample growing up in the natural magnetic field is directed close to SW or at least that SW is encompassed within the 95% confidence limits of the sample mean vector.

However, **sometimes it is not sufficient to consider the (sample or the) grand mean vector.**

In the example on Fig.5 and based in the **individual mean vectors**, the orientation of five out of eight birds deviates significantly from due S at the 0.05 (95%) level. So what to do? Shall we rely on the grand mean vector of the sample or the individual mean vectors of the birds? A first approach to the answer should be that if the amount of variation between individuals contributes significantly to the total variation (which is the sum of the within and between variation of the individuals) then normally we can not rely alone on the grand mean vector. And in the present case (i.e. Fig.5) the contribution of the between variation is very significant ( $P \ll 0.001$ , Stephens 1972, see also Thorup et al. 2007).

So what is the conclusion if the orientation considered at Fig.5 was an example from real life. Well, because five out of eight birds deviate significantly from due S the orientation of the eight birds can **not** reasonably be considered as a stochastic outcome of due S orientation in (the sample of) all eight birds. Five out of eight seems too many but the exact number of birds which could be allowed to deviate significantly at – say – a  $P < 0.05$  level will depend on an appropriate statistical test procedure (which should not be outlined or discussed here).

Now, three individual birds deviated significantly to the right and two birds significantly to the left, i.e. E of S. If the standard direction is SW what then about these two latter birds/individual mean vectors. Do they count? Yes, in the present context they count **if** the research hypothesis is that the birds based on the stars alone are programmed to take a course directly away from the point of celestial rotation.

### **Remarks**

Ecological and behavioural science is nowadays much a matter about testing one or another (simple) hypothesis such as for example the one put forward in the title of the present paper. Furthermore, publishing a paper in a distinguished scientific journal is clearly facilitated if one or another acknowledged hypothesis or popular scenario is confirmed. At present a popular scenario is that magnetic orientation is most important calibrating or setting orientation in reference to celestial cues in a significant way. However, true science is not only about publishing papers; it is also – and most importantly – about finding out what is going on in the real world. Therefore it is important that at least a few people are critical about the established hypotheses and scenarios. It is also important that critical papers are published, but unfortunately this is not so easy in the referee-system used. As an example Rabøl et al. (2002) was several years and journals under its way before finally accepted by a journal - and its presence and significance still not seems to be recognized by people advancing the hypothesis of a magnetic inclination compass. Also Rabøl (1998a) demonstrating stellar gradient navigation is still largely ignored.

Within the field of bird orientation the scene has been much dominated by the Wiltschkos and co-workers and according to my point of view the significance of magnetic orientation is over-rated and also not so well as understood as one may get the impression when reading one of the many surveys by the Wiltschkos. If the scene has to be changed towards a more balanced and realistic state it is necessary – besides new critical experiments – patiently and in details to review and dissect the classical papers behind the myth(s); here the reader should be prepared upon the many different conditions under which the birds were raised, caged and tested. What for a superficial consideration seems to be about the same as another experiment is perhaps something quite different, and it is very difficult to overview the field and keep in check with all the details. Because of this boundlessness it is tempting for such people as the Wiltschkos writing many review papers to concentrate on a certain experiment – or part of an experiment - and generalize on such selected material. Correspondingly, it is difficult for other people to see through that doubtful generalizations are carried out.

In the next sections the “classical” conflict experiments focusing on the orientation of first-time migrants **raised in captivity** are reviewed and dissected.

### ***Weindler et al (1996, 1997)***

These two papers – and the first in particular - constitute the hard core behind the hypothesis that celestial rotation in itself only provides due S orientation.

Weindler et al. (1996) compared the orientation of two groups of Garden Warblers taken on the nests and **spending the pre-migratory period under a rotating “16-star-sky”** and in the normal magnetic field (the controls, i.e. magnetic N = 360°) or in a vertical magnetic field (the exp.s). In

the migratory season both groups were **tested under a stationary “16-star-sky”** and in a vertical magnetic field. The migratory season was divided in two period, Aug.-Sep. and Oct.-Nov. because of the well known shift in the standard direction from about SW to about SSE around 1 Oct. (e.g. Gwinner & Wiltschko 1978). Weindler et al. (1996) focused on the orientation in the first half of the autumn – probably because the shift in orientation from 232° (first half) to 267° (second half) in the grand mean vectors of the **controls** made no sense according to the expectation. Testing these two mean vectors against each other as two independent samples (which is not correct) and applying a W-W test results in  $t = 1.79$  ( $0.05 < P < 0.10$ ), i.e. it is close to a significant shift - in the **wrong** direction! Testing the single birds as their own controls the shift is 32° to the right and the mean vector concentration 0.428 corresponding to  $0.05 < P < 0.10$  ( $n = 15$ ). Clearly, Weindler et al. (1996) are in trouble with this orientation in the second half of autumn and therefore come up with an ad hoc “explanation”: *“Apparently, the population-specific course of the second part of migration also requires magnetic information. This suggests a transfer process analogous to that described for establishing the first direction”*. Weindler et al. (1996) do not consider the possibility that the westerly orientation in the controls in both early and late autumn was influenced by some kind of artefact or that perhaps another steering system than simple vector-orientation was in charge.

Anyway, the orientation of the **exp.s** in Aug.- Sep. was significantly different compared with the controls in Aug.-Sep.; the grand mean vector is 173° - 0.90\*\*\* ( $n = 11$ ), and this difference constitutes the hard core of evidence for the claim that celestial rotation in itself only provided the Garden Warblers with a due S course. Clearly, the grand mean vector of the exp.s during Aug.-Sep. does not deviate significantly from due S, whereas the deviation from SW is highly significant ( $P \ll 0.01$ , confidence interval test). Considering the individual mean vectors two out of eleven exp.s deviate significantly from due S at the  $P < 0.05$  level, i.e. at least for some of the birds the hypothesis seemingly does not fit. During Oct.–Nov. the grand mean vector of the exp.s was insignificant (176° - 0.46,  $n = 10$ ).

Weindler et al. (1997) investigated the influence of the rotation of the “16-star-sky” in the **clockwise** direction, i.e. in the reverse direction of the normal counter-clockwise direction. In three samples the direction of “celestial” rotation was towards geographical E, S and W, respectively. Otherwise, the experimental set up and test procedure were the same as in Weindler et al. (1996).

In comparison with the orientation of the controls in Weindler et al. (1996) the orientation of all three groups in **early** autumn was not significantly different from due S in relation to stellar rotation – according to Weindler et al. (1997). However, one of the grand mean vectors (E3) deviated significantly (151° - 0.72\*\*\*,  $n = 12$ , the 95% confidence limits are  $\pm 28^\circ$ ) at the 0.05 level. Only two out of 31 individual mean vectors were directed significantly different from due S.

The grand mean vectors in **late** autumn in general show smaller concentrations than in early autumn and in two out of three groups the mean direction was close to due S. Anyway, seven out of 31 individual sample mean vectors deviated significantly from due S at the 0.05 level.

Now the birds in the two papers of Weindler et al. were from **two different years**, so perhaps the difference in orientation was more influenced by year than by direction of “celestial” rotation. This possibility is not discussed by the authors. Perhaps the directional discrepancy between magnetic N and rotational N during raising in the three samples of Weindler et al. (1997) influenced the subsequent orientation under the stationary “16-star-sky” in such a way that due S orientation came out. Neither this possibility is discussed by the authors.

According to Weindler et al. (1996) there is a *“transfer of information from the magnetic field to celestial cues during the premigratory period”*. Furthermore, *“the deviation from this basic*

*direction (i.e. a) magnetic South or b) away from celestial rotation, JR) defining the population-specific migration course is coded only with respect to the magnetic field". Weindler et al. (1996) also write the following: "It is possible that the innate magnetic information does not specify a particular course, such as 230° southwest, but specifies a deviation from a reference point, something like `50° to the right` of a basic direction. This would mean that the migratory course is established in two stages". The same message is repeated in more or less the same words by Weindler et al. (1997), Wiltschko et al. (1998) and Wiltschko & Wiltschko (2003). Furthermore, Weindler et al. (1997) concluded that the interplay between the magnetic compass and celestial rotation "depends on the direction of rotation and is disrupted when the sky is rotating in the reverse direction from normal". Wiltschko et al. (1998) added "- - that with reversed rotation, the information on the deviation from the reference direction coded with respect to the magnetic field could not be combined with the reference given by celestial rotation. As a result, the birds had to rely on the information provided by celestial rotation alone, namely away from its center".*

However, before accepting these explanations the crucial point is whether the outcome of experiments carried out under a stationary "16-star-sky" have any relevance to what is going on under the natural starry sky. Obviously, Wiltschko et al. (1998) believe in a simple translation when writing "*Thus in nature, celestial and magnetic cues interact during the premigratory period to convert genetically coded information into the starting course of migration, celestial rotation normally providing the reference direction and the magnetic field providing the population-specific deviation from this reference*". However, all these scenarios and "explanations" could be considered as ad hoc adaptations rooted in a strong wish to keep the magnetic compass in front of the game.

In the next section two experiments based on birds raised and tested in a useless magnetic field but exposed for the **natural starry sky** are presented and clearly we need more such tests before the far-reaching interpretation of the Wiltschkos and co-workers can be generalized. Obviously, we also have to know the orientation of birds **tested** under a **rotating** "16-star-sky"; perhaps the claimed due S orientation is just an artefact produced by the stationary "sky" and has nothing to do with the presence/absence of the magnetic field or the direction of "celestial" rotation.

### ***Rabøl & Dabelsteen (1983) and Bingman (1984)***

Rabøl & Dabelsteen (1983) tested the orientation of four juvenile Pied Flycatchers taken on the nest in June and caged in the pre-migratory period in a strong vertical and heterogenous magnetic field presumed to be useless for magnetic orientation. 11 nights in this period the birds spent outdoors in their (magnetically destroyed) cages under the natural starry sky. When tested in funnels under the starry sky and in strong vertical magnetic fields during August (i.e. the supposed standard direction is about SW) the sample mean vector based on the single bird/nights was significant ( $191^\circ - 0.531^*$ ,  $n = 16$ ). However, considering the overall grand mean vector ( $195^\circ - 0.780$ ,  $n = 4$ ) the orientation was not quite significant. Clearly, none of these two mean vectors deviated significantly from due S (or SW), but considering the individual grand mean vectors of the birds one did at the 0.02 level ( $257^\circ - 0.977^*$ ,  $n = 3$ ). Another bird also came fairly close ( $146^\circ - 0.927^*$ ,  $n = 4$ ). The right hand of the 95% confidence limit is about  $186^\circ$ ).

In the very same autumn (1982) Bingman (1984) – quite independently – carried out essentially the same experiment with the same species. However, the experiment of Bingman was much more elaborated and also contained a control group (the controls of Rabøl & Dabelsteen 1983 was killed

during pre-migratory exposure by a Tawny Owl!) and a third group in which magnetic N during the pre-migratory caging phase was deflected 105° to the left (i.e. to about WSW) of geographical N. It is not clear how many birds contributed with directions, but initially ten birds were caged in each of the three groups. The birds of Bingman were also tested outdoors under the stars and in a vertical magnetic field. The tests were carried out during September i.e. in the first half of the migratory season where the presumed standard direction is about SW.

Unfortunately, the results are presented in a way which makes it impossible to find out whether the orientation of any **single** bird deviated significantly from due S. The mean vectors of Bingman (1984) are resting on total of bird/nights.

The orientation of the **controls** was puzzling. The sample mean vector was 128° - 0.40\*\* (n = 35) and due S is outside the domain of the 95% confidence limits (+/- 35°). Of course, the deviation from the standard direction in about SW is even more outstanding. Bingman did not comment on - or appreciated - this very significant deviation from SW of the controls.

The orientation of the **magnetically deprived** birds was about the same – at least there was no significant difference (158° - 0.36\*, n = 35). However, this mean vector was not deviating significantly from due S (the 95% confidence limits are about +/- 39°).

Also the orientation of the **magnetically deflected** birds was in the SE-quadrant (177° - 0.38\*\*, n = 36), and according to Bingman the difference compared with the controls was not statistically significant. However, as far as I can calculate  $P < 0.05$  (W-W-test). The 95% confidence limits are about +/- 35°. If the magnetic compass **calibrates** the stellar compass the orientation should be 120° in relation to stellar/rotational N if the course in relation to magnetic N is in the standard direction, i.e. SW. However, if the course for some reason is (about) SE (following the orientation of the controls) the course should be (about) 30°. Both 120° and 30° are far outside the 95% confidence interval of the mean vector 177° - 0.38\*\*. If the role of the magnetic compass during raising is **setting** of the course in relation to stellar rotation the course should be 45° to the right of rotational S (corresponding to a standard direction of SW), i.e. we expect the orientation in reference to stellar N to be 225°. However, as told, the confidence limits of the mean vector observed do not encompass the standard direction. Nor do they encompass SE (which – perhaps – is the theoretical direction of the controls). Now 177° is between 120° and 225°, and therefore could be “explained” as a **compromise** between the influence from a magnetic and a stellar compass.

In conclusion, the orientation of the magnetically deprived birds neither supports nor rejects the hypothesis of the Wiltschkos. The orientation of the sample of birds growing up in the deflected field leads to the next section.

### ***Wiltschko et al. (1987) and Weindler & Wiltschko (1991)***

Consider an example; magnetic N is deflected towards W (in reference to rotational/geographical N) and the standard direction is SW, which – in terms of the Wiltschkos - is “45° to the right of magnetic S” situated in E, i.e. the magnetic compass tells the bird to go SW whereas the stellar/rotational compass (according to the Wiltschkos) only enable the birds to go straight away from the centre of rotation, i.e. due S. Clearly, the Wiltschkos will expect birds raised under a rotating “16-star-sky” and in a deflected magnetic field – if tested under a stationary “16-star-sky” – to orient in the standard direction towards SW. Now a SW orientation will not in itself be an indication of a transfer from the magnetic compass to the stellar rotational compass; we have to see due S orientation also in a group of birds raised in a vertical/useless magnetic field (as in Weindler et al. 1996).

W. Wiltschko (in litt.) confirms this scenario but **if** the condition is a bird growing up in the deflected field outdoors under the natural stellar sky and later on tested outdoors under the natural stellar sky he is “- not sure, since our results and those of Ken Able are in disagreement. Able finds that the birds prefer the stars during the whole migratory season, while we find that this is only true for exposures in the premigratory season. But in all cases, where we find outdoors a recalibration of stellar cues via magnetic cues, the birds had already started to migrate and thus had already experienced that the appearance of the sky has changed”.

Now, Able apparently never tested his birds under an outdoor natural sky (or a stationary “16-star-sky”) in a vertical/weakened magnetic field. However, according to Able & Able (1996) Bingman (1983) did so: “Although Moore (1978, 1980) could find no compelling evidence that Savannah Sparrows possess a star compass, Bingman’s (1983) hand-raised birds that grew up outdoors showed axial northeast-southwest orientation when tested under starry skies in a vertical magnetic field (i.e. no magnetic information available). A group of sparrows raised outdoors within a shifted magnetic field showed identical orientation under stars, indicating that the development of stellar orientation is unaffected by magnetic influences. Similar results have been found in other species (Bingman, 1984; Wiltschko, 1982; Wiltschko et al. 1987; but see Katz et al. 1988)”.

**Wiltschko et al. (1987)** carried out experiments with Garden Warblers.

In **Series I** five birds were **raised** in the normal magnetic field and under a **rotating** “16-star-sky” where the centre of rotation was in geographical N coinciding with magnetic N. When tested under a stationary “16-star-sky” and in a vertical magnetic field the sample mean vector of all bird/nights was  $197^\circ - 0.48^{***}$  ( $n = 57$ ). The 95% confidence limits ( $\pm 22^\circ$ ) are encompassing due S, i.e. the course can not be distinguished from due S. Another 5 birds were **raised** under a **stationary** “16-star-sky” and as the first-mentioned 5 birds also in the normal magnetic field. The latter 5 birds were tested under a stationary “16-star-sky” and in a vertical magnetic field. Apparently no information were transferred from the magnetic compass to the stationary “stars” as the sample mean vectors of all bird/nights was insignificant ( $139^\circ - 0.15$ ,  $n = 45$ ). These results are not understandable in terms of the findings/interpretations of Wiltschko & Wiltschko (1976).

In **Series II** three other groups of Garden Warblers were raised in the normal magnetic field and under a rotating “16-star-sky” where the **centres of rotation** now were directed towards 1)  $60^\circ$ , 2)  $180^\circ$  and 3)  $300^\circ$ , respectively compared with geographical/magnetic N. When tested in a vertical magnetic field and under the stationary “16-star-sky” the orientation – based on all bird/nights - in **relation to the former centre of rotation** were as follows. 1)  $214^\circ - 0.54^{***}$  ( $n = 27$ ), 2)  $174^\circ - 0.30^{***}$  ( $n = 86$ ), and 3)  $170^\circ - 0.34^{***}$  ( $n = 95$ ). In 1) the 95% confidence limits ( $\pm 27^\circ$ ) were not encompassing due S, i.e. in this group the deviation from due S was statistically significant.

The question is how to interpret this Series II experiments. If the rotational compass was **calibrated** by the magnetic compass and the course in relation to magnetic N was SW ( $225^\circ$ ) we should expect the following directions – in reference to the former centre of rotation: 1)  $165^\circ$ , 2)  $45^\circ$ , and 3)  $285^\circ$  (if instead the course in relation to magnetic N was S ( $180^\circ$ ) we should expect 1)  $120^\circ$ , 2)  $360^\circ$ , and 3)  $240^\circ$ ). Clearly, the rotational compass was not calibrated by the magnetic compass which furthermore seems without any influence, because 2) is almost due S and the angular difference between 1) and 3) is to the wrong side. However, in principle the course could had been programmed as  $10^\circ$  or  $20^\circ$  to the right of magnetic S (i.e.  $190^\circ - 200^\circ$ ) and transferred to  $10^\circ$  or  $20^\circ$  to the right of celestial rotation, i.e. **setting** the course by means of the magnetic compass is a possibility. Clearly, the 95% confidence limits around the mean vectors 1), 2) and 3) mentioned above are encompassing  $190^\circ - 200^\circ$ .

Wiltshko (1982, Fig.4) presented what probably are the results (bird/nights) of Series II above when about half (118) of the experiments were finished. When depicted in relation to former rotational N the sample mean vector was (about)  $180^\circ - 0.42^{***}$ , whereas the sample mean vector in relation to former magnetic N was (about)  $130^\circ - 0.08$ , i.e. insignificant. However, as mentioned by Wiltshko the latter pattern was significantly bimodal ( $P < 0.05$ ). Wiltshko did not specify the axis which, however, seems to be in about NNW/SSE. Rabøl (1988, Fig.92) explained the outcome of the two patterns observed using a simple quantitative model building on vector combination where the influence of the rotational compass was 3 times stronger than the influence from the magnetic compass. In this model the orientation in relation to both compasses was S. However, compared with the larger dataset presented of Wiltshko et al.(1987) this model does not apply in the simple form.

**Weindler & Wiltshko (1991)** is a little different. Here three groups of Garden Warblers are investigated. The **controls** are raised under a rotating “16-star-sky” and in the normal/undisturbed magnetic field, and later tested under a stationary “16-star-sky” and in a weakened magnetic field supposedly unqualified for magnetic orientation. The orientation of the controls was  $246^\circ - 0.35^{***}$  (75). An **exp. group I** was raised under the same conditions, and tested under a stationary sky and in a magnetic field where magnetic N was turned into stellar W. The orientation of these birds was  $211^\circ - 0.56^{***}$  (59) in reference to stellar N, i.e.  $121^\circ - 0.56^{***}$  (59) in reference to magnetic N. Compared with the controls it seems as if the course is in reference to stellar N (“- - sie richteten sich offensichtlich trotz widersprechender Information vom Magnetfeld nach den Sternen”). An **exp. group II** was raised under a rotating “16-star-sky” but in a weakened magnetic field unqualified for magnetic orientation. When tested in the weakened magnetic field and under a stationary sky the orientation is close to due S ( $175^\circ - 0.60^{***}$ , 75). Considering the three groups in symphony an interpretation could be that the presence of a qualified magnetic field (in the pre-migratory period) is necessary for the development of a course in reference to stellar N deviating significantly from due S.

Now these experiments were apparently carried out in the **first half** of the autumn where the standard direction of German Garden Warblers is about SW. At least Weindler & Wiltshko (1991) write that “*In der zweiten Hälfte der Versuchssaison*” the exp. group II is still oriented about due S ( $181^\circ - 0.36^{***}$ , 61), whereas exp. group I orients E of S ( $168^\circ - 0.73^{***}$ , 46). This counter-clockwise turn on  $43^\circ$  in the latter group is significant and in accordance with the shift in the standard direction to about SSE in the second half of autumn. Also the controls shifts a little counter-clockwise ( $228^\circ - 0.31^{**}$ , 67), but this insignificant shift to SW can not appropriately – together with the shift in exp. group I – be described by the words of Weindler & Wiltshko “*Sie bevorzugten weiter östlich liegende Richtungen*”. In fact, the orientation of the controls is in contradiction with the results and interpretation of Gwinner & Wiltshko (1978). This is never mentioned in the surveys of the Wiltshkos.

### ***Influence of stellar rotation on the magnetic orientation***

Concerning the “**reverse**” **interplay**, i.e. the influence of stellar rotation on the orientation in reference to the magnetic compass Wiltshko et al. (1998) write “- even when the magnetic compass course was altered by exposing birds to celestial rotation in deflected magnetic fields, species that normally head magnetically southwest preferred the magnetic direction that corresponded to southwest during exposure and not the one that had corresponded to south as directly away from the center of rotation (Weindler and Wiltshko 1991, Prinz and Wiltshko

1992). It means that even when the magnetic compass course is overruled by celestial rotation, information coded with respect to the magnetic field has a part in establishing the migratory course. This seeming paradox can be best explained by the assumption that the crucial information on the population-specific course is not coded as a certain magnetic course, but as a deviation from a reference direction. In case of the Garden Warblers, this would mean that the innate information does not specify `225° SW` with respect to the magnetic field, but something equivalent to `45° clockwise` of a reference direction. This reference direction can be provided by both celestial rotation and the geomagnetic field, corresponding to geographic South and magnetic South, respectively". I.e. no matter about the angular relation between magnetic N and stellar/rotational N in the pre-migratory/raising phase, the orientation comes out as the standard direction if the birds were tested under the starry sky and in vertical/useless magnetic field. On the contrary, the picture of the opposite relationship – i.e. birds tested without celestial cues but in a normal or a deflected but useful magnetic field – will be as illustrated by the following two examples: If magnetic N is pointing towards stellar/rotational W then the subsequent orientation will be NW in relation to the magnetic compass. If magnetic N is pointing towards stellar/rotational E then the subsequent orientation will be SE in relation to the magnetic compass.

Concerning this interplay between the magnetic and stellar/rotational compass Prinz & Wiltschko (1992) are a little annoyed with the notion “*calibration of the magnetic compass by celestial rotation*” used by Bingman (1983), Bingman et al. (1985) and Able & Able (1990a, b). Instead the magnetically more positive notion “*change in the intended course for the magnetic compass*” is used. However, the latter wording is more diffuse and tends to obscure the outcome of the process.

The reference in Wiltschko et al. (1998) to Prinz & Wiltschko (1992) makes sense concerning the group where magnetic N in the pre-migratory period was deflected towards 240°, but not for the group where the magnetic deflection was in 120°. The birds were **raised outdoors under the natural day and night sky, and later on tested indoors in the (close to) natural magnetic field and without access to celestial cues**. As the controls were heading WSW (237° - 0.51\*\*\*, n = 41) the observed N-orientation in relation to the magnetic N in the first group (356° - 0.57\*\*\*, n = 110) made sense whereas the more scattered but significant N-orientation in the second group (12° - 0.19\*, n = 87) is not easily interpretable. Clearly, the expectation is an orientation about 120°. Also the rather low activities and the smaller concentrations in the individual mean vectors of the second group were significant/outstanding (the individual birds in the three groups each were tested between 10 and 14 times). However, focusing on the grand mean vectors – which is not done by the authors – these are 358° - 0.864\*\* (n = 8) for the first group and 9° - 0.700\* (n = 7) for the second group. On basis of these results – and some other results – Prinz & Wiltschko (1992) come out with ad hoc “explanations” about asymmetries and different influences according to whether the magnetic shift was in the same or in opposite direction of celestial rotation. According to Prinz & Wiltschko (1992) unpublished data of Bingman contained a group where magnetic N during ontogeny was deflected towards 115° and as in the corresponding group (i.e. the 120° group) of Prinz & Wiltschko this “*also showed a breakdown in orientation*”. Another possibility is that the northerly orientation in relation to magnetic N could also be perceived as reverse orientation in relation to the magnetic compass because of conflicts in the raising period between the magnetic and celestial compasses (cf. Magnet2).

Bingman et al. (1985, Fig.3) found more or less the same in another group of Pied Flycatchers raised under conditions of access to the day and night sky and in a magnetic field where magnetic N was deflected towards 245°. When later tested without celestial cues and in the local magnetic field the birds oriented NW-NNW (sample mean vector based on all bird/nights 332° - 0.25\*, n = 70). In

comparison the controls were oriented SSE-S ( $172^\circ - 0.44^{***}$ ,  $n = 62$ ). Anyway, the expectation of the orientation of the exp.s - based on the orientation of the controls - was a course on about  $245^\circ - 172^\circ = 73^\circ$  to the left of magnetic N. However, the course was  $28^\circ$  to the left and the discrepancy thus  $45^\circ$ . Modifying these observations into a two-sample test (W-W) the difference between the two distributions ( $287^\circ - 0.44$  (62) and  $332^\circ - 0.25$  (70)) is significant at the 0.05 level, i.e. the orientation of the exp.s is not explained alone by the hypothesis of a simple and full transfer from rotational-N to magnetic-N. Another part of the explanation - i.e. the too northerly orientation - could be reverse orientation in relation to the magnetic compass (Magnet2).

Weindler et al. (1998) also investigated the influence of the **direction of “stellar” rotation** on the magnetic compass. Pied Flycatchers **raised** under condition of an inclination of  $73^\circ$  (corresponding to Latvia where the birds were taken on nests) were divided in three groups: 1) under a planetarium sky rotating in the **normal, counter-clockwise** direction, 2) under a planetarium sky rotating in the **clockwise** direction, and 3) without celestial cues. The two latter groups - **tested** in the natural magnetic field and without access to celestial cues - showed axial SW/NE (i.e. standard/reverse) orientation, whereas the first group displayed “*a significant unimodal preference of their migratory direction*“, and it is hypothesized that because of the rather steep Latvian inclination the birds need a normal, counter-clockwise celestial rotation in order to develop normal, i.e. unimodal standard orientation. Now, 1) the inclination was not steep compared with the much steeper inclination in the Canada experiments of Åkesson et al. (2001, 2002) and Muheim & Åkesson (2002) - and here it is claimed that two species of passerine birds make use of a magnetic compass during almost vertical inclinations. Furthermore, 2) the 1)-group of Weindler et al. (1998) was not displaying unimodal orientation. In particular the sub-sample of 12 birds with higher concentrations (above 0.50) was almost significantly axially NW/SE-oriented - and this tendency (though clearly insignificant) was also apparent in the total sample of 27 birds ( $305^\circ/125^\circ - 0.134$ ). Anyway, the control-sample of Weindler et al. (1998) is acting so peculiar that it is difficult to give good explanations of the standard/reverse bimodality the two experimental groups.

Finally, the Savannah Sparrow experiments of Bingman (1983) and Able & Able (1990a, 1990b, 1993, 1996) should be shortly presented and discussed. The birds were **tested** in funnels and **always in the normal magnetic field without access to celestial cues**, whereas the birds were **raised** under various conditions of the natural night sky and/or the natural day sky, or a rotating “16-star-sky”. Normally, the birds were raised in the normal magnetic field but sometimes in a deflected field (magnetic N =  $110^\circ$ ). Some groups were also raised under condition of covering with polaroid sheets rotating the E-axis  $45^\circ$  clockwise. In short, the orientation in the exp.s always shifted in a way showing that **the magnetic compass was calibrated by the stars/celestial rotation**.

Comparing the experimental procedures of the Wiltschkos and the Ables the small amount of overlap is remarkable. Therefore, there is not much to disagree about. However, one important point is the constant claim of the Wiltschkos that magnetic orientation in course of the autumn takes over and dominates stellar orientation. This could not be confirmed by Able & Able (1995) and Able & Able (1996) conclude “*That magnetic orientation may be calibrated repeatedly and apparently indefinitely suggests that the plasticity that characterizes early development persists throughout the life of these birds. Celestial rotation assessed via visual cues appears to be of overriding importance in both early development and in adulthood*”. Neither Rabøl et al. (2002) could confirm the claim of the Wiltschkos.

### ***Summing up the evidence for the significance of the magnetic compass setting a migratory course different from due S***

The following is a conclusion for the claims and findings in the preceding sections.

A priori, there are no reasons or logic why a migratory course – different from due S - should be genetically rooted only in relation to the magnetic compass. An innate message like “obliquely away to the left of stellar rotation” seems to be just as easy or more easily programmed than “obliquely ahead to the right of magnetic S”. Obviously, both messages signal a SW course in human terminology and under normal conditions.

Clearly, the interpretation of the interplay between the magnetic compass and a celestial rotation compass as outlined above is a variant of the ancient theme of the Wiltschkos that the one and only – or at least most important and primary - innate compass in migrant birds is the magnetic compass (Wiltschko & Wiltschko (2003) still maintain this view – and in fact write it up - in case of Homing Pigeons). Then the Ables – followed by the Wiltschkos – demonstrated that celestial rotation in the pre-migratory period calibrated the magnetic compass, i.e. it looked like the magnetic compass was secondary though still innate and sufficient for establishing migratory orientation if celestial cues were absent. But the Wiltschkos found their way out and now consider orientation based in celestial rotation as reduced to a kind of “nonsense” orientation which has to be modified by a message coded in relation to the magnetic compass. This means that magnetic orientation is back in front of the game.

Anyway, in principle the interpretation of the Wiltschkos may be correct. The devastating problem is that the hypothesis is weakly supported by only a few selected observations. The question also is whether the raising and testing conditions have been so artificial that the results cannot be used to deduce what is going on under natural conditions. Furthermore, the interpretation of the Wiltschkos is contradicted by other results such as the Whitethroat orientation as reported by Rabøl & Thorup (2006).

My conclusion is that the migratory direction is genetically programmed both in relation to celestial rotation and to the magnetic compass, but if conflict in the pre-migratory period the former will overrule the magnetic compass and **under natural conditions** there is no setting of the course from the magnetic to the stellar compass.

### ***Is magnetic orientation in migrant birds well understood?***

According to one or another of the many reviews on magnetic orientation by the Wiltschkos (e.g. W. Wiltschko et al. 1998) – and also recent papers by the Swedes such as Sandberg et al. 2000 and Åkesson et al. 2002 – it appears that the field is well understood: 1) 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, there are problems with and uncertainties about all these four points.

- 1) The Wiltschkos observed that when the magnetic inclination is **inverted** – e.g. from +70° to -70° (unchanged polarity) – the orientation shifts 180°, i.e. it is **reversed**. This is considered an unambiguous indication of an inclination compass in action. However, sometimes the orientation also reverses under unchanged magnetic conditions (e.g. Rabøl 1994, 1995) or in

conflicts between stellar and magnetic compasses (Magnet2). This means that **reverse orientation is not in itself a sufficient signal for the presence of an inclination compass in action**; reverse orientation may also arise because of a changed **motivation**. Furthermore, Rabøl et al. (2002) found no indications of an inclination compass – i.e. the orientation was not reversed – when inverting the magnetic inclination in four samples of migrant passerines. These results of Rabøl et al. (2002) are much better in accordance with the influence of a magnetic polarity compass.

- 2) The experimental evidence behind the second point is presented and discussed in the present paper and obviously the expectation is not (always) met.
- 3) Recent conflict experiments (Magnet2) with three independent samples of first-time migrants trapped en route showed that it is not possible to generalize the statement that the magnetic compass calibrates the stellar compass. When magnetic N was deflected towards E or W in the sunset/early night phase – under conditions of a clear sunset and a starry sky – there was no shift in the subsequent orientation under the starry sky and in the natural magnetic field, i.e. there was no sign of a magnetic calibration of the stellar compass.
- 4) The conflict experiments by Rabøl (Magnet2) also showed that in the **exp.s** spending the sunset/early night in a deflected magnetic field and later on tested in the same deflected field and under a starry sky **in about half the cases the stellar compass dominated the magnetic compass**. However, just as often exp.s spending the sunset/early night in a deflected magnetic field and later on tested in the same deflected field and 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. Clearly, this finding is also central for the question whether birds are endowed with an inclination compass or just display reverse orientation under adverse or conflicting conditions.

Looking forward, there is **much need for 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 under a stationary “16-star-sky”, and also b) that the birds when caged in between the funnel/cage testing in most experiments and for extended periods have been deprived of celestial but not magnetic information (cf. Able and Able 1995). 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** experiments to balance the generalizations based in the many sunset/early night experiments (which often are spuriously co-influenced by **sunset-taxes**). Finally, in particular there is much need for **long-term, steady (i.e. 24 hours) conflicts** between magnetic and celestial information.

### *The magnetic compass in pigeons*

The hypothesis of Wiltschko & Wiltschko (2003) that in **homing pigeons the magnetic compass is the only innate compass** should be tested. As in case of stars there is no theoretical reason why

celestial rotation based in the sun cannot be an innate compass too, and the conflict experiments between the sun- and magnetic compass performed until now (Wiltschko et al. 1983, Wiltschko & Wiltschko 1990) are not easily interpreted – and in the discussion of Wiltschko & Wiltschko (1995) the implicit message is that magnetic compass at an early stage but not later dominates the sun compass which however well may be innate too. If the magnetic compass is the only innate compass calibrating all other compasses including the sun-compass then young pigeons growing up in a destroyed magnetic field and released with attached bar-magnets should be dis-oriented. To my knowledge such experiments are not yet performed.

### *The standard direction of the Endelave Whitethroats*

In the summer/autumn 1996 we trapped and tested local juvenile Whitethroats on Endelave very much in the same way as in 2001. The exp.s were caged and tested in inverted magnetic fields (inclination  $-70^\circ$ ) whereas the intensity and direction of magnetic N mirrored those of the natural magnetic field. The controls were caged and tested in the natural magnetic field (Rabøl 1998b, Rabøl et al. 2002). The birds were caged and tested in a more open landscape than in the forest glade used in the years 2000, 2001 and 2002, and the controls were caged close to the ground and not quite so exposed to the sun and stars as in the later experiments. However, when tested in the funnels the controls were up on a table and freely exposed for the night sky.

The starry night orientation of the **controls** in 1996 (17 Aug. through 17 Sep.) was more scattered than in 2000. The sample mean vector based on all bird/nights was  $202^\circ - 0.291^{**}$  ( $n = 59$ ), and the grand mean vector based on the individual mean directions  $201^\circ - 0.562^*$  ( $n = 11$ ). Applying the M-W-W-test on the grand mean vectors the difference between the controls in 1996 and 2000 is statistically significant ( $0.01 < P < 0.02$ ).

The sample mean vector based on all bird/nights of the starry night orientation of the **exp.s** in 1996 was  $158^\circ - 0.241$  ( $n = 39$ ), and the grand mean vector  $162^\circ - 0.731^*$  ( $n = 6$ ). The difference between the grand mean vectors of the exp.s and controls in 1996 was not quite significant (M-W-W-test,  $0.05 < P < 0.10$ ). Clearly, the orientation of the exp.s in 1996 was not different from the orientation of the controls and exp.s in 2000.

Normally, the standard direction of Danish Whitethroats is supposed to be SSW-SW as the birds are wintering in tropical W-Africa. However, perhaps the picture is not so simple; it seems like the birds from Jutland migrate towards SSW-SW whereas the birds from Zealand migrate more like the Swedish Whitethroats towards SE-SSE (Jesper J. Madsen, Danish ringing officer, pers.comm.). The population from Endelave may have both potentialities. Thus, the question is whether the observed SSE orientation in 2000 was spuriously influenced or deflected by the surroundings such as asymmetries in sounds, light, visible parts of the magnetic coils, forest silhouette, or procedure of treatment. In short, I do not think so – and a good argument is the much varying orientation from night to night in most individuals (Table 1). Another possibility is that the standard direction during first part of autumn is more easterly than generally supposed. A third possibility is that our expectations about a simple vector orientation system is not valid; perhaps the birds (in the start phase and when tested in funnels/cages) are not always proceeding in the standard direction but display right angle direction (e.g. Rabøl 1997). Anyway, the point and opinion of mine is, that the observed SSE-orientation is well qualified to answer the question put in the title of the paper. Significant deviations from the standard direction are often found (though never commented much upon). To mention just two obvious examples, the control birds of Bingman (1984) were SE-oriented far from the standard orientation in about SW, and the bimodal NW/SE orientation of the

Savannah Sparrows (Bingman 1983) is about perpendicular to the presumed standard direction in SW.

This leads to the next section.

### *The orientation/navigation system of migrant birds*

Due S orientation **could** also – and certainly according to the judgement of mine, **should** also – be considered as a sort of basic reaction in relation to stellar rotation coming out under the very deprived and unnatural conditions used. It is important to realize that experimental results are not necessarily reflecting or can be translated directly to what is going under natural, un-manipulated conditions.

Furthermore, as discussed by Rabøl (1985, 1994) compass orientation and gradient/coordinate navigation – normally considered to be two different **processes** (though the latter in its second step contains and is supposed to be steered by compass orientation, e.g. Able 2001) – are probably just only different **expressions** of same process/system. Possibly, the basic compass reaction in relation to celestial rotation is directed in one of the directions of the N/S gradient, i.e. there is something about the results of Weindler et al. (1996, 1997) though the interpretation of the results is somewhat different from the one given. Also within the field of magnetic orientation/navigation there seems to be a melting together of the two concepts of compass orientation and gradient navigation. Reports on navigatory responses in magnetic gradient based on intensity or inclination in birds (the Australian Silvereye *Zosterops lateralis*), spiny lobsters, turtles, newts and alligators (Fischer et al. 2003, Boles & Lohmann 2003, Lohmann & Lohmann 1994, 1996, 1998, Lohmann et al. 2001, Fischer et al. 2001, Rodda 1984) could also be understood as reverse orientation in a magnetic compass system..

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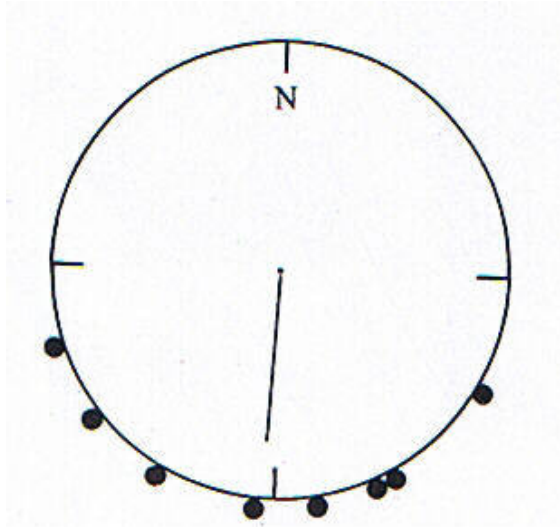
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**Fig.5:** Constructed example. The dots show the mean directions of 8 birds the sample mean vectors of which were:  $120^\circ - 0.60^*$  ( $n = 10$ ),  $150^\circ - 0.70^{**}$  ( $n = 12$ ),  $155^\circ - 0.80^{***}$  ( $n = 14$ ),  $170^\circ - 0.90^{***}$  ( $n = 8$ ),  $185^\circ - 0.60^*$  ( $n = 12$ ),  $210^\circ - 0.90^{***}$  ( $n = 10$ ),  $230^\circ - 0.70^*$  ( $n = 8$ ), and  $250^\circ - 0.80^{***}$  ( $n = 11$ ). The 95% confidence limits are  $\pm 45^\circ$ ,  $\pm 32^\circ$ ,  $\pm 22^\circ$ ,  $\pm 25^\circ$ ,  $\pm 40^\circ$ ,  $\pm 21^\circ$ ,  $\pm 41^\circ$ , and  $\pm 27^\circ$ , respectively. The grand mean vector is  $183^\circ - 0.764^{**}$  ( $n = 8$ ).