J. Rabøl: Do migrant European chats and warblers use magnetic gradient navigation? – Dansk Orn. Foren. Tidsskr. 108 (2014): 232-250

Appendix 2

Investigations indicating or claiming magnetic navigation

The obvious problem of mine is that (almost) all scientists are convinced that magnetic navigation is a significant real world phenomenon.

I doubt so. At least I think the phenomenon is much overrated and misconceived. But can so many people be mistaken? In principle, they can. Man is a social animal and opportunistic too. Scientists want publications in the leading journals, and there is a highway open for carrying out their ambitions.

Probably also data fabrications are more common than normally appreciated. Perhaps fabrications invaded papers on magnetic navigation? At least, the reward/risk fabrication-balance seems significantly skewed towards the reward.

1. Pied Flycatchers

Results presented by Beck & Wiltschko (1988) and Wiltschko & Wiltschko (2003b) – with reference also to Beck (1984) and Beck & Wiltschko (1982) – are relevant for the question about whether migrant birds make use of magnetic navigation.

German Pied Flycatchers *Ficedula hypoleuca* taken on nest and reared and tested without access to celestial cues presented all autumn for a magnetic intensity of 0.39G and an inclination of 35° (corresponding to a position in North Africa) ”never showed a meaningful directional preference” or were “disoriented” according to Beck & Wiltschko (1988) and Wiltschko & Wiltschko (2003a), respectively. However, these statements are not that simple. Considering sample mean vectors (Beck & Wiltschko 1988) in the four periods 1) 22 Aug. - 20 Sep., 2) 21 Sep. - 14 Oct., 3) 15 Oct. - 5 Nov. and 4) after 6 Nov., the following were found 1) 339° - 0.04 (n = 77), 2) 309° - 0.19∗ (n = 85), 3) 321° - 0.20 (n = 60) and 4) 8° - 0.11 (n = 23). If the whole autumn is considered, the total sample mean vector was 320° - 0.13∗ (n = 245). The question is whether this so called **third** group of flycatchers believe they are in ‘North-Africa’ and navigate back towards their standard migratory route between Germany and Spain. Certainly, this possibility is overlooked by Beck & Wiltschko and other people.

Now, in these flycatcher-experiments people always focus on the orientation of two other groups.

In the **first** group the magnetic intensity and inclination was constant throughout the autumn, 0.46G and 66° corresponding to Frankfurt. Here the orientation was SSW during the first two periods (see above), and then broke down in the last two periods (according to Beck & Wiltschko).

In the **second** group, the magnetic intensity and inclination were 1) 0.46G and 66º, 2) 0.42G and 52º, 3) 0.39G and 35º, and finally 4) 0.32G and 10º, where 1), 2), 3) and 4) correspond to the periods above. The orientation was SSW during the first two periods and then changed to SE, i.e. the orientation followed the predicted shift in the migratory route and progress. The most parsimonious interpretation here is a vector orientation system in operation depending on a shift to lower magnetic inclinations/intensities during late autumn. According to Gwinner & Wiltschko (1978), such a magnetic shift is not necessary for a directional shift in another long-distance migrant, the Garden Warbler *Sylvia borin*. In the second group of Pied Flycatchers, the lower intensity and/or inclination could be considered as a sort of **navigatory marker** (according to e.g. Freake *et al*. 2006). I.e. the flycatchers are not performing true magnetic navigation, as I tentatively interpreted the NW-orientation of the third group of flycatchers mentioned above.

A more parsimonious overall interpretation is that the NW-orientation in the third group and the SE-orientation in the second group are right angles responses to the initial standard orientation in about SW, i.e. a **cross-axis system** (Rabøl 1983, 1985) is operating. For a more thorough presentation and discussion, see Rabøl (2006).

2. The ancient Frankfurt cage experiments

Wiltschko (1968, 1972, 1978) carried out several experiments where the magnetic intensity and inclination were different from those in the local magnetic field. These three papers constitute the basic reference for the claim that the magnetic intensity has to be within 20-30% of the normal value in order for birds (i.e. mostly European Robins *Erithacus rubecula*) tested in Frankfurt cages to be able to compass orientate in (about) the standard direction. Clearly (but normally this is not emphasised or stressed) this claim may not hold true for – say – Pied Flycatchers tested in funnels.

The question is whether there are some indications in this material on **magnetic navigation**? Apparently, W. Wiltschko never considered this possibility. In short, the answer is no, because then some of the sample mean vectors should be more or less reverse to the standard direction, and no reverse orientation is found in any of the different constellations of changed intensity and inclination. Only standard orientation is found, or dis-orientation, or sometimes in spring NNW-orientation (considered as aberrant standard orientation towards NNE-NE). However, in most constellations of altered intensity/inclination, the change is not up/up or down/down as under natural conditions. Anyway, there is a single ‘displacement’ towards ‘S’ to 0.16G/31º. In this case a significant SSW standard orientation was observed in birds adapted to the low intensity, whereas such birds tested on the Frankfurt intensity/inclination (0.46G/66°) were dis-oriented. I.e. no (more or less) reverse orientation was observed as expected if the birds interpreted the lower intensity/inclination as a geographical displacement.

3. Tasmanian Silvereyes

The experiments of mine were much inspired of Fischer *et al*. (2003), who **simulated geographical displacements** by shifting the magnetic inclination and inclination. Freake *et al*. (2006) commented on Fischer *et al*., who only investigated adult birds. Deutschlander *et al*. (2012) extended the experiment to include juvenile birds.

Grey-breasted Silvereyes *Zosterops lateralis* were displaced from the breeding ground on Tasmania on latitude 42.5º S to Armidale in eastern Australia on 30.5º S. According to Freake *et al*. (2006) and Deutschlander *et al*. (2012), Armidale is situated in the northern part of the wintering area.

The silvereyes were displaced during summer and caged indoors on the magnetic parameters of Armidale (55 nT and -62º) for the next two months until the autumn migratory season started.

First, the 11 birds of Fischer *et al*. were tested on the magnetic conditions of Armidale – and indoors under diffuse light without the sight of the sun or stars. The sample mean vector was 22º - 0.52*** (n = 83). Then the birds were divided into two groups; SimN which were caged and tested on 50 nT and -59º, and SimS on 60T and -65º. According to Fig. 5 in Freake *et al*. (2006), the first condition corresponds to a latitude N of the wintering area (the intensity), or about the northern border of the wintering area (the inclination). The SimS condition corresponds the southern border of the wintering area (the intensity), or the middle of the wintering area (the inclination). The numbers of birds were six in SimS and five in SimN, and the two sample mean vectors were 38º - 0.75** (n = 30) and (according to the measurements and calculations of mine; Fischer *et al*. give no data) 132º - 0.30 (n = 28), respectively. According to the measurements of mine, the grand mean vectors were 40º - 0.93** (n = 6) and 125º - 0.62 (n = 5), respectively.

In short, the patterns displayed were taken as an indication of magnetic navigation, where the insignificant SE-orientation in the SimN birds could be perceived as if the birds considered themselves within the northern part of the wintering area (the inclination), or a little N of the wintering area (the intensity). This conclusion of the authors may be right. Anyway, the procedure is not optimal. Why displace the birds to Armidale? Clearly, the experiments should have been carried out on Tasmania. Also both the intensity and inclination in the SimN birds should have been clearly N of the wintering area.

In a recent paper, Deutschlander *et al*. (2012) also simulated magnetic ‘displacements’ in **juvenile** silvereyes. The paper starts with the usual ‘conventional wisdom’ talk about juveniles which – contrary to adults – are supposed only to display vector orientation (see, however, Thorup & Rabøl 2007).

Deutschlander *et al.* (2012) “… used larger changes in the magnetic field than used previously (Fischer *et al.* 2003) to ensure locations that were specified were well outside the range of this subspecies.” The latter is only partially true because the SimS inclination (-67º) isoline runs through the southern part of Australia N of Tasmania including southern part of the wintering area.

As in Fischer *et al*. (2003), Tasmanian silvereyes were trapped “in the breeding areas prior to autumn migration” and transported to Armidale. The birds – 18 juveniles and 22 adults – were tested **indoors**. First five times at Armidale magnetic conditions and then six times under either SimN or SimS conditions (two different groups). In short, all combinations showed significant northerly orientation, except **adults on SimN conditions**. In the calculation of mine, the axial grand mean vector is **300º**/120º - 0.717** (n = 9). This is about at right angles to the ‘NNE’ orientation in the five other groups combined. The conclusion of the authors is “The reorientation of the SimN adults, perpendicular to their seasonal appropriate migratory direction, does not allow us to distinguish between map-based navigation or “sign post” navigation by adults.” I agree though perhaps the designation ‘reorientation’ is flawed. In fact, the right angle axial pattern observed in the adults in the SimN situation is expected by none of the two hypotheses.

The question is whether there is a significant difference between the adults in the SimN conditions of Fischer *et al*. and Deutschlander *et al*.? The grand mean vector of the former is 125º - 0.618 (n = 5), i.e. on about the 300º/120º axis of the Deutschlander adults. If the two distributions are considered together, the axial grand mean vector is 120º/300º - 0.433 (n = 14). P is close to statistical significance at the 0.05 level. Applying the Fisher-test, five in ‘SE’ and 0 in ‘NW’ (Fischer) are different from three in ‘SE’ and six in ‘NW’ (Deutschlander) (P = 0.031).

In conclusion, using even more dramatic changes in the SimN condition perhaps will evoke changes also in the orientation of the juveniles – and reverse responses in both groups (SimN) – **if the birds navigate by magnetic means**. But I doubt they do so in a strict gradient-based sense**.**

4. White-crowned Sparrows

Åkesson *et al*. (2005) displaced White-crowned Sparrows *Zonotrichia leucophrys* in North America from W towards E (longitude 135º W to 66º W in Canada) – and from sites where magnetic N (mN) was clockwise of geographic N (gN) to sites where mN was counter-clockwise of gN. The migratory orientation changed dramatically from E-SE to W-NW in both adults and juveniles, and under both a clear sky and a simulated overcast sky.

The orientation on the eastern sites were cautiously interpreted as magnetic navigation (towards the site of trapping in Alaska) based on the shifted declinations. However, a more simple explanation could be reverse orientation in a simple compass system – at least under clear sky conditions and in reference to mN (Åkesson *et al*. 2001). Another explanation, not seriously considered by Åkesson *et al*. (2005), could be connected to the on average more than two hours’ time difference between the western and eastern sites. From Tab. 1 in Åkesson *et al*. (2005) I calculated that the median dates for experiments on the western and eastern sites are around 12 Aug. and 25 Aug., respectively. So there is no need for a very precise internal clock in order to deduce the easterly displacement.

In conclusion, the differences between the orientation on the eastern and western sites could be understood as reverse or right angle responses (in reference to mN), and there is no need of invoking some kind of navigation towards the breeding site, as proposed by Gould (2005). The orientation after the displacement **is directed** towards (about) the breeding site, but **this is no proof (not even an indication) that the process behind this direction is based in magnetic navigation.**

The question also is how Gould (2005) imagines a navigation system building on declination, because a system based on pre-migratory explorations in the breeding area is not appropriate for coping in a harmonic manner with the very large declination-shifts further E.

5. Procellariiformes

These birds should be considered obvious candidates for using magnetic navigation towards their breeding islands or foraging grounds: great stretches of an (at least apparently) uniform and featureless oceanic landscape, and at least in some regions an appropriate magnetic grid system where the isoclines of e.g. magnetic intensity and inclination form large angles of intersection (Åkesson & Alerstam 1998).

However, experimental evidence of magnetic navigation is totally lacking. Benhamou *et al*. (2003) and Mouritsen *et al*. (2003), among others, attached bar-magnets to the head of petrels and albatrosses but the magnets apparently had no effect at all. Very probably, these birds make use of olfactory navigation (e.g. Nevitt 2008).

6. Swedish chats and warblers

6.1. Fransson *et al*. (2001) investigated Trush Nightingales *Luscinia luscinia* caught in Sweden just before their first migration and exposed them to a magnetic field simulating the one in northern Egypt just before the Sahara crossing. "We found that that this magnetic field stimulated the birds to extend their fat-deposition period, indicating that magnetic cues may help small migratory birds to confront large ecological barriers." This conclusion has been widely accepted (e.g. Alerstam 2006 and Boström *et al*. 2010) as an example on magnetic navigation, or at least as a navigatory marker, in case of hatchling turtles (e.g. Lohmann & Lohmann 1994, 1996) and Pied Flycatchers (Beck & Wiltschko 1988). However, Fransson *et al*. never tested the orientation of the birds, and my conclusion is that an indication of magnetic navigation is at best very marginal.

6.2. Boström *et al*. (2010) reported on experiments performed with juvenile Northern Wheatears *Oenanthe oenanthe* trapped in autumn as grounded migrants at Ottenby, Sweden. Seven birds were subjected to a magnetic treatment intended to simulate the magnetic conditions met on their normal migratory route through western Europe down to Mauretania. Starting on the natural magnetic conditions of 1) Tovetorp (S of Stockholm) on 31 Aug. - 4 Sep., the birds experienced the magnetic conditions of 2) France ('Toulouse') on 5 Sep. - 9 Sep., 3) Morocco ('Casablanca') on 10 Sep. - 14 Sep., and 4) Mauretania on 15 Sep. - 19 Sep. Eight other wheatears experienced the same treatment as 1). Then steps 2), 3) and 4) were the magnetic conditions of a position 2) a little S of Cape Farewell (Greenland), 3) a position in the Atlantic Ocean S of 2) at the same latitude as 'Toulouse', and finally 4) a position further S in the Atlantic Ocean at the same latitude as 'Casablanca'.

The authors intended to simulate a displacement to the positions along the normal migratory route in the controls and to the three positions in the Atlantic Ocean in the experiments. No **orientation experiments** were carried out, and the amount of **migratory restlessness** was not monitored (or at least not reported). Two parameters were monitored: a) the **daily food intake** per bird, and b) the **daily weight** of the birds: a) "There was no significant difference in food intake between the birds in the two treatments", and b) ”The birds displaced parallel to the west of the normal migratory route increased more in body mass towards the end of the experiment than controls birds …". These results led to: "we … show that birds, during their first migratory event, can use geomagnetic cues to compensate for a displacement away from their normal migratory route, by adjusting their fuel deposition rate." The higher weight gain in the experimentals was taken as a positive indication of the hypothesis in charge. Anyway, the (treatment of the) results are too much manipulated: The reasons for omitting three birds (Tab. 2) are not legal and highly speculative, and without the omission the difference between the samples is insignificant.

At last, some positive comments to this paper: People now **think** in navigatory terms (at least if these are magnetic), also in juvenile birds – or at least **report** orientations in juvenile birds difficult to understand if not rooted in a navigational process (e.g. Gschweng *et al*. 2008).

6.3. Boström *et al*. (2012) is a follow up on the preceding paper. It is a highly speculative paper where the conclusions are not supported to any significant degree by the all too restricted and meagre results. But as usual, even weak suggestions of a magnetic navigation system are welcomed and easily published in the leading scientific journals.

6.4. Henshaw *et al*. (2010) presented orientation experiments with Lesser Whitethroats *Sylvia curruca* trapped as grounded migrants in spring S of Stockholm and transported to nearby Tovetorp.

The birds were tested indoor in wooden huts under low artificial light conditions and assigned to one of two groups tested in manipulated magnetic fields mirroring the magnetic conditions at a) a position of 'Bodø' (in Norway N of their breeding area, 33 birds) or b) a position said to be in the 'Czech Republic' (32 birds). However, the very large positional uncertainties are not appreciated (the isolines of inclination and intensity run almost in parallel).

The birds 'displaced' to 'Bodø' were disoriented (the sample concentration 0.30 is insignificant (P = 0.08) according to the Rayleigh test), whereas the birds 'displaced' to the 'Czech Republic' were significantly northerly oriented. The mean direction of the Norwegian sample is not presented – probably because of lack of statistical significance. However, according to my calculation it was 323º and thus close to the significant N-direction in the 'Czech Republic'. Applying a V-test, the 'Bodø' sample was significantly oriented in the standard direction NNW (P < 0.05), but not towards due N. The authors are not considering this possibility. However, the results could be interpreted in terms of magnetic compass orientation in the standard direction.

In conclusion, Henshaw *et al*. (2010) is an important paper because of the results. The interpretations are not unreasonable, but strongly skewed in favour of magnetic navigation. One may wonder why the clear indications of stellar navigation (Rabøl 1998, Thorup & Rabøl 2007) are not mentioned. Furthermore, the authors seem unaware of the long-distance displacements of mine to the Canary Islands (Rabøl 1981) and Kenya (Rabøl 1993), where at least the adult Robins and adult Garden Warblers did not display compensatory (magnetic nor celestial) navigation.

7. Magnetic pulse treatments

There have been several reports (e.g. Wiltschko *et al*. 1994, 1998, 2006, 2007, 2009) and Wiltschko & Wiltschko (1995b) on a change in migratory orientation ~~on~~ of about 90º towards E following the application of a very strong and short-termed magnetic pulse *aligned E/W with the head of the birds in the position termed south-anterior*. This change is taken as an indication of a navigation system based in magnetism. The reasons and (inherent?) logic for such a point of view are: a) the change is found only in **adult/experienced** birds – and most scientists within the field pretend to know that only adult and not juvenile migrants are able to navigate. Furthermore, b) as the magnetic **compass** is (supposed to be) an inclination compass based in processes in the avian eye not influenced by the pulse treatment the reaction is logically considered to be a **map-factor in a navigational system**. I understand this kind of logic, which nevertheless is flawed.

Apparently, this 90º deflection to E – both spring and autumn – has only been demonstrated in adult birds of the Tasmanian race of Grey-breasted Silvereye. Juvenile birds on their first autumn migration showed no deflection (Munro *et al*. 1997a, b). There is no significant deflection in adult European Robins, but during the first two days after the pulse the sample concentration is very low (Wiltschko & Wiltschko 1995b). Furthermore, the phenomenon is reported in Bobolinks *Dolichonyx oryzivorus* and pigeons (Beason *et al*. 1995, 1997, see below). However, the shift here is dependent on the direction of the pulse magnetization and is much less than 90º in the pigeons, and in fact appears insignificant. In adult Catbirds *Dumetella carolinensis*, Holland *et al*. (2009) found no deflection following a magnetic pulse (see 8.below).

Wiltchko *et al*. (2006) showed that birds following the pulse when tested in an inverted magnetic field reacted in such a way that the deviation was still (about) 90º but now to the opposite side indicating that the response was steered by an inclination compass. For Wiltschko *et al*. (2006) this is a **clear indication of a navigation system where the compass and a map components are totally separated**, i.e. it is a confirmation of Kramer's map-and-compass perception, as this is interpreted of almost all scientists within the field, including Able (2000) (see, however, Rabøl 2001 and Wallraff 2005). Another possibility is that **the magnetic compass for aligning of the magnetic gradients is of the polarity type**. However, Wiltschko & Wiltschko (1995a, pp. 64-65) do not seem to agree in this scenario of Phillips (1986): Newts from about 20 km E-ESE of the laboratory displayed **shoreward** orientation established in reference to a magnetic inclination compass – as inversion of the inclination (without changing the polarity) in the test-phase leads to an orientation shifted about 180°. On the other hand, the **homeward** orientation was unaffected by the inversion, and this leads Phillips to the obvious conclusion that the newts make use of a compass steered by the polarity of the magnetic vector for navigation – with the words of Phillips "a distinct magnetoreception pathway with polar response properties is involved in homing and is possibly linked in some way to the navigational map." My comment is that the navigational map of the newts needs (integration with) a compass, and this compass is a polarity compass if the gradients are based in the magnetic field. When the homeward orientation is unaffected, this also means that there is no transference from the polarity compass to an inclination/axial compass in the test-phase (as reported by Wiltschko *et al* 2006, see above).

Wiltschko *et al*. (2007) is about a second pulse applied 16 days after the first pulse (in silvereyes). Now the reaction was different: In the first two days the scatter was increased but no significant directional deviation was observed. Then the orientation turned back to normal. The interpretation of Wiltschko et al. is along the usual line that everything could and should be explained: The reaction on the days immediately following the first pulse "implies that this pulse had caused the receptors to provide the birds with some kind of false information, i.e. **the birds behaved as if they believed that they had been displaced to a westerly location and hence headed east**." This is a surprise for the authors because "one would intuitively expect that magnetic 'map' components mainly indicate north-south displacements." Next "The disoriented behavior observed during the following days seems to suggest that the information no longer made sense to the birds." However, the question is whether the right angle response instead should be considered as a reaction of a magnetic **polarity** compass. Certainly it looks much more a as right angle response in a compass system (Rabøl 1983, 1985). Clearly, we are lacking responses following other alignments of the pulse. If a map factor is involved, the alignment should be N/S investigating both north-anterior and south-anterior.

8. Catbirds

Holland *et al*. (2009) is about orientation in the short/medium-distance migrant **Catbird** trapped in autumn in New Jersey (NJ; adults and juveniles) and Illinois (adults only) and **radio tracked** when released at Princeton, NJ. Each sample was divided in three sub-samples: controls, magnetic birds (treated with a strong, very short magnetic pulse) and anosmic birds.

The orientation of the **controls** trapped and released in NJ was SSW-SW in the **adults**, whereas the **juveniles** were heading S-SSW. The difference between adults and juveniles was significant, but two juveniles turned clockwise after some time, and their final track was SSW-SW just like in adults. Probably (my interpretation), the juveniles oriented in about the standard direction of the population involved, whereas the adults navigated towards their former wintering area.

Fig. 2 shows the **NJ adult** orientation. The **anosmic** birds display S orientation, whereas the two other groups were SSW-SW-oriented. The difference is significant.

Fig. 3 shows the **NJ juvenile** orientation. The **anosmic** birds were S oriented, whereas the **controls** – as mentioned – oriented S-SSW. The **magnetic** birds were in between. The difference was not significant.

Fig. 4 shows the **Illinois adult** orientation. The **anosmic** birds were S-SSW oriented, whereas the two other groups oriented about SSW-SW. As the standard direction – and direction from Illinois towards the wintering area – is probably E of S, the orientation of the two latter groups was probably compensatory, whereas the S-SSW orientation of the anosmic birds was probably not standard (as it would had been if NJ birds).

Fig. 5 shows the orientation of **adult controls/magnetic birds from NJ and Illinois**. The orientation of the latter was skewed to the right (SW) and on the fringe of being significantly different from the SSW-SW orientation of the NJ birds.

An important point is whether the southerly orientation of the anosmic adults was due to the same mechanism as the S orientation in the juveniles. Perhaps it just looks like. Furthermore, it may be that the orientation in the control and magnetic adults was an olfactory based compensatory ‘navigation’ towards the wintering area.

Clearly, the magnetic pulse treatment had no effect.

The conclusion of mine is the Catbird – a short/medium-distance migrant – perhaps developed a navigation system based in olfaction much in the same way as pigeons (more complicated, because also a wintering area is involved). For a better understanding, releases from Illinois (both adults and juveniles) and NJ (juveniles from Illinois) are much wanted.

9. Reed Warblers

Chernetsov *et al*. (2008) trapped Reed Warblers *Acrocephalus scirpaceus* in spring at Rybashy on the Russian Baltic coast and displaced the birds 1000 km eastwards to Zvenigorod SE of Moscow. The birds were supposed to be on their way to a breeding area in the Ladoga-area/SE Finland. The birds were funnel-tested during starry nights and oriented significantly NE at Rybashy and NNW after the displacement to Zvenigorod. The mechanism behind this significant compensation is unknown.

Kishkinev *et al*. (2010) investigated the possibility that the compensatory mechanism was based in a double clock system, and simulated a displacement to Zvenigorod by shifting the light/dark rhythm one hour ahead. The birds were tested indoors at Rybashy and showed NNE-orientation not significantly different from the N-NNE orientation of the controls. The conclusion was that the birds were not using a double clock system for compensating an eastern displacement.

Kishkinev *et al*. (2013) repeated the displacement of Chernetsov *et al*. (2008) but now included experimentals with an intersected ophthalmic branch (V1) of nervus trigeminus. The orientation of both controls and experimentals were NE at Rybashy.

A third sample of experiments were sham treated (i.e. the upper beak region was operated but V1 not cut). After displacement to Zvenigorod these experimentals were significantly oriented a little W of N, and the sample orientation was significantly different from the NE orientation at Rybashy. According to Kishkinev *et al*. (2013), the difference between these sham treated birds and the V1 sectioned birds at Zvenigorod was on the border of significance ($P = 0.05$).

The conclusion of Kishkinev *et al*. (2013) is cautious, but clearly they consider it most probable that the V1 intersection has impaired a magnetic map factor responsible for the compensatory orientation in the controls.

In short, I do not disagree with the Kishkinevs, but probably the scenario is or could be more nuanced.

The obvious questions are a) how the NE-orientation is established in the V1 disected birds, and b) whether the NNW-orientation after displacement to Zvenigorod is a logical and expected reaction if based in a magnetic navigational system. In short, a) could be explained as a simple compass reaction based in a celestial compass or in the magnetic compass, which is supposed to be rooted in retinal processes and therefore not influenced by the V1 cutting.

Looking at the **intensity** isoclines, these are running about NW/SE in the region embracing Rybachy, SE Finland and Zvenigorod (Fig. 3; Kishkinev *et al*. 2013), i.e. the gradient-axis is about SW/NE. The intensity in the presumed breeding area is about the same as in Zvenigorod, i.e. we are expecting no compensatory NNW-orientation after displacement (if the birds navigate using the magnetic intensity as a navigatory parameter). However, if the birds at Zvenigorod are navigating towards an intermediary goal area between Rybashy and the breeding area (Y), we should expect a compensatory SW-orientation..

The **inclination** isoclines are running close to E/W (100º/280º). Zvenigorod has an intermediate inclination between Rybashy and the breeding area, so it is difficult to have an expectation on S or N compensation after displacement to Zvenigorod for an intermediary goal area, whereas N compensation seems the most obvious if the birds are navigating towards the breeding area.

The **declination** – with isoclines running about NW-NNW/SE-SSE – seems a promising parameter, as the difference between Rybashy and Zvenigorod is 4.5º, between Rybashy and the breeding area 3.3º, and – of course – between Zvenigorod and the breeding area 1.2º. If the declination is a navigatory parameter, we should expect weak SW orientation both towards the breeding area and a more strong SW response if navigating towards an intermediary goal area between Rybashy and the breeding area.

Considered in symphony, a magnetic based compensatory NNW response as a mixture between N (inclination) and SW (declination in particular, and intensity) seems rather promising. Perhaps as a coincidence, the intact birds displaced to Zvenigorod (Fig. 1, Kishkinev *et al*. 2013) shows a major N and a minor SW peak.

We are now waiting for **simulated magnetic displacements** – preferably small changes in intensity, inclination and declination in the same order of magnitude as the differences between Rybashy, Zvenigorod and the presumed breeding area.

The responses to the displacements of Rabøl (1998) and Thorup & Rabøl (2007) – and in particular the **simulated** displacements – indicate that the stellar sky can be used for navigation. The obvious question then is why the V1 dissected Reed Warblers of Kishkinev *et al*. (2013) did use their stellar navigation and compensated the geographical displacement.

This question is obvious because the tests of Kishkinev *et al*. (2013) were carried out on starry nights, and the birds were pre-exposed under the sunset-sky for one hour before to one hour after sunset. Experiments were started at the beginning of astronomical twilight and lasted for 40 minutes.

This means that at least the major stars were visible during all of the test period, whereas no stars (or very few at last) were visible in the pre-exposed sunset-period. Perhaps this procedure somewhat impaired the birds' ability to compensate the displacement by means of the starry sky. However, the evidence of Rabøl (1997) and Thorup & Rabøl (2007) for stellar based compensation were much more pronounced in autumn than in spring. Perhaps stars are not used in spring for navigation close to the breeding area, and one may envisage a **local** navigation system based in odours and visible landscape and – perhaps – a **regional** navigation system based in magnetism.

Finally, the usual problem concerning orientation experiments: omission of evidence for other interpretations. Kishkinev *et al.* (2013) write "Nevertheless, recent East-West displacement experiments (3), (4) have shown that several species of night-migratory birds can correct … and thus can compensate for longitudinal displacements." (3) is the Thorup *et al.* (2007) White-crowned Sparrow paper and (4) the first Reed Warbler paper of Chernetsov *et al*. (2008). There is no reference to Thorup & Rabøl (2007) nor Rabøl (1998), as there should be. The scene grows even more grotesque when it is claimed later in the introduction that "The stars are also unlikely to provide useful east-west positional information to night-migratory songbirds (25)." (25) is a paper by Mouritsen & Larsen (2001), where the design is not optimal and seems unsuitable to show stellar navigation.

10. Homing pigeons

During many years much work and attention has been devoted to demonstrate magnetic navigation in pigeons, but no real confirmation – only a lot of weak indications have accumulated.

In their survey “**Magnetic maps in animals: A theory comes of age**“ Freake *et al*. (2006) are confident about magnetic navigation in pigeons. However, they are not able to find direct experimental evidence of magnetic navigation in pigeons, only indirect evidence relying on an old review of Wallcott (1991). Formerly, Wallcott was positive about magnetic navigation in pigeons. However, later on he changed – not referred to by Freake *et al*. – to a much more sceptical and in fact rejecting attitude (Wallcott 1996).

Let us consider some central papers claiming magnetic navigation in pigeons.

10.1. Wiltschko & Wiltschko (2003b) is a truly remarkable paper: In eleven well written pages in a distinguished scientific journal it is very convincingly demonstrated that the departure directions of homing pigeons released within a magnetic anomaly were in no significant ways influenced by the magnetic field intensity[1]. However, the authors gave some good reasons why the magnetic field was not used or ignored.

10.2. Dennis *et al*. (2007) also released pigeons within a magnetic anomaly. However, the randomization method used to figure out the orientations was not clearly described. Therefore, it is not easy to find our whether the conclusions of the authors are reasonable.

Adult/experienced pigeons were released in and around the Auckland Junction Magnetic Anomaly (JMA). “The source of the JMA is a deep-seated structural dislocation app. 1.6 km below the Earth´s surface and is not correlated with surface topography.” The peak of (total) magnetic intensity in the anomaly is said to be 400 nT above regional main-field intensity. According to Fig. 1.4 in Wiltschko & Wiltschko (1995b) the latter is about 55,000 nT, i.e. 400 nT is less than 1% of the regional level, probably meaning that the directions of magnetic N in reference to geographical N is barely affected.

Pigeons were trained from several releases up to several 100 km S of the loft. Fig. 1 **implies that the birds were released “N” of the loft** (home-directions between 130° and 220°, six out of 15 release sites are depicted). The intensity isoclines of the anomaly looks like a lens oriented with the long axis running 150º/330º. According to Fig. 1.4 in Wiltschko & Wiltschko (1995b), the intensity isoclines in general are oriented about 110°/290° in the New Zealand area. When displaced “N”, the pigeons anyway will experience increased intensities, i.e. supposedly releases within the anomaly will just increase the “feeling” of being displaced “N”. Clearly, we need a map with the anomaly, the 15 release sites, the loft and the magnetic intensity isoclines. Furthermore, we need to know the borders of the area from where the “randomly oriented bearings of the intensity field” are taken.

The flight trajectories of Fig. 1 are compatible with a PCD in about SE-SSE – and therefore perhaps it is only a coincidence that most flights are in parallel to the isoclines. This is not discussed by the authors. However, an appropriate randomization procedure should compensate for such a coincidence – but is the randomization procedure appropriate? Their probabilities of the alignment of the trajectories in parallel or perpendicular appears so low that perhaps the procedure is inappropriate. Anyway, the randomization procedure is not described properly; we need some

---

[1] The Wiltschkos claim a single minor influence: “– pigeons released for the first time within the anomaly tended to have longer mean vectors with increasingly steeper gradients.” However, in any kind of Bonferroni thinking (such as Rice 1989) such a single affirmative variable in an array of other variables showing nothing has to be considered insignificant.

calculated examples of trajectories to accept the procedure. As realized by the authors “Why pigeons initially fly after release in directions with respect to that of the local intensity field begs explanation” (p. 1155, first sentence in Discussion). In my interpretation this could be a spurious correlation to a PCD directed SE-SSE

10.3. Beason *et al*. (1997) state in the Abstract: “After treatment with a 0.5 T magnetic pulse, homing pigeons (Columbia livia) showed headings that deviated from the mean direction of untreated controls. (1) These deviations ranged up to 60° and were most pronounced at distances beyond 100 km from the home loft. (2) When birds treated with a pulse south-anterior and birds treated with south-left were released together, they deviated to opposite sides of the untreated controls, indicating that the direction of the pulse determined its specific effects. (3) On the day of treatment, a south-left pulse caused a significantly larger deflection than a south-anterior pulse. (4) The duration of the effects was not entirely clear; the number of releases with significant deflections seemed to decrease as time passed and birds had made additional homing flights. (5) Our findings agree with the hypothesis that magnetite-based receptors provide the pigeons with orientational information. (6) The manifestations of the effect indicate that the magnetic ‘map’ rather than the magnetic compass is involved. (7) Apparently, the pulse alters map information″. The markings (1-7) are mine and are referred to below in 10.3.1-6.

However, almost nothing happens in evidence of a magnetic map factor.

10.3.1. The mean numerical deviations are 32° and 17° for controls compared with pulse south–left (n = 10), and controls compared with pulse south-anterior (n = 21), respectively (only data from Tab. 1 and 2 are included). The corresponding mean vectors are 13° - 0.843*** and -2° - 0.933***, resp. Clearly, there are no significant differences between the controls and the two sets of experiments. Furthermore, the difference (15°) between the two sample mean vectors is not significant (Watson/Williams test, 0.10 < P < 20). It is true that the deflections were most statistically pronounced at distances beyond 100 km from the home loft – in case of controls/south-anterior. The opposite tendency was found in controls/south-left.

10.3.2. This is correct. However, the deviation was sometimes to the right and sometimes to the left, and there was no system in the deviations in relation to the homeward direction.

10.3.3. This is correct five times out of six (Tab. 1). Including Tab. 2 the statement is right seven times out of 10. However, these tendencies are not statistically significant.

10.3.4. There is no such general tendency. Considering south-anterior and omitting the three deviations (-102°, -36°, -127°) based on very small sample concentrations (0.10, 0.26, 0.21) the correlations coefficient (Pearson) is 0.087 (n = 27), whereas the correlation coefficient (-0.682***, n = 14) is significant in the subsample of south-left. Taking the two subsamples together, there is no statistically significant tendency (r = -0.217, n = 41).

10.3.5. This is not clear, because no clear predictions were made.

10.3.6. This is not clear. As far as I know, a light/retina dependent magnetic compass is strongly inferred in passerine birds but not in pigeons. Perhaps pigeons have a compass based on magnetite

– or both kind of magnetic compasses as claimed in newts (Phillips 1986, see also Wiltschko & Wiltschko 1995 p. 64 and 65).

Whereas magnetic navigation seems to be doubtful there seems to be no doubt about an influencing and important **magnetic compass** in pigeons (as recently rendered most probable by Gagliardo *et al*. 2009). The general conclusion of the four papers in J. Exp. Biol. of Wallcott (1996), Able (1996), Wiltschko (1996) and Wallraff (1996) was that magnetic navigation in pigeons was doubtful whereas olfactory navigation was an important fact. This point of view has recently been confirmed of Gagliardo *et al*. (2008). However, people convinced of the significance of magnetic navigation continue to claim evidence of the phenomenon. E.g. Fleissner *et al*. (2008) report on a structure in the upper beak of pigeons: "Due to its 3D architecture and physiochemical nature, the dendritic system should be able to separately sense the three vector components of the Earth's local field, simultaneously allowing birds to detect their geographic position by the magnetic vector, i.e. amplitude and direction of the local magnetic field, irrespective of the animal's posture or movement and photoreception." Winklhofer & Kirschwink (2008) could not confirm, and Treiber *et al*. (2012) in details dismantled the system. Next, a heavy discussion appeared in the RIN-forum. The alarming point is how two so different views could originate in the essential same base of observations. A cautious conclusion is that people believing in magnetic navigation are too far fledged in their expectations and interpretations.

10.4. Schiffner & Wiltschko (2011). This paper has clear affinities to the Gernsheim-paper (10.1).

According to the Abstract: "Tracks of pigeons, recorded with the help of GPS-receivers from two sites 30 km N and S of the Frankfurt loft, were analyzed in view of an influence of irregular fluctuations of the geomagnetic field. The data obtained were correlated with indices characterizing different aspects of these fluctuations".

Schiffner & Wiltschko investigated a multitude of variables and their correlations. For various reasons or by chance some correlations were significant and a selected amount of these were taken as indications for a navigational process in pigeons rooted in earth magnetism. In the opinion of mine, Schiffner & Wiltschko made a clear over-rating of the data.

10.5. Mora & Walker (2009). The title of this paper is "Do release-site biases reflect response to the Earth's magnetic field during position determination by homing pigeons?"

Release-site biases are the rule more than the exception when pigeons are released, and at least part of the 'explanation' is the so called PCD (preferred compass direction): When released in a certain region, the departure directions of the pigeons are often consistently skewed compared with the home-direction, say directed towards WNW when the home-direction is SW. Rabøl (2001) – based on Wallraff (1974) – considered this as a systemic phenomenon based on uncertainties and zero-axis navigation. Nowadays, Wallraff (e.g. 2005) has a different opinion about the nature of the PCD. In principle, PCDs as considered by Rabøl (2001) may arise in a magnetic navigation system. However, this is not the message of Mora & Walker (2009) who consider that the pigeons are following magnetic intensity slopes **or** contour directions when released. If e.g. the intensity isocline is running E/W then pigeons depart predominantly in the directions of N, E, S and W.

The argumentation and documentation of Mora & Walker are not easy to accept, and in a RIN-forum discussion in 2009 even the Wiltschkos were not happy about the logic in Mora & Walker.

Furthermore, Wallraff in several thorough comments severely dismantled Mora & Walker. I have to agree with Wallraff: Mora & Walker is a mixture of imagination and inappropriate data treatment.

10.6. Wu & Dickman 2012 "… describe neuronal responses in the pigeon´s brainstem that show how single cells encode magnetic field direction, intensity, and polarity; qualities that are necessary to derive an internal model representing directional heading and geosurface location." We have to wait for further evidence and considerations, but certainly it looks promising for the presence and importance of a magnetic GPS system.

11. Turtles

11.1. Freake *et al.* (2006) mention the **hatchling** loggerhead turtle *Carreta carreta* experiments by Lohmann & Lohmann (1994, 1996, 1998) and Lohmann *et al*. (2001) as indicative of some sort of magnetic navigational response intended to be meaningful and adaptive in relation to the movement of the turtles round in the North Atlantic gyre. Freake *et al*. are thinking in terms of **navigational markers** alias **position markers** alias **sign post navigation** which essentially is a compass reaction. However, the interpretation of mine is that different magnetic treatments sometimes are followed by orientations which differ significantly from each other – whereas their coupling/causal relationship with the positions in the gyre are not clear and in all probability spurious.

Freake *et al*. note that "the case for magnetic map navigation has been greatly strengthened by a more direct line of evidence: **juvenile** green sea turtles *Chelonia mydas* captured on feeding grounds off the coast of Florida and tested in magnetic fields found approximately 300 km north or south of the capture location, oriented themselves in the appropriate general direction that would return them to the capture site (Lohmann et al. 2004)." I agree, but the result of this single experiment with rather few animals involved needs to be reconfirmed.

Concerning **adult** green turtles, Freake *et al*. is much concerned about the possibility of magnetic navigation in the Ascension Island turtles (see also section 11.6). Breeding female turtles "displaced to the northwest showed the highest homing success and tended to have straighter paths." Freake et al. deliver a lengthy and redundant set of explanations rooted in a calculation that the geographical position of the magnetic coordinates of Ascension has moved steadily and about 700 km towards northwest in the period 1970 until 2005. Anyway, the distance of displacements was much shorter (Luschi *et al*. 2001, Hays *et al*. 2003) and – given the considerable age of the adult turtles in consideration – it seems difficult to figure out whether the former magnetic coordinates of the island is to the NW or SE of its present position. Luschi and co-workers gives a much more reasonable reason of the high homing success from the NW: Olfactory (or auditory) orientation from the leeward site of the island (prevailing winds from the SE). This possibility is mentioned shortly by Freake *et al*.

11.2. Lohmann & Lohmann (1994, 1996, 1998), Lohmann *et al*. (2001) and Putman *et al*. (2011) investigated the orientation of hatchling loggerhead turtles emerging during night on an about N/S oriented Florida beach. Guided by the low horizontal glow from the sea, the hatchlings move about E towards and into the sea. Their first orientation is guided by the waves, which irrespective of wave direction ashore come in from the E perpendicular to the coast. It is shown that the direction towards the horizontal glow and wave-direction is secondarily transferred to the magnetic compass.

Emerging hatchlings placed in a circular water-tank by night were not oriented when tested in darkness in the magnetic field alone. When tested with a low light from the E, most hatchlings moved towards the light. When the light afterwards was taken away, the hatchlings proceeded in the same direction and the course was maintained in relation to the magnetic compass. The hatchlings were tested only once in the local magnetic field or a field where the intensity, or inclination or both were changed.

Well out in the sea, the hatchling is supposed to proceed eastwards presumably guided by its magnetic compass and after some time enters the North Atlantic gyre where the animals grows up spending the next years before returning to Florida. The gyre first flows northeast and east towards Portugal, then south towards Senegal where it turns west towards Cuba. It is considered important for the Florida turtles to stay within the gyre and in particular avoid following a NE-directed branch near Portugal. This leads to colder water and death for the turtles.

Lohmann & Lohmann (1996) concluded that *“…* sea turtles [i.e. the hatchlings] possess the minimal sensory abilities necessary to approximate global position using a bi-coordinate magnetic map.” This point of view is further elaborated in Lohmann *et al*. (2001) where both inclination and intensity were changed simultaneously to simulate displacements to three magnetic regions in the gyre: “These results imply that young loggerheads have a guidance system in which regional magnetic fields function as **navigational markers** [my highlighting] and elicit changes in swimming direction at crucial geographic boundaries.”

Clearly, Lohmann and co-workers consider it likely that the hatchlings in the very first hours of their beach-emergent life are able to express an appropriate “navigational” response based on (parameters in) the Earth magnetic field. These responses have no immediate survival value; their benefit will first occur in some remote areas in the remote future.

The central question is whether this is reasonable and possible as the hatchlings are not even endowed with an innate magnetic start-direction; i.e. there is nothing like an innate standard/nonsense direction established in relation to the magnetic compass.

In the Florida hatchling turtles, **time** is not involved as an influential variable. **Position** is the only influential variable and could be every position in the route at the same time. There is no coupling between time and position as in case of goal area migration in juvenile birds (Rabøl 1985). Therefore, in most cases it is possible for the author to place the turtles in a position somewhere in or in the vicinity of the gyre where the observed orientation makes meaning. Clearly, this is not science but close to manipulation.

The general observation of the hatchling experiments of the Lohmann’s is that the orientation often shifts when the magnetic intensity and/or inclination are changed, but there is no urgent need interpreting the results in terms of magnetic navigation or navigational markers; more simple reactions in a **cross-axis system** (Rabøl 1983, 1985, 1994) describe just as well or better.

Clearly, we need more experiments before the hypothesis of magnetically based positional markers are accepted.

The Lohmanns performed very few experiments with hatchling turtles: 1) Six samples (1994), where the inclination varied between 75º and 15º whereas the intensity was constantly 44-45 mT. In three samples the sample mean vector was not significant, and in one sample the expectation was badly fitted. This sample was omitted in the 1998-paper. 2) Two samples (1996) where the intensity was 52 and 43 mT, respectively, whereas the inclination in both was 57º. 3) Three samples (2001) in which both intensity and the inclination varied between samples. No figures were given for the pair-wise intensities, and for inclinations only three markings of the positions in reference to the gyre on Fig. 1. Here, the three orientations fit the expectation. Focusing on the six plus two samples in 1994 and 1996, in only a single sample there was a significant angle of dissection between the isolines of magnetic intensity and inclination, and here the orientation towards 90º looks reasonable according to the expectations. In most other samples the orientation seems out of context with one or both isolines. Clearly, there are more fabulations than documentations in these hatchling experiments by the Lohmanns.

In the beginning, the Lohmanns believe that the hatchlings are able to navigate in a magnetic gradient field. However, this system is never considered in an operational way; it is only out there somewhere in the vague intuition. In the 2001-paper a 'navigational marker' system is proposed – but still in a vague, non-operational way because the orientation on the three sites in the gyre as shown on Fig. 1 is more indicative of (a sort of) goal-area navigation in the sense of Rabøl (1969, 1985) or perhaps even better resembles the (by Sauer 1957 proposed) orientation-system of the outstanding single Lesser Whitethroat 'Müllerchen'.

In a final paper of Putman *et al*. (2011), hatchlings were taken from their beach and tethered in a water arena surrounded by magnetic coils. For ten minutes, a dim right light came from the east, and then was switched off, and soon after "… the magnetic field was simultaneously changed to either (1) a field replicating one near Puerto Rico or (2) a field replicating one near the Cape Verde Islands." Puerto Rico and Cape Verde are both situated on a latitude of 20º N, but the longitudes are very different (65.5º W, and 30.5º W, respectively).

The 'Puerto Rico' hatchlings oriented 50º - 0.39* (n = 22), and the 'Cape Verde' hatchlings 217º - 0.34* (n = 35).

The Atlantic gyre runs about WNW at Puerto Rico and WSW at Cape Verde, so the orientations are marginally acceptable – mostly because the "navigatory markers" expectations are very broad and plastic.

A more simple – and biological meaningful – interpretation should be that the NE-orientation at 'Puerto Rico' is a compass reaction not significantly different from due E (the direction towards the red light), and the SW-orientation at 'Cape Verde' is a reverse compass reaction, but of course such a scenario is all too simple for the Lohmanns (and the referees too).

Their final conclusion that "… our results provide the first demonstration that longitude can be encoded into the magnetic positioning system of an animal" is absolutely too far-fetched and close to pure fantasy.

And as said before: how should these just newborn hatchlings on their emerging beach with a magnetic sense of direction depending on light-calibration be able to react in a meaningful magnetic navigational way in a site and context somewhere in the remote and distant future?!

And now from **hatchling** turtles to some important **juvenile** and **adult** turtle investigations.

11.3. Avens & Lohmann (2004): Juvenile loggerhead and green turtles inhabiting inshore waters of North Carolina, US were tested after displacements 30-168 km along circuitous routes while deprived of visual cues. The turtles were several years old and were supposed to have undertaken and terminated the long gyre migration round in the Atlantic Ocean.

Turtles were displaced to Beaufort from two main areas 1) Core Sound and Pamlico Sound towards ENE (74°), and 2) an area WSW (255°) as seen from Beaufort. At Beaufort they were tested – tethered in the same way as the hatchling turtles – in a circular arena. Obviously, the local seawater of the testing site was used. The walls of the tank blocked the view of the horizons and surroundings.

During summer (i.e. May to September) both species showed reasonably clear homeward orientation, in particular towards ENE (loggerheads 83° - 0.29***, n =122, and green turtles 50° - 0.71**, n = 9). Only loggerheads were displaced from WSW, and the westerly orientation (271° - 0.43, n = 11) was only significant in context of the V test and not the Rayleigh test.

Avens & Lohmann considered these results as indicative of homing towards the capture grounds towards ENE and WSW. They were cautious about the compasses and maps involved. The **magnetic compass** and a compass based on the **sun** or patterns of skylight polarisation were mentioned. ″Among several potential sources of **positional information** are **location-specific chemical cues** … and information from the **Earth′s magnetic field** … (and) from celestial cues such as the elevation (height above the horizon) of the **sun** at specific times of the day″ [my highlighting]. The last possibility was considered unlikely.

Avens & Lohmann also tested both species during autumn (i.e. October and November) where the turtles are supposed to migrate towards about south out in the Atlantic Ocean. At this time of the year, the displaced loggerheads oriented 190° - 0.61**, n = 15, and the greens 199° - 0.76*, n = 7).

The authors forgot to tell or recognize that magnetic map navigation is also rather unlikely as all magnetic gradients in the region (except declination) run about NNW–SSE i.e. perpendicular to the displacement directions. The same objection is valid in case of spiny lobster *Panulirus argus* displacements (Boles & Lohmann 2003, see below). On the other side, Avens & Lohmann should be acknowledged for mentioning the chemical ‘olfactory’ possibility. Boles & Lohmann never did that.

In conclusion – and as far as we can see – the conditions for chemical navigation must be rather perfect, as seawater is probably running up and down along the coast and sounds, and the testing site is placed at the coast and local seawater is used in the test arena.

11.4. Lohmann *et al.* (2004): Juvenile green turtles were trapped on the foraging grounds on the eastern/mid Florida coast, where experiments were carried out in the local laboratory water following simulated displacement about 337 km to the N and S (shifted magnetic fields to 61.2º, 49.2 microT and 55.4º, 45.4 microT. The sample orientations were 172º - 0.70** (n = 11), and 16º - 0.54* (n = 12), i.e. **it looks like magnetic navigation – as in the N/S-‘displaced’ spiny lobsters and newts** (see sections 13 and 14). I would like to see this experiment repeated. On the map shown in Lohmann *et al*. (2004) two dots denote to where the turtles were ‘displaced’. However, these ‘displaced’ positions are not too well defined, as the isolines of magnetic intensity and inclination are running almost in parallel.

11.5. Lohmann (2007): This is a more cautious paper compared with his first papers – and the hatchlings are now not supposed to be able to navigate in a magnetic gradient system, but the inclination and intensity ‘only’ serve as **navigatory markers** eliciting “changes in swimming direction at crucial points in the migratory route where the turtles might otherwise stray off course.” Later on in the text it grows even less precise “when exposed to regional magnetic fields that exist in widely separated locations along the their migratory route, turtles that had never before been in the ocean responded by swimming in directions that would, in each case, facilitate movement along the migratory pathway.” The problems for K. Lohmann is 1) there is no clear testable research/null-hypothesis (by keeping it loose he may ‘adapt’ his results), and 2) he made all too few experiments – in particular with combinations of intensity and inclination.

In this paper, Lohmann relies much on the navigatory responses of (1) simulated magnetic ‘displacement’ with juvenile turtles (reported in section 11.4), and in particular by (2) the Luschi *et al*. (2007) experiments with geographically displaced adult turtles. (1) is reported above and looks convincing, but we need to see such simulated displacements repeated before making generalizations. (2) is reported below (section 11.6) and the conclusion of both Luschi (in litt.) and me is that there is no direct indication of magnetic navigation, but certainly the results are indicative of something else than just simple magnetic compass orientation. But this something may be navigation in another system than a magnetic one.

11.6. Luschi *et al.* (2007): 20 green turtles were displaced about 100 km from Mayotte (Comoro Islands) to three areas to the SE, SW and NE.

The turtles were divided in three groups (number of individuals within parentheses): 1) Controls (**C**; 7), 2) Magnet Homing (**MH**; 7), i.e. turtles equipped with a strong and movable bar-magnet on head at the release site, and 3) Magnet Transport (**MT**; 6), i.e. turtles disturbed by a strong and movable bar-magnet under the transport from Mayotte to the release site. I.e. there was no fourth group carrying magnets both when displaced and when released.

C and **MH** turtles were displaced to NE (2), SE (3) and SW (2).

MT turtles were displaced to SE only.

The SW and NE transports were in one year (2004), and the SE transports in another year (2005). I.e. the MH and MT turtles were mostly displaced in different directions and in different years making comparisons between the two experimental groups difficult.

Therefore, the applied three-sample ANOVA testing including all turtles is perhaps not very rewarding. It seems better just to compare the SE releases.

All turtles – except one – actually homed to Mayotte, i.e. **the magnetic treatments did not destroy the homing process** to the same extent as cutting the olfactory nerves in pigeons. However, certainly the magnetic treatments have some effects.

The main effect – when looking at Fig. 1 – is that the **homing tracks of the HM and HT turtles are much longer than in case of the C turtles.**

However, there are also important **similarities** between the controls and the experimentals. All turtles released from SE departed more or less NNE-NE and then bended N and finally approached Mayotte from NE. A mirror image of this pattern was seen in (at least three out of four) turtles released from SW: The departure direction was about NW then bending N and Mayotte was finally approached from the NW. The four C and MH turtles released in NE approached the island on more straight courses.

If distinguishing in a simple way between action of a magnetic compass **or** magnetic gradient navigation without considering processes in between, the conclusion of mine – based on the patterns of MH and MT turtles considered in concert – should be that probably only the magnetic **compass** is influenced by the two treatments.

However, the authors moved in between the two concepts, e.g. in their final words "… geomagnetic information has a major, albeit still not exclusive, role in pinpointing isolated targets." Certainly, the authors with the words "major" and "pinpointing" infer a significant kind of something more 'navigational' than just simple compass orientation. The question is whether this is mostly a 'political' compromise between different basic views of Luschi and Lohmann concerning the orientation system?

11.7. Cain *et al.* (2005): In case of the hatchlings, the results of Lohmann *et al*. (2001) are presented as the most prominent example of the magnetic field delivering information as **navigational markers** (Fig. 1).

The following quotations are interesting: "straying beyond the latitudinal extremes of the gyre is often fatal", and "An ability to recognize the latitudinal extremes of the gyre, and to respond by orienting in an appropriate direction, might therefore have considerable adaptive value." We could all agree and then **wonder about the disorientation shown by turtlings 'displaced' to the inclinations of 75º and 15º** (Fig. 2, Lohmann & Lohmann 1994).

Cain *et al*. also maintain that "… hatchling loggerheads **evidently** emerge from their nests already capable of detecting two different magnetic field elements that vary across the Earth's surface and might provide positional information useful in guiding a long-distance migration." If one is very friendly this is perhaps vaguely correct in an indirect way but using the word "evidently" is far too much. Remember that the hatchlings are not even endowed with a magnetic 'standard direction' when emerging on the beach. What is the reality of this scenario: emergent hatchlings struggling towards the light of the sea transferring this direction to a magnetic compass reference looking in their remote future in the Atlantic Gyre reacting in a meaningful way on specific values of intensity and inclination of the Earth's magnetic field simultaneously under attacks from voracious ghost crabs?

11.8. Lohmann *et al.* 2008: This clear survey refers many of the papers above. According to the Abstract "… a reasonable hypothesis is that sea turtles use multiple cues to navigate in the marine environment, perhaps relying on a magnetic map to navigate into the vicinity of a distant target and then use non-magnetic cues to guide themselves to the final goal." Thus this paper seems a Lohmann/Luschi-mixture with dominance of the former.

12. Alligators

Sub-adult alligators *Alligator mississipiensis* displaced by Rodda (1984) were supposed to make use of “magnetic map information to select their homeward directions.” Freake et al. (2006) agreed about the “… possible role of geomagnetic inclination in navigation.” “The data suggest that alligators may be sensitive to changes in magnetic inclination of as little as 0.01-0.02º (roughly 1-2 km).” On the contrary **yearlings** were supposed to make use of (compass based) route-reversal, as yearlings were not homeward oriented except in cases of almost rectilinear displacements.

Homeward distances after displacement were between 11.6 and 34.3 km, and **homeward directions** SE, E, NE, N, NW and NW, i.e. rather (radial) symmetrical, but the distances were so short that magnetic gradient navigation seems difficult to effectuate.

The alligators were released in an arena, and there was no difference in orientation whether the experiments were carried out in overcast or under sunny conditions. Therefore, quite reasonably, the focus is on magnetic orientation, but apart from what could be considered to be a **biased and spurious ad hoc correlation**, there was no evidence of magnetic map navigation, but only route reversal based in a magnetic – and/or a sun-compass – or perhaps even more probable olfactory navigation or inertial ‘navigation’. In short, there is no real logic behind the dip angle calculations of Rodda (1984) but several filtrations and ad hoc adaptations.

The ‘evidence’ for magnetic map navigation presented was a statistically significant negative correlation between **homeward score** and **dip-angle deviation** (deviations between night level dip angles and dip angles measured at the time of the release). The same relation holds true but a little weaker in case of (deviations in) horizontal magnetic intensity as the independent variable (but not for vertical and total intensity). However, the data from May 1979 when considered separately showed an insignificant positive correlation and were omitted from the analysis because of the presence of several magnetic storms in this period (according to Rodda this correlation is negative but according to Fig. 4 it is about +0.45). If May 1979 is included there is no significant negative correlation. Also other ad hoc adaptations were carried out to the maximal magnetic fit. Furthermore, the magnetic measurements used were carried out a long distance away and therefore a lot of noise was probably involved.

Rodda discussed three possible systems of orientation/navigation in the alligators:

12.1. Olfactory orientation/navigation. This possibility was rejected because of the observed reversal of the wind-directions inside the arena (caused by the high collars surrounding the arena). However, according to our present knowledge (Wallraff 2005) we should not expect the process of olfactory orientation/navigation as a heading into the wind of a certain scent, but as measures of olfactory (ratio) intensities and knowledge of olfactory gradients in reference to a compass (solar or magnetically based). In my opinion (the presence of) olfactory (short distance) navigation in alligators is a much more reasonable possibility than magnetic navigation, but there is no direct evidence.

12.2. Route-based navigation. First, some very reasonable reservations were made against en route based navigation. Anyway Rodda’s conclusion in case of the orientation of the yearlings “suggest routebased navigation.” John Phillips told him about the hypothesis of the Wiltschkos concerning very young pigeons shifting from route based orientation (route reversal) into gradient navigation when becoming older and more experienced. Phillips (and Rodda) expect the same system in alligators but brings no significant evidence.

12.3. Multi-coordinate navigation. This means “an accurate sensitivity to large scale gradients in at least two directions.” Furthermore, “These arena data raise the possibility that geomagnetic dip angles or horizontal intensities could provide one gradient for multi-coordinate navigation in alligators.” Rodda found possible evidence for this point of view because the correlation coefficient between homeward bearing and dip angle deviations peaked at the moment the alligators started moving away from the middle of the arena (on the average 14 minutes after release). However, clearly there were no significant differences between the six correlation coefficients calculated from 30 minutes before to 30 minutes after the release. These varied between (about) -0.25 and -0.58, and three were significant on the 5% level. However, as mentioned the atypical May 1979 scores were omitted. Thus the indirect kind of proving magnetic navigation is increased by an ad hoc manipulation.

Anyway, Rodda (1984) is a very sober paper remarkably good for its time of publication. However, there are (spurious/biased) special treatments and interpretations in favour of magnetic navigation. No one can use this investigation as a significant signal of magnetic navigation in alligators. It is a possibility, but more probable systems are route reversal or olfactory navigation.

Rodda (1985) is another paper on the orientation of alligators. Compared with the 1984 paper this is a more cautious paper where Rodda followed displaced alligators marked or radio-tracked. There are very significant indications of homing following displacements of 2-20 times the diameter of the home range in 258 **yearling** alligators. Roddas interpretation of the orientation/navigation system is the one of gradient navigation and not en route based reversal (as for the yearlings in the 1984 paper), but he is very cautious and in fact never proposes magnetically based navigation. However, olfactory (gradient) navigation is mentioned as a possibility.

13. Newts

According to Freake *et al*. (2006) the experiments with eastern red-spotted newts *Notophtalmus viridescens* give “The most direct evidence for magnetic map navigation ...” **I agree that the results of Phillips and co-workers in course of the years have developed to confirm this conclusion**. Considered in isolation Fig. 4 in Freake *et al*. – showing newt-orientations following simulated geographical displacements – confirms the hypothesis of gradient navigation in reference to magnetic inclination.

I appreciate the last sentence of Freake *et al*.: “Future work should include precise geomagnetic surveying at and around the home ponds of the newts to test for a match between the orientation behavior observed in the experiments and the actual gradient patterns.” One may wonder why such work was not initiated long time ago. In particular, we need knowledge of the gradient-axis of the inclination – in reference to both magnetic and geographical N. The declination seems to be about 8º-10º to the W. The local axes (at the two important home-pond areas) may be different from the general gradient-axis – probably close to N/S – of the Indiana region. Unfortunately, Phillips and co-workers give no information.

The main problem for us before accepting magnetic gradient navigation in the newts are not the experimental results but the extremely small home-range of these animals: The adult newts spend most of their time in the home-pond or in other ponds or on land up to 1 or 2 km away. **The conditions for developing a magnetic navigation system (but of course not a magnetic compass) seem far out of contexts**.

Also the methods and results of these newt experiments are not easily overviewed and integrated – even after several re-readings of the many papers published. 1) At first I suspected spurious connection between shoreward and homeward orientation, i.e. the latter could – perhaps – be reduced to some (motivational conditioned) cross-axis deviant of the former, but a thorough and critical inspection of the extensive material reveals no obvious reason for such a suspicion. However, to be sure we need to see homeward orientation also after staying in a **radial symmetrical outdoor water-tank** where there is a shore all way around (or in the middle) and not just in one of the long ends of a rectangular tank. 2) All displacements from the home-ponds to the laboratory area came from SSW or E-ESE. We need to see the orientation also of newts displaced from the two opposite directions – and field experiments where newts from a certain home-pond are displaced in the four cardinal directions (as in the homing pigeons of H.G. Wallraff). 3) The homeward orientation of newts from E-ESE (Phillips *et al*. 1995) is very difficult to understand, as the difference in inclination between the home-pond and the tank/testing area is as minute as 0.02º-0.03º (calculation based on a said difference of 0.17º between the home-pond in SSW and the tank/testing area (Phillips *et al*. 2002a), and a supposed inclination gradient running about N/S). Furthermore, if the newts navigate in a mono-coordinate system by means of the inclination the response should be S and not E-ESE. 4) If the newts make use of bi-coordinate-navigation – and the declination is the other coordinate/gradient – then the homeward orientation of the E-ESE newts becomes much more understandable, as the difference in declination is E-directed and about 0.1º (the sample mean vector was 126º - 0.52**, n = 19). Furthermore, in a bi-coordinate system the orientation of the newts from the home-pond towards SSW is now expected to be SW and not S as the declination-vector is about 0.16º and directed towards W (the sample mean vector was 221º - 0.59***, n = 18). 5) However, if we maintain the proposition of a bi-coordinate navigation system the results of the final simulated displacements of Fischer *et al*. (2001) and Phillips *et al*. (2002a) become less understandable: the orientation following the ‘displacement’ **downward** the inclination 0.15º, 0.48º, and 2º, respectively, should be about 270º, 325º, and 340º, respectively. In fact, they were random (328º - 0.08), 25º - 0.52*** and 56º - 0.47***, respectively. 6) In principle, the newts in the outdoor tanks should be able to ‘measure’ the declination as the sun is available for establishing geographical N. However, the extremely small differences in declination needed seem out of context, and in fact Phillips and co-workers are not proposing the probability. 7) One should note that the SSW and NNE-NE orientations on a general SSW/NNE-axis in Phillips *et al*. (2002a) come close to the bimodal ‘fixed-axis’ orientation on SSW/NNE after exposure for long-wave light in the tank-phase (Phillips *et al*. (2002b). On the whole, the different reactions/changes in orientation as the result of exposures for different wavelength of light in particular in the shoreward orientation adds to insecurity about the mechanisms behind homeward directed orientation. 8) In conclusion, the homeward orientation in the experiments performed should not be considered a proof that the newts under natural circumstances make use of magnetic navigation. In my opinion, too many ‘degrees-of-freedom’ in the procedures are involved. But certainly, the results are promising.

We have to realize, that **the newts – in the scenario of P – are carrying out the process of gradient navigation while spending their time in the outdoor watertanks**. Here the homeward compass direction is transferred to the magnetic compass and maintained and expressed in reference to this compass when later on tested indoors.

Several kinds of gradient navigation systems may be involved, among these a magnetic one based in the inclination (as supported by some of the experiments changing the inclination).

Now Phillips at least nowadays believe much in orientation in reference to polarized light patterns in passerine bird orientation (e.g. Muheim *et al*. 2006a, b) – and in fact already many years ago he was positive about the influence of reflected light in his interpretations of the deflector loft experiments with pigeons (e.g. Phillips & Waldvogel 1982). As the water tanks containing newts from the ponds towards SSW and ESE are oriented with the long axis perpendicular to each other, some deflections based on (polarized) light patterns may be responsible for the orientation, i.e. **perhaps gradient navigation is not at all involved**.

When the experimental newts are transferred indoors to the test table they almost certainly experience a minor decrease or increase in the magnetic inclination compared to the one present in the outdoor tanks, so the question is whether the newts behave as suggested above, or whether they react on the changed magnetic condition experienced at the test table?

14. Spiny lobsters

The spiny lobster experiment of Boles & Lohmann (2003) is referred to in Freake *et al*. (2006) and my comment is that both these authors seem unaware of the possibility of chemical/olfactory navigation in the displaced lobsters[2]. Concerning the simulated displacements the following orientations certainly look like at least mono-coordinate magnetic map responses – just like the newts of Phillips and co-workers. Freake *et al*. write the following wise words: “A criticism common to both the newt and lobster studies is that the simulated displacement distances exceed the distances over which they are known to perform true navigation and, therefore, are not representative of the real world.”

The conclusion of Boles & Lohmann (2003) is “our results demonstrate for the first time that an invertebrate animal is capable of true navigation.” Furthermore, “These results provide the most direct evidence yet that animals possess and use magnetic maps.” However, whereas true navigation is probably involved, the indications of the use a magnetic map could be challenged.

---

[2] I contacted Boles (with the text above) several times. He never answered. I then contacted Hans Wallraff writing “If the displaced lobsters (Figures 1-2) were tested in local seawater (they probably were!), olfactory/chemical navigation may be involved.” Wallraff already earlier contacted Boles, and based on Boles’ answer he concluded to me “that in this case olfaction is sufficiently excluded.” However, Wallraff’s conclusion could be wrong. Probably, he misunderstood something about the words “tank” and “arena”, which for Boles are clearly the same, or the word “laboratory.” Boles wrote that “The water for the tanks was filtered sea-water from the laboratory’s flow through system.” Furthermore, “The water comes from the nearby ocean.” This probably means that the lobsters were tested in the local water of TS1 when displaced to TS1, and in the local water of TS2 when displaced to TS2, and if the water was only mechanically filtered and not charcoal filtered (or something like that as in the pigeons of Wallraff) the chemical composition of the water was not changed.

First, **if** the displaced lobsters (Figure 1 and 2) were **tested in local water**, ‘olfactory’ (chemical) navigation may be involved in much the same way as demonstrated in pigeons by Benvenuti & Wallraff (1985). If so, the magnetic field was probably involved only as a compass reference. The authors are aware – and mention – that magnetic navigation may be difficult because the displacements are closer to an E/W-axis than a N/S-axis, and the isoclines of both magnetic inclination and intensity are running close to E/W in the area of investigation.

This leads to the next point: Fig. 3 is depicting simulated magnetic displacements to **positions** about 400 km N and S of home, respectively. The two mean vectors calculated are pointing close towards home, so the combination of Figs 1, 2 and 3 appears very convincingly explained as guided by magnetic navigation. However, the longitude – 80.5º W – given in the ‘Experimental protocol’ for both positions of displacement is bound to be very uncertain. Both magnetic inclination and intensity vary ‘much’ with latitude but close to nothing with longitude, so the simulated displacement is not towards a position to the N but towards a long row of ‘positions’ between – say – WNW and ENE as seen from the home position. In the same way, the position in S is a long row of ‘positions’ between ESE and WSW. In short, the homeward orientations as depicted are maximum solutions to the hypothesis in charge. The figure may also be misleading in another aspect: If navigating in a close-range magnetic system, the orientation depicted may or may not be home-directed.

Now, the lobsters on Fig. 3 were captured at CS2 and tested in TS1, and clearly there is no significant difference between the orientation of the lobsters ‘displaced’ 400 km to the ‘N’ (199º - 0.51) and the other(?) sample of lobsters displaced from CS2 to TS1 depicted in the lower right of Fig. 1 (222º - 0.65). This leaves the possibility that the orientation of the lobsters ‘displaced’ 400 km to the ‘S’ is not a navigational response but only reverse orientation in a compass system elicited by ‘something’ that of course in principle could be the magnetic inclination and/or intensity and if so could be considered (it is mostly a matter of words) as a simple form of uni-coordinate navigation.

15. Pacific salmon

Until now I refrained from discussing magnetic orientation in fishes but obviously the following has relevance to turtle orientation.

Putman *et al*. (2014) report orientation - long before the fishes actually enters the Pacific Ocean - in a juvenile freshwater stage of the Chinook salmon *Oncorhynchus tshawytscha* which is interpreted as indicative of the presence of meaningful ‘navigational markers’ (based on magnetic inclination and intensity). Clearly the results could be interpreted in such a way but as in the hatchling turtles simple compass could be involved. I wonder whether a similar system could be found in juvenile migrant birds before migratory readiness appears. I cannot believe so.

This paper has much in common with the turtling chronicles of Kenneth Lohmann with the same over-rating interpretations about the presence/importance of magnetic sign-post/’mono-coordinate’ navigation (the isoclines of magnetic intensity and inclination are running almost in parallel).

The actors were about one year old, 5-10 cm juvenile Chinook salmons tested in small buckets (30.5 cm diameter) with freshwater. The fishes were in the parr stage "the stream-dwelling juvenile stage. Thus, it appears that the fish possess orientation responses necessary for successful ocean navigation prior to even migrating toward the sea." In the rearing tanks the magnetic intensity was 526 micro-Tesla, and the inclination 67º. As adults, the salmons are migrating out into the Pacific Ocean (very large area from Oregon in the east to Asia in the west) bordered by the about east/west running isoclines 555 and 444 micro-Tesla in the north and south, respectively, and inclinations 73º and 56º, respectively. The isoclines 555 mT and 73º ran almost in parallel and close to each other. The same holds true for the isoclines 444 mT and 56º.

The fishes were tested under five magnetic conditions: 1) northern border, i.e. 555 mT/73º, 2) southern border 444 mT/56º, 3) home/rearing conditions 526 mT/67º, and the two nonsense constellations 4) 555 mT/56º, and 5) 444 mT/73º. The fishes oriented significantly SSW-SW at 1) and NNE at 2), otherwise random.

The five sample concentrations were very low (at highest 0.135 and 0.163 at 1) and 2)), and n was very high (between 232 and 240). The tests were performed during daytime, and I am a little insecure whether the single fish was tested a) only once in only a single constellation, or b) only once but in all five constellations assigned randomly; apparently a). The individual orientation used was the one of the head of the fish pointing relative to magnetic north ("a digital image of each fish was taken 8 min. after the field changed …"). Head directions were measured to the nearest 5º, which appears mysterious because at the figures the directions are shown in sections of 15º, and every second 15º section is larger than the preceding and following section. However, this mysterious compilation should have no significant influence on the sample direction and concentration.

Clearly, the Putman's have **not demonstrated "An inherited magnetic map"** as proclaimed in the title. May be we just see a standard and a reverse magnetic compass response. Why the standard response is SSW-SW is a weak/unclear point in my proposal. Anyway, one should expect an about W-response under 3) the home-condition as the ocean and the foraging ground (the presumed goal) is situated about W as seen from the home-site in Oregon.

The authors conclude that appropriate values for both intensity and inclination should be present in order for the fishes to be oriented, but perhaps the fishes are not disoriented but bimodally SSW-SW/NNE or NNE/SSW-SW oriented meaning that about half the fishes orient in reference to the inclination and the other half reverse in reference to the intensity. The two sample concentrations are so low that a combination appears random/disoriented.

Perhaps there is a point that marine/aquatic organism use the magnetic field for (sign post) navigation (if their interpretation is correct). Unlike birds, such creatures cannot (?) see the star patterns/movements appropriately.

Clearly, this paper could be taken as another brick-in-the wall indication of the presence of magnetic (sign post) navigation. However, as in the turtlings the weak point is that the orientation is recorded in a stage preceding the circumstances where the reactions/orientations have meaning. Could similar orientations be recorded in migrant birds tested before they entered the stage of a migratory mood?

A further point is that perhaps some samples with other combinations of intensity/inclination are omitted. At least there is a previous case where Lohmann omitted some samples for future presentations.

Postscript

In the remote year of 2030, the leading bird navigation scientists of our time have passed away. In the context of orientation and navigation by animals, the magnetic universe collapsed some years ago, and people still wonder what happened. How could so many people be so misled for so many years? The prime explanation is that humans are social and opportunistic animals with strong personal bonds, and these people were persistent leaders firmly believing in their – as it turned out to be – by and large spurious world and paradigm.

Now, the question is whether we learned of this story? Almost certainly we did not. Next time in another context we will – in principle – do the same mistake, because our way to understand and figure out complex nature has to pass the threshold of acceptance by other people who are more interested in the social hierarchy in the local village than being a brick in the wall embracing the universe.

References

Able, K.P. 2000: The concepts and terminology of bird navigation. – J. Avian Biol. 32: 174-183.

Alerstam, T. 2006: Conflicting evidence about long-distance animal navigation. – Science 313: 791-794.

Avens, L. & K.J. Lohmann 2004: Navigation and seasonal migratory orientation in juvenile turtles. – J. Exp. Biol. 207: 1771-1778.

Beason, R.C., N. Dussourd & M.E. Deutschlander 1995: Behavioural evidence for the use of magnetic material in magneto-reception by a migratory bird. – J. Exp. Biol. 198: 141-146.

Beason, R.C., R. Wiltschko & W. Wiltschko 1997: Pigeon homing: effects of magnetic pulses on initial orientation. – Auk 114: 405-415.

Beck, W. 1984: The influence of the earth magnetic field to the migratory behaviour of Pied Flycatchers (*Ficedula hypoleuca* PALLAS). - in: Varju & Schnitzler (eds.) Localization and orientation in biology and engineering, pp. 357-359. Springer Verlag Berlin Heidelberg.

Beck, W. & W. Wiltschko 1982: The magnetic field as a reference system for genetically encoded migratory direction in Pied Flycatchers (*Ficedula hypoleuca* Pallas). - Z. Tierpsychol. 60: 41-46.

Beck, W. & W. Wiltschko 1988: Magnetic factors control the migratory direction of Pied Flycatchers (*Ficedula hypoleuca* Pallas). - In: Quellet, H. (ed.) Acta XIX Congr. Int. Ornith., Vol.II, pp.1955-1962.

Benhamou, S., F. Bonadona & P. Jouventin 2003: Successful homing of magnet-carrying white-chinned petrels released in the open sea. – Anim. Behav. 65: 729-734.

Benvenuti, S. & H.G. Wallraff 1985: Pigeon navigation: site simulation by means of atmospheric odours. – J. Comp. Physiol. A 156: 737-746.

Boles, L.C. and K.J. Lohmann 2003: True navigation and magnetic maps in spiny lobsters. – Nature 421: 60–63.

Boström, J.E., T. Fransson, I. Henshaw, S. Jacobsson, C. Kullberg & S. Åkesson 2010: Autumn migratory fuelling: a response to simulated magnetic displacements in juvenile wheatears, *Oenanthe oenanthe*. – Behav Ecol Sociobiol DOI 10.1007/s00265-010-0985-1.

Boström, J.E., C. Kullberg & S. Åkesson (2012): Northern magnetic displacements trigger endogenous fuelling responses in a naive bird migrant. – Behav Ecol Sociobiol 66: 819-821.

Cain, S.D., L.C. Boles, J.H. Wang & K.J. Lohmann 2005: Magnetic orientation and navigation in marine turtles, lobsters and molluscs: concepts and conundrums. – Integr. Comp. Biol. 45: 539-546.

Chernetsov, N., D. Kishkinev, & H. Mouritsen 2008: A long-distance avian migrant compensates for longitudinal displacement during spring migration. – Curr. Biol. 18: 188-190.

Dennis, T.E., M.J. Rayner & M.M. Walker 2007: Evidence that pigeons orient to geomagnetic intensity during homing. – Proc. R. Soc. B274: 1153-1158.

Deutschlander, M.E., J.B. Phillips & U. Munro 2012: Age-dependent orientation to magnetically-simulated geographic displacements in migratory Australian Silvereyes (*ZOSTEROPS L. LATERALIS*). - Wilson J. Orn. 124: 467-477.

Fischer, J.H., M.J. Freake, S.C. Borland and J.B. Phillips 2001: Evidence for the use of a magnetic map by an amphibian. – Anim. Behav. 62: 1–10.

Fischer, J.H., U. Munro and J.B. Phillips 2003: Magnetic navigation by an avian migrant? – In: ″Avian Migration″ Berthold, P., E. Gwinner and E. Sonnenschein (eds.), pp.424–432. Springer, Berlin.

Fleissner, G., B. Stahl, P. Thalau, G. Falkenberg & G. Fleissner 2008: A novel concept of Fe-mineral-based magnetoreception: histological and physicochemical data from the upper beak of homing pigeons. – Naturwissenschaften DOI 10.1007/s00114-007-0236-0.

Fransson, T., S. Jacobsson, P. Johansson, C. Kullberg, J. Lind & A. Vallin 2001: Magnetic cues trigger extensive refuelling. – Nature 414: 35-36.

Freake, M.J., R. Muheim & J.B. Phillips 2006: Magnetic maps in animals: a theory comes of age? – Quart. Rev. Biol. 81: 327-347.

Gagliardo, A., P. Ioale, M. Savini & M. Wild 2008: Navigational abilities of homing pigeons deprived of olfactory and trigeminally mediated magnetic information when young. – J. Exp. Biol. 211: 2046-2051.

Gagliardo, A., M. Savini, A. De Santis, G. DellÒmo & P. Ioale 2009: Re-orientation in clock-shifted homing pigeons subjected to a magnetic disturbance: a study with GPS data loggers. – Behav Ecol Sociobiol 64: 289-296.

Gould, J.L. 2005: Animal navigation: Northern exposure. – Current Biology, Vol.15: R653-R655.

Gschweng, M., E. K. V. Kalko, U. Querner, W. Fiedler & P. Berthold 2008: All across Africa: highly individual migration routes of Eleonora´s falcon. – Proc. R. Soc. B 275: 2887-2896.

Gwinner, E. & W. Wiltschko 1978: Endegenously controlled changes in the migratory direction of the garden warbler, *Sylvia borin*. – J. Comp. Physiol. 125: 267-273.

Hays, G.C., S. Åkesson, A.C. Broderick, F. Glen, B.J. Godley, F. Papi & P. Luschi 2003: Island-finding ability of marine turtles. – Proc. R. Soc. London B 270: S5-S7.

Henshaw, I., Fransson, T., Jacobsson, S. & Kullberg, C. 2010: Geomagnetic field affects spring migratory direction in a long distance migrant. – Behav Ecol Sociobiol 64: 1317-1323.

Holland, R.A., K. Thorup, A. Gagliardo, I.A. Bisson, E. Knecht, D. Mizrahi & M. Wikelski 2009: Testing the role of sensory systems in the migratory heading of a songbird. – J. Exp. Biol. 212: 4065-4071.

Kishkinev, D., N. Chernetsov, & H. Mouritsen 2010: A double clock er jetlag mechanism is unlikely to be involved in detection of east-west displacements in a long-distance avian migrant. – Auk 127: 773-780.

Kishkinev, D., N. Chernetsov, D. Heyers, & H. Mouritsen 2013: Migratory Reed Warblers need intact trigeminal nerves to correct for a 1,000 km eastward displacement. – PloS ONE 8(6): 1-10.

Lohmann, K.J. 2007: Sea turtles: navigating with magnetism. – Current Biology 17: R102-R104.

Lohmann, K.J. and C.M. Lohmann 1994: Detection of magnetic inclination angle by sea turtles: a possible mechamism for determining latitude. – J. Exp. Biol. 194: 23–32.

Lohmann, K.J. and C.M. Lohmann 1996: Detection of magnetic field intensity by sea turtles. – Nature 380: 59–61.

Lohmann, K.J. and C.M. Lohmann 1998: Migratory guidance mechanisms in marine turtles. – J. Avian Biol. 29: 585–596.

Lohmann, K.J., S.D. Cain, S.A. Dodge and C.M. Lohmann 2001: Regional magnetic fields as navigational markers for sea turtles. – Science 294: 364–366.

Lohmann, K.J., M.F. Lohmann, L.M. Erhart, D.A. Bagley & T. Swing 2004: Geomagnetic map used in sea-turtle navigation. – Nature 428: 909-910.

Lohmann, K.J., P. Luschi & G.C. Hays 2008: Goal navigation and island-finding in sea turtles. – J. Exp. Mar. Ecol. 356: 83-95.

Luschi, P., S. Åkesson, A.C. Broderick, F. Glen, B.J. Godley, F. Papi & G. Hays 2001: Testing the navigational abilities of ocean migrants: displacement experiments on green sea turtles (*Chelonia mydas*). – Behav Ecol Sociobiol 50: 528-534.

Luschi, P., S. Benhamou, C. Girard, S. Ciccione, D. Roos, J. Sudre & S, Benvenuti 2007: Marine turtles use geomagnetic cues during open-sea homing. – Current Biology 17: 126-133.

Mora, C.V. & M.M. Walker 2009: Do release-site biases reflect response to the Earth´s magnetic field during position determination by homing pigeons? – Proc R Soc B, Online Early DOI: 10.1098/rspb.2009.0872.

Mouritsen, H. & O.N. Larsen 2001: Migratory sonbirds tested in computer-controlled Emlen funnels use stellar cues for a time-independent compass. – J. Exp. Biol. 204: 3855-3865.

Mouritsen, H., K.P. Huyvaert, B.J. Frost & D.J. Anderson 2003: Waved albatrosses can navigate with strong magnets attached to their head. – J. Exp. Biol. 206: 4155-4166.

Munro, U., J.A. Munro, J.B. Phillips 1997a: Evidence for a magnetite-based navigational ´map` in birds. – Naturwissenschaften 84: 26-28.

Munro, U., J.A. Munro, J.B. Phillips & W. Wiltschko 1997b: Effect of wavelength of light and pulse magnetisation on different magnetoreception systems in a migratory bird. – Australian Journal of Zoology 45: 189-198.

Muheim, R., F.R. Moore & J.A. Phillips 2006a: Calibration of magnetic and celestial compass cues in migratory birds – a review of cue-conflict experiments. – J. Exp. Biol. 209: 2-17.

Muheim, R., J.B. Phillips & S. Åkesson 2006b: Polarized light cues underlie compass calibration in migratory songbirds. – Science 313: 837-839.

Nevitt, G.A. 2008: Sensory ecology on the high seas: the odor world of the procellariiform seabirds. – J. Exp. Biol. 211: 1706-1713.

Phillips, J.B. 1986: Two magnetoreception pathways in a migratory salamander. - Science 233: 765–767.

Phillips, J.B. & J.A. Waldvogel 1982: Reflected light cues generate the short-term deflector-loft effect. – In: “Avian Navigation” Papi, F- & H.G. Wallraff (eds.), Springer-Verlag, Berlin Heidelberg New York, pp. 190-202.

Phillips, J.B., K. Adler & S.C. Borland 1995: True navigation by an amphibian. – Anim. Behav. 50: 855-858.

Phillips, J.B., M.J. Freake, J.H. Fischer and S.C. Borland 2002a: Behavioral titration of a magnetic map coordinate. – J. Comp. Physiol. 188: 157–160.

Phillips, J B., S.C. Borland, M.J. Freake, J. Brassart & J. Kirschwink 2002b: ´Fixed-axis` magnetic orientation by an amphibian: non-shoreward-directed compass orientation, misdirected homing or positioning a magnetite-based map detector in a consistent alignment relative to the magnetic field? – J. Exp. Biol. 205: 3903-3914.

Putman, N.F., C.S. Endres, C.M.F. Lohmann, & K. Lohmann 2011: Longitude perception and bicoordinate magnetic maps in sea turtles. – Curr. Biol. 21: 463-466.

Putman, N.F., M.M. Scanlan, E.J. Billman, J.P. O`Neil, R.B. Couture, T.P. Quinn, K.J. Lohmann & D.L.G. Noakes 2014: An inherited magnetic map guides ocean navigation in juvenile pacific salmon. – Current Biology 24: 446-450.

Rabøl, J. 1969: Orientation of autumn migrating Garden Warblers (*Sylvia borin*) after displacement from western Denmark (Blaavand) to eastern Sweden (Ottenby). A preliminary experiment. – Dansk Orn. Foren. Tidsskr. 63: 93–104.

Rabøl, J. 1981: The orientation of Robins Erithacus rubecula efter displacement from Denmark to Canary Islands, autumn 1978. – Ornis Scand. 12: 89-98.

Rabøl, J. 1983: Evolution of orientation in migratory birds. – Ornis Fenn. Suppl.3: 17-19.

Rabøl, J. 1985: The moving goal area and the orientation system of migrant birds. – Dansk Orn. Foren. Tidsskr. 79: 29-42.

Rabøl, J. 1993: The orientation systems of long–distance passerine migrants displaced in autumn from Denmark to Kenya. – Ornis Scand. 24: 183–196.

Rabøl, J. 1994: Compensatory orientation in Pied Flycatchers *Ficedula hypoleuca* following a geographical displacement. – Dansk Orn. Foren. Tidsskr. 88: 171-182.

Rabøl, J. 1997: Star-navigation in Pied Flycatchers *Ficedula hypoleuca* and Redstarts *Phoenicurus phoenicurus*. – Report, Department of Population Ecology, Copenhagen.

Rabøl, J. 1998: Star navigation in Pied Flycatchers Ficedula hypoleuca and Redstarts Phoenicurus phoenicurus. – Dansk Orn. Foren. Tidsskr. 92: 283-289.

Rabøl, J. 2001: Do pigeons follow their noses? – Dansk Orn. Foren. Tidsskr. 95: 9-17.

Rabøl, J. 2006: The orientation system of migratory birds: The classical cases of vector orientation Gwinner & Wiltschko (1978) and Beck & Wiltschko (1988). – http://www.jorgenrabol.dk/files/gwinner2.pdf

Rice, 1989: Analyzing tables of statistical tests. – Evolution 43: 223-225.

Rodda, G.H. 1984: The orientation and navigation of juvenile alligators: Evidence of magnetic sensitivity. – J. Comp. Physiol. 154: 649–658.

Rodda, G.H. 1985: Navigation in juvenile alligators. – Z. Tierpsychol. 68: 65-77.

Sauer, E.F.G. 1957: Die Sternenorientierung nächtlich ziehender Grasmücken (*Sylvia atricapilla, borin* und *curruca*). – Z. Tierpsychol. 14: 29-70.

Schiffner, I. & R. Wiltschko 2011: Temporal fluctuations of the geomagnetic field affect pigeon`s entire homing flight. – J. Comp. Physiol. A 197: 765-772.

Thorup, K. & J. Rabøl 2007: Compensatory behaviour after displacement in migratory birds. A meta-analysis of cage experiments. – Behav Ecol Sociobiol 61: 825-841.

Thorup, K., I.-A. Bisson, M.S. Bowlin, R.A. Holland, J.C. Wingfield, M. Ramenofsky & M. Wikelski 2007: Evidence for a navigational map stretching across continental U.S. in a migratory songbird. – Proc. Nat. Acad. Sciences USA 104: 18115-18119.

Treiber, C.D., M.C. Salzer, J. Riegler, N. Edelman, C. Sugar, M. Breuss, P. Pichler, H. Cadiou, M. Saunders, M. Lythgoe, J. Shaw & D.A Keys 2012: Clusters of iron-rich cells in the upper beak of pigeons are macrophages not magnetosensitive neurons. – Nature 484: 367-370.

Wallcott, C. 1991: Magnetic maps in pigeons. - In: Berthold, P. (ed.) Orientation in birds. Birkhäuser Verlag, Basel, pp.38-51.

Wallcott, C. 1996: Pigeon homing: Observations, experiments and confusions. – J. Exp. Biol. 199: 21-27.

Wallraff, H.G. 1974: Das Navigationssystem der Vögel. – Oldenburg.

Wallraff, H.G. 2005: Avian navigation: pigeon homing as a paradigm. – Springer, Berlin.

Wiltschko, W. 1968: Über den einfluss statischer magnetfelder auf die zugorientierung der Rotkelchen *(Erithacus rubecula)*. – Z. Tierpsychol. 25: 537-558.

Wiltschko, W. 1972: The influence of magnetic total intensity and inclination on directions preferred by migrating European Robins *(Erithacus rubecula)*. – In: ″Animal Orientation and Navigation″ Galler, S.R., K. Schmidt-Koenig, G.J. Jacobs & R.E. Belleville (eds.). U.S. Govt. Printing Office Washington, D.C., pp.569-578.

Wiltschko, W. 1978: Further analysis of the magnetic compass of migratory birds. - In: ″Animal Migration, Navigation and Homing″. Schmidt-Koenig, K & W.T. Keaton (eds.). Springer-Verlag, Berlin Heidelberg New York, pp.302-310.

Wiltschko, W. & R. Wiltschko 1995a: Migratory orientation of European Robins is affected by the wavelength of light as well as by a magnetic pulse. – J. Comp. Physiol. A. 177: 363-369.

Wiltschko, R. & W. Wiltschko 1995b: Magnetic orientation in animals. – Springer, Berlin.

Wiltschko, R. & W. Wiltschko 2003a: Mechanisms of orientation and navigation in migratory birds. - In: Berthold, P., E. Gwinner & E. Sonnenschein (eds.) Avian Migration. Springer-Verlag Berlin Heidelberg, pp.433-456.

Wiltschko, R. & W. Wiltschko 2003b: Orientation behaviour of homing pigeons at the Gernsheim anomaly. – Behav Ecol Sociobiol 54: 562–572.

Wiltschko, W., U. Munro, R.C. Beason, H. Ford & R. Wiltschko 1994: A magnetic pulse leads to a temporary deflection in the orientation of migratory birds. – Experientia 50: 697-700.

Wiltschko, W., U Munro, H. Ford & R. Wiltschko 1998: Effect of a magnetic pulse on the orientation of Silvereyes, *Zosterops l. lateralis,* during spring migration. – J. Excp. Biol. 201: 3257-3261.

Wiltschko, W., U. Munro, H. Ford & R. Wiltschko 2006: Bird navigation: what type of information does the magnetite-based receptor provide? – Proc. R. Soc. B 273: 2815-2820.

Wiltschko, W., H. Ford, U. Munro, M. Winklhofer & R. Wiltschko 2007: Magnetite-based magnetoreception: the effect of repeated pulsing on the orientation of migratory birds. – J. Comp. Physiol. A. 193: 515-522.

Wiltschko, W., U Munro, H. Ford & R. Wiltschko 2009: Avian orientation: the pulse effect is mediated by the magnetite receptors in the upper beak. – Proc. R. Soc. B 276: 2227-2232.

Winklhofer, M. & J. Kirschwink 2008: Does avian magnetoreception rely on both magnetite and maghemite. – Phys. Biol. Phys., http://arxiv.org/abs/0805.2249.

Wu, L.-Q. & J.D. Dickman 2012: Neural correlates of a magnetic sense. – Science 336: 1054-1057.

Åkesson, S. 2003: Avian long–distance navigation: Experiments with migratory birds. In ″Avian Migration″ Berthold, P., E.Gwinner and E.Sonnenschein (eds.) pp.471–492, Springer, Berlin.

Åkesson, S. & T. Alerstam 1998: Oceanic navigation: are there any feasible geomagnetic bi-coordinate combinations for albatrosses? – J. Avian Biol. 29: 618-625.

Åkesson, S., J. Morin, R. Muheim, and U. Ottosson 2001: Avian orientation et steep angles of inclinations: Experiments with migratory White-crowned Sparrows at the magnetic North Pole. – Proc. R. Soc. Lond. B. Biol. Sci. 268: 1907-1913.

Åkesson, S., J. Morin, R. Muheim, and U. Ottosson (2005): Dramatic orientation shift of White-Crowned Sparrows displaced across longitudes in the high arctic. – Current Biology, Vol.15: 1591-1597.