Dominance and calibration of magnetic, sunset and stellar compasses in cue conflict experiments with night-migrating passerines

Jørgen Rabøl

(Med et dansk resumé: Kalibrerer trækfuglene deres kompasser før nattens træk?)

Abstract Compass calibrations around sunrise and sunset are generally supposed to be important and necessary for the process and progress of bird migration. However, the question remains whether this is an established fact or just conventional wisdom. Migrant passerines were tested on Christiansø island (55.3°N, 15.2°E) in the Baltic Sea on the first or second sunset or night after trapping (and presumably arrival). More than 1300 birds were tested on more than 70 sunsets or nights. Apparently, in general a magnetic compass was not in action, and (therefore) indications of compass calibrations were almost non-existent.

Introduction

According to conventional wisdom, juvenile passerines in their first autumn make use of compass orientation only (e.g. Wiltschko & Wiltschko 2003). Therefore compass conflict experiments make sense and must be considered a highly relevant science in order to find out which compass dominates and/or calibrates the other compasses. Migratory birds may orient by compass with reference to the sun, the sunrise sky, the sunset sky, the magnetic field, or the stellar sky (both star patterns and Polaris/rotational point) (Wiltschko & Wiltschko 1995). The migratory direction may be established in reference to one compass and then transferred to and maintained in reference to another compass. This process is named compass calibration (Rabøl 2010).

The periods around sunrise and sunset are in particular considered to be the most relevant and vital for the interplay between the compasses and for the establishment/maintenance of subsequent orientation for day and night migration, respectively (Muheim *et al.* 2006a). The magnetic compass is available all day and night, whereas the sun and star compasses are only available during day and night, respectively, if it is not too cloudy. The sunrise and sunset compasses, which are believed to be primarily based on the polarization pattern of the sky (Muheim *et al.* 2006b), are available

Tab. 1. Four different kinds of experiments were conducted.
Fire forskellige slags forsøg blev foretaget.

Standard	Cross	Direct	Half-cross
The control birds were caged and funnel-tested in the natural magnetic field, whereas the experimental birds were caged and tested within the deflected magnetic fields.	The controls were caged in the natural magnetic field but tested in a deflected magnetic field. The experimentals were caged in a deflected magnetic field but tested in the natural magnetic field.	The controls and experimentals were transferred directly from the garden into the funnels in the natural and deflected magnetic fields, respectively.	The controls were caged in the natural magnetic field and the experimentals in the deflected magnetic fields. All birds were tested in the funnels in the natural magnetic field.
Standard forsøg. Kontrolfuglene blev holdt i bure og testet i tragte i det naturlige magnetfelt, medens forsøgsfuglene blev holdt i bure og tragt-testede i afbøjede magnetfelter.	*Krydsforsøg. Kontrolfuglene blev holdt i bure i det normale magnetfelt, men senere tragt-testede i de afbøjede magnetfelter. Forsøgsfuglene blev holdt i bure i de afbøjede felter men tragt-testet i det normale magnetfelt.*	*Direkte forsøg. Både kontroller og forsøgsfugle blev overført direkte fra haven midt på øen til tragtene henholdsvis i det naturlige og det afbøjede magnetfelt.*	*Halv-kryds forsøg. Kontrollerne blev holdt i bure i det normale magnetfelt, og forøgsfuglene var i bure i de afbøjede felter. Alle fugle blev tragt-testede i det normale magnetfelt.*

only for short (say one to two hour) periods if it is not too cloudy.

This study is about birds tested during sunset/early night or during the night. For a bird initiating a migratory process and step during the sunset period, the following compasses are potentially available as references for migratory orientation: the sun, the sunset, and the magnetic compasses. Furthermore, the stellar compasses are also available at the very end of the sunset period. During night when the last trace of sunset has disappeared, only the magnetic and stellar compasses are potentially available. The most important processes are supposed to be: 1) the sunset compass which calibrates the magnetic compass and the stellar compass; 2) the magnetic compass which calibrates the sunset compass; 3) the magnetic compass which calibrates the stellar compass; 4) the stellar compass which calibrates the magnetic compass (for use if the night sky turns overcast).

Rabøl (2010) found no clear evidence of compass calibrations in the sunset/early night period for long-term caged birds tested on Endelave island (55.7°N, 10.2°E) during night in autumn. In general, a compass related to geographical N, in all probability a stellar compass, was the dominant one for orientation in the standard direction during night. However, a magnetic compass sometimes apparently dominated and steered a reverse orientation during night. The main object and question in the present experiments was whether short-term caged Christiansø birds reacted in the same way or differently from the long-term caged birds on Endelave.

Material and methods

Funnel experiments were carried out in autumn 2006, 2007, 2008, 2011 and 2012 during 36 nights and 37 sunset/early nights, which involved, respectively, 659 and 646 birds. The purpose of the experiments was to find 1) the dominant compass-reference and 2) the compass that calibrated the other compasses. Magnetic, sun, sunset and stellar compasses were supposedly potentially available to the birds.

Juvenile nocturnal passerine migrants were trapped on Christiansø in the morning hours. Captured birds were retained until testing in plastic funnels the same night or the next night or sunset. The birds were caged in pairs in plastic baskets covered on top with a plywood plate. The baskets were placed outdoors in depot in a garden in the middle of the island and in the undisturbed magnetic field.

In late afternoon the birds selected for experiments were transported a few hundred meters to the experimental site, where some of the birds, the experimentals, were caged within a deflected magnetic field with the same intensity and inclination as the local magnetic field, magnetic N (mN) = geographical W (gW) or E (gE), whereas the rest of the birds, the controls, were caged in the undisturbed magnetic field. During the first hour or two the baskets were covered with a plywood plate as protection against Sparrowhawks *Accipiter nisus*, but these plates were removed no later than at sunset so that the birds were fully exposed to the sunset and later on to the stellar sky. In the night experiments the birds were transferred to the funnels two hours after sunset when all trace of the sunset sky had disappeared. With

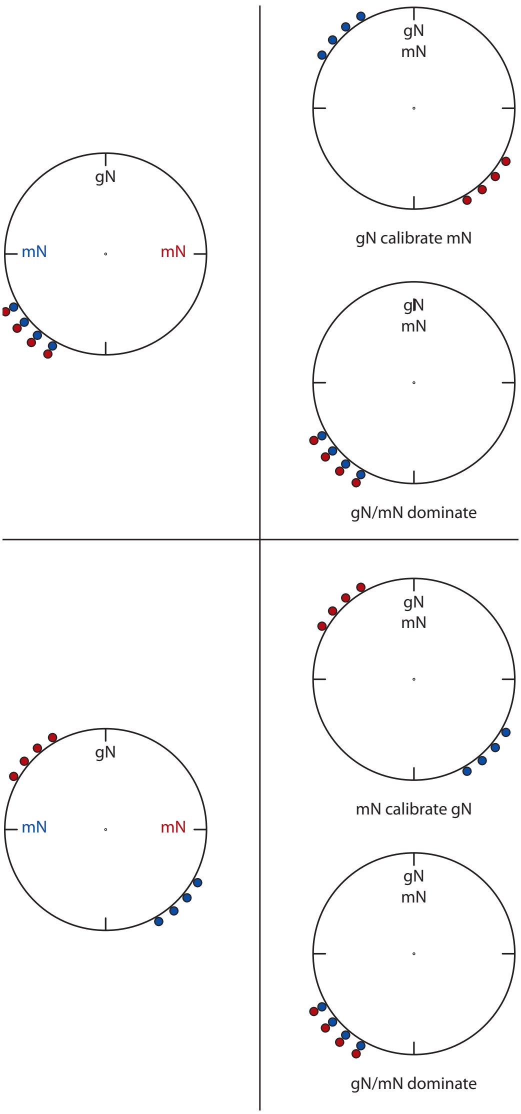

Fig. 1. Experimentals in cross experiments (see Tab. 1). In the upper left the birds in the cage in the sunset phase orient SW with reference to geographical N (gN). The eight birds spent the presumed compass calibration period sunset/early night in a basket within the deflected magnetic fields. For four birds (blue), mN was deflected towards gW, and for another four birds (red), mN deflected towards gE. If the sunset/stellar compass (gN related) calibrates the magnetic compass, orientation during night will appear as shown in the upper right: the W experimentals orient NW and the E experimentals orient SE. In the lower left, if the magnetic compass calibrates the gN related compass, the orientation during night appear as shown in row three to the right: the W experimentals orient SE and the E experimentals orient NW. The two outcomes are easily distinguished and are the only solutions. A dominant compass reaction in the test phase (right) will invariably reveal itself as SW orientation, and we cannot know whether gN or magnetic N (mN) is the dominant compass reference. Therefore the reaction of the experimentals in a cross (or half-cross) experiment is the most powerful way to demonstrate a calibration process – and whether gN or mN is the calibrating compass.
Forsøgsfugle i krydsforsøg (se Tab. 1). Dette er den ideelle betingelse for at kunne skelne mellem her og nu-dominans og forudgående kalibrering. Kalibrering medfører modsatrettet NV/SØ orientering af V- og Ø-forsøgsfuglene i tragtene, og førstnævnte er i henholdsvis NV og SØ ved kalibrering af henholdsvis geografisk N (gN) og magnetisk N (mN). Hvis orienteringen er i SV, kan man ikke skelne mellem om gN eller mN er det dominerende her og nu-kompas. Orienteringen af forsøgsfuglene i krydsforsøg er den bedste og mest entydige måde til at påvise kompaskalibrering, og hvilket kompas der er kalibreret, og hvilket der er det kalibrerende.

regard to the sunset experiments, the birds were sometimes caged during early sunset and then later tested during late sunset on the same day. However, in most sunset experiments (direct, see below), the birds were transferred directly from the garden to the funnels. Four different kinds of experiments were carried out (Tab. 1):

(1) *Standard*: The controls were caged and funnel tested in the natural magnetic field, whereas the experimentals were caged and tested within the deflected magnetic fields. (2) *Cross*: The controls were caged in the natural magnetic field but were tested in deflected magnetic fields. The experimentals were caged in deflected magnetic fields but were tested in the natural magnetic field. (3) *Direct*: The controls and experimentals were transferred directly from the garden into the funnels in the natural and deflected magnetic fields, respectively. (4) *Half-cross*: The controls were caged in the natural magnetic field and the experimentals were caged in the deflected magnetic fields. All birds were tested in the funnels in the natural magnetic field.

The purpose of experiments 1 and 3 was to find out which compass dominated the actual sunset or night orientation, i.e. either no preceding calibration was carried out in the sunset/early night phase, or such a calibration was overridden by a process that occurred during sunset or night. The purpose of experiments 2 and 4 was to find out whether the stellar compass was calibrated by the magnetic compass during sunset or sunset/early night and whether this calibration was maintained during the sunset or night to come. Or whether the magnetic compass was calibrated by the sunset compass during sunset/early night and whether this calibration was upheld during the ensuing night (principles outlined in Fig. 1).

On some occasions, the birds were caged in plastic cans (instead of baskets) which set the horizon higher (about 30°) and gave no view of the landscape. On other occasions, the birds were tested with aluminum collars (height 8 cm) placed on top of the funnels (creating a high horizon). Such procedures were intended to influence the compass hierarchy and affect which compass was the calibrating or dominant one, respectively.

On many occasions the birds were tested under the condition of "overcast" which meant that the opening of the funnel, in addition to a cloth net, was covered with an opaque plastic sheet. This sheet was translucent but not transparent, i.e. objects such as the stars and the wooden frame housing the magnetic coil field could not be seen through the plastic sheet. It is also supposed – but not actually measured – that patterns of polarized light in the sky could not be detected by the bird from its position inside the funnel. However, a blurred image of the sun was visible through the plastic sheet, and very probably the lighter part of a clear sunset sky was also detectable, i.e. the light intensity of the funnel ceiling on clear evenings was probably unevenly distributed as seen by the bird inside of the funnel. The open question is whether the direction of the lighter sunset sky alone (i.e. if or when patterns of polarized light in the sky are not detectable) may be used as a compass reference for sunset/early night orientation.

About half of the birds were long-distance Africa migrants, mostly European Pied Flycatchers *Ficedula hypoleuca* followed by Garden Warblers *Sylvia borin* and Common Redstarts *Phoenicurus phoenicurus*. The other half was medium-distance migrants like European Robin *Erithacus rubecula* and some Eurasian Blackcaps *Sylvia atricapilla* (Appendix 1).

Results with brief comments

Prior to the experiments, clear examples of both compass dominance and compass calibrations were expected. However, only a few and weak indications of calibrations were found. On the other hand, many clear cases were observed of dominance of a compass related to geographical N – including in nights or sunsets where the sky was overcast and a stellar or sunset compass would therefore be unable to exert influence. No significant differences were found between the species.

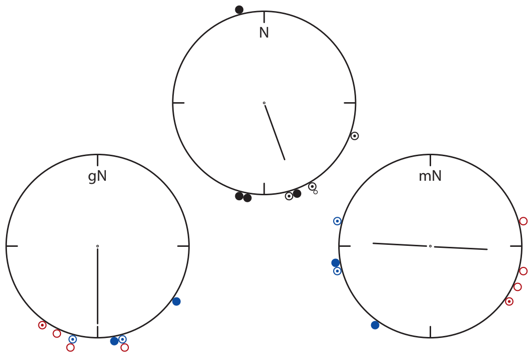

Fig. 2. Direct experiment (see Tab. 1) on 8 September 2008 at night under a clear starry sky with Africa migrants (Pied Flycatchers, and two Redstarts). The orientation of the controls (upper figure) was 160° - 0.662* (n = 8). The orientation of the experimentals (lower figures) was 180° - 0.893** (n = 8) with reference to gN (left) or 92°/272° - 0.633* (n = 8) with reference to mN (right). Blue dots show W experimentals, and red dots E experimentals.
Direkte forsøg (se Tab. 1) om natten den 8. september 2008 under en klar stjernehimmel. Kontrollerne er testet i det naturlige magnetfelt, medens forsøgsfuglene er testede i kunstige magnetfelter, hvor magnetisk N i det resulterende felt er drejet henholdsvis til geografisk V og geografisk Ø. Kontrollerne i midten er SSØ-orienterede, medens forsøgsfuglene er S-orienterede i forhold til geografisk N (nederst til venstre). I forhold til magnetisk N (til højre) er orienteringen to-toppet med V-fuglene i V (blå prikker) og Ø-fuglene i Ø (røde prikker). Orienteringen peger på manglende indflydelse af et magnetkompas (som forklaret i Rabøl 2010).

Night experiments
Two hundred and forty standard experiments (see Tab. 1) were carried out on 15 nights. Controls without collars showed significant SSW-orientation, whereas controls with collars were not significantly SSW-oriented (2007).

Thirty one direct experiments (see Tab. 1) were carried out on two clear nights. On both nights the orientation of the experimentals was clearly steered by a compass related to geographical N (gN). On the first night, the orientation of the controls was SSE and the experimentals oriented S in reference to gN (Fig. 2). On the next night, the controls oriented NW, and the experimentals also oriented NW in reference to gN. This looked like a phototaxis directed towards the sunset. However, the sunset to the WNW was gone when the birds were tested.

One hundred and seventy six cross experiments (see Tab. 1) were carried out on eight nights. No signs of compass calibrations were found as there was no significant difference between the orientations of the experimentals deflected gW or gE (in short "W and E experimentals"). In the period 16-26 September 2006 (four

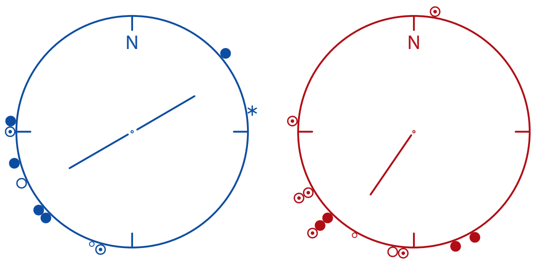

Fig. 3. Cross experiments (see Tab. 1) at night. Experimentals tested in the natural magnetic field 21- 26 September 2006, clear sky. Only basket birds are shown here. The distribution of the W-deflected birds (blue) appears to be bimodal, and doubling the angles leads to 240°/60° - 0.638* (n = 10). If the angles are not doubled, the sample mean vector is 234° - 0.517 (n = 10). The mean vector of the E-deflected birds (red) is 214° - 0.677** (n = 12). If the W and E deflected birds are combined, the sample mean vector is 222° - 0.595*** (n = 22).
Krydsforsøg (se Tab. 1) på tre nætter i september 2006. Krydsforsøg betyder, at kontrollerne i solnedgangsfasen i burene var eksponerede for det normale magnetfelt, solnedgangen og den spirende stjernehimmel, medens de om natten under stjernerne og i tragtene blev testet i magnetfelter, der var drejet mod henholdsvis gV og gØ. For forsøgsfuglene var det omvendt, og på denne figur er kun forsøgsfuglene er vist, ligesom kun forsøgsfugle, der var i kurv i solnedgangs-fasen, er vist. Til venstre var magnetisk N drejet i geografisk V (blå) og til højre i geografisk Ø (rød). Der er ingen signifikant forskel på SV-orienteringen i de to grupper, og således ikke noget der tyder på en forudgående kompas-kalibrering.

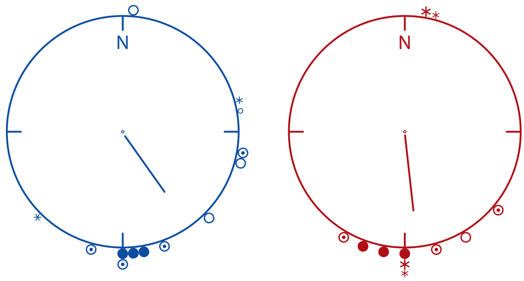

Fig. 4. As for Fig. 3 but here only birds held in cans were considered. The sample mean vector of the W-deflected birds (blue) is 145° - 0.649** (n = 11). The sample mean vector of the E-deflections (red) is 174° - 0.702* (n = 9). Doubling the angles improves the description (180°/360° - 0.727**, n = 10). If the W and E-deflected birds are combined, the sample mean vector is 159° - 0.652*** (n = 20). The difference between the two combined sample mean vectors of Figs 2 and 3 is significant (P < 0.01, Watson-Williams test). The same holds true concerning the difference between the two sample mean vectors of the W-deflected birds considered separately, whereas the difference between the two E-deflected samples is close to significance at the 0.05 level.
Som Fig. 3 men nu kun forsøgsfugle, der i solnedgangsfasen var anbragt i spande. Der er ingen signifikant forskel på den SSØ-lige orientering i de to grupper, og således ikke noget der tyder på kompas-kalibreringer.

experiments, clear starry sky), half of the experimentals spent the sunset/early night in cans with a high artificial horizon whereas the other half were caged in the normal baskets. When both groups were tested in the local magnetic field, the birds in baskets were SW-oriented whereas the birds in cans were SSE-oriented and significantly deflected more than 60° counter clockwise (Figs 3 and 4). I have no explanation for this deflection. In the controls there was no difference between birds tested in magnetic N deflected towards gW or gE (Fig. 5). On 28 August 2006 (clear sky), following a preceding stormy and rainy night (recall that the birds were caged outside in baskets covered on top with a wooden plate), both W and E experimentals were very significantly NNW-N oriented, probably as a reaction to the preceding bad weather (Fig. 6). Once again, there was no difference between W and E experimentals as there should have been if a compass calibration had taken place. The controls (not shown) tested in the deflected magnetic fields showed nonsignificant bimodal NW/SE-orientation with reference to gN, and SW/NE-orientation with reference to mN.

Two hundred and twelve half-cross experiments (see Tab. 1) were carried out on 11 nights. The birds experienced a more or less clear sunset sky in the baskets while exposed at the test site. On a single night the sky became totally overcast and on two nights the birds were tested under ”overcast” conditions. On two clear nights the birds were tested in a strong vertical heterogeneous magnetic field which in all probability was unsuitable for magnetic orientation. Regardless of how the results were conceptualised and analysed there were no clear or significant tendencies for compass calibrations. On two nights the birds showed approximately reverse orientation, and in most nights geographical N seemed to be the dominant compass reference – also on the three nights under conditions of overcast or ”overcast”. On such occasions orientation could of course not be explained as attraction towards light or other unevenly distributed sources of stimuli.

Sunset experiments
Sixty four standard experiments (see Tab. 1) were carried out during four sunsets/early nights in 2008. The sunset sky was overcast or almost so. Furthermore, the birds were tested under the condition of ”overcast”. However, no influence/dominance of a compass related to magnetic N was observed.

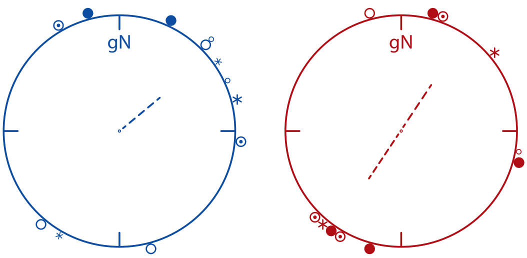

Fig. 5. Cross experiments (see Tab. 1) at night. Controls in deflected magnetic fields on 16, 21, 24 and 26 September 2006. The figure to the left depicts the orientation of the W-deflected controls (blue). The sample mean vector is 50° - 0.467 (n = 10), or 40°/(220°) - 0.357 (n = 11) if the angles are doubled. The figure to the right depicts the orientation of the E-deflected controls (red). The sample mean vector is 33°/213° - 0.500 (n = 11). If the two distributions are added together, the sample mean vector after doubling the angles is 36°/216° - 0.425* (n = 22). If depicted with reference to magnetic N, the single night directions (and sample mean vectors) of the W-deflected and E-deflected birds should be rotated 90° clockwise and 90° counter-clockwise, respectively, i.e. an overall "SE/NW" pattern arises (126°/306° - 0.425*).
Kontroller i krydsforsøg (se Tab. 1) på fire nætter i september 2006. Orienteringen indenfor magnetfelterne, hvor magnetisk N var drejet mod geografisk V (blå) og geografisk Ø (rød) er vist henholdsvis til venstre og højre. De viser begge tendenser til NØ/SV-orientering, og der er ikke signifikant forskel på fordelingerne.

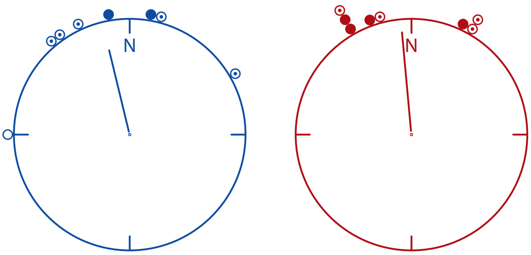

Fig. 6. Cross experiment (see Tab. 1) at night, Garden Warblers, experimentals tested in the natural magnetic field, 28 August 2006, clear sky. No significant difference between W experimentals (346° - 0.765*, n = 8, blue) and E experimentals (355° - 0.897***, n = 8, red).
Krydsforsøg (se Tab. 1), 28. august 2006. Til venstre ses de fugle, hvor magnetisk N i solnedgangsfasen var drejet mod geografisk V (blå). Til højre de fugle, hvor magnetisk N var drejet mod geografisk Ø (rød). Der er ingen signifikant forskel på den NNV-N-lige orientering i de to grupper, og således intet der tyder på kompaskalibreringer i solnedgangsfasen. Den omvendte orientering skyldes formentlig dårligt vejr (regn og kraftig vind) natten forud for forsøget (fuglene stod ude i overdækkende kurve denne nat).

Four hundred and twenty nine direct experiments (see Tab. 1) were carried out in 28 sunsets. In 2006, 128 experiments were carried out in eight sunsets/early nights. In the controls – but not in the experimentals – a significant orientation towards the sunset was apparent. In 2007, 48 birds were tested in three clear sunsets. The experiments were carried out under clear sky conditions, and collars were applied in half of the birds. The purpose of these experiments was to test the hypothesis that screening away the lower part of the sky increased the importance of the magnetic compass. The implication is that the expected orientation of the collared experimentals with reference to mN would be more concentrated towards SW or bimodally SW/NE than in the case of the experimentals not tested with collars. This expectation was not met, and in fact gN seems to be the obvious dominant compass reference in experimentals both with and without a collar. In 2008, 253 birds were tested on 17 sunsets, about half of which were clear. For the other half of the birds tested, the sky was overcast and/or the birds were tested under "overcast". In the clear sunsets the controls oriented very significantly W-WNW, i.e. there appeared to be a sunset taxis. The experimentals showed no sunset taxis, and both W and E experimentals were much dispersed with reference to both gN and mN. There seemed therefore to be orientation steered (more) by a compass related to gN than a magnetic compass under circumstances (overcast or "overcast") where no celestial compasses were available.

Forty cross experiments (see Tab. 1) were carried out during two sunsets. (a) In the first experiment, eight controls and 16 experimentals were tested. The birds spent the first part of the sunset period in the baskets exposed to a clear sunset sky. Later, half of the experimentals were tested under a clear sky, but the remaining experimentals and the controls were tested under conditions of "overcast". The controls tested in the deflected magnetic field showed a significant orientation in approximately the normal direction of migration with reference to gN, and nonsignificant axial NNW/SSE orientation with reference to mN. This is surprising because the "overcast" condition should prevent use of a sunset compass. The experimentals tested in the normal magnetic field under the "overcast" condition showed axial WNW/ESE orientation with (most) W experimentals in WNW and (most) E experimentals in the ESE peak. The interpretation would be that the sunset compass calibrated the magnetic compass. However, due to small sample size, the otherwise clear pattern was statistical nonsignificant. The orientation of the eight experimentals tested under a clear sunset sky was axially NNE/SSW with W experimentals in the NNE peak and E experimentals in the SSW peak. This is not easily understood compared with the WNW/ESE pattern of the experimentals tested under an "overcast" sky. Probably, calibration is not involved because the birds show axially standard/reverse orientation. (b) In the second cross experiment, no controls were involved and the 16 experimentals experienced a clear sunset in the baskets in the two previous sunsets before being tested under "overcast" in the third sunset. The birds oriented axially NNE-NE/SW-WSW with all E experimentals in the SW-WSW peak and most W experimentals in the NE-ENE peak. In fact, the difference between the W and E experimentals was statistically significant. The patterns observed could be taken as an indication of a calibration of the magnetic compass by the sunset compass – for a NW course (principles outlined in Fig. 1).

Eighty-nine half-cross experiments (see Tab. 1) were carried out in four clear sunsets. The controls, the W and E experimentals all oriented approximately standard and there was no sign of compass calibrations.

Discussion

2006-2012 findings and interpretations

As regards night experiments and taking stochastic events into consideration, there was virtually no indication of the influence of a magnetic compass as the dominant and/or calibrating compass. Some results indicated a sunset/early night compass that calibrated a magnetic compass but, in general, support for compass calibrations during sunset/early night was weak or lacking. The general picture was that orientation at night was steered by a dominant geographical N (gN) related (probably stellar) compass. Screening the lower approximately 30% of the sky during sunset/early night exposure (i.e. cans versus baskets) was not accompanied by an increased amount of magnetic orientation, but the orientation did shift significantly counter-clockwise (from SW to SSE). The cause of this shift remains unclear; there was no difference between W and E experimentals. Therefore no calibration process seems to have been involved.

Regarding sunset experiments, clear phototaxis during sunset – in the controls – was apparent when birds were tested with access to a clear sunset sky. Weak indications of compass calibration by the sunset compass into the magnetic compass were observed. A compass related to gN seems to be the one responsible – and also (mysteriously) occurred in several cases of overcast/"overcast" conditions. No clear influence of collars at the top of the funnels was found, and no difference could be demonstrated in subsequent orientation for birds exposed during early sunset in baskets and cans. When the lower part of the sunset sky was visible, the sunset compass did not calibrate the magnetic compass unlike as was proposed by Muheim *et al.* (2006a, 2006b).

Comparison with Endelave investigations 2001 and 2002

Rabøl (2010) carried out similar night experiments with three groups of juvenile Pied Flycatchers and Redstarts on Endelave in autumn 2001 and 2002. The birds were trapped as migrants on Christiansø and taken to Endelave where they were caged for several days or even weeks. A control group of these birds was held in the natural magnetic field and a group of experimentals was held within magnetic fields where resultant magnetic N was deflected towards gW or gE. Most of the time the birds were freely exposed to the celestial sky, and from time to time the birds were taken out of their baskets for testing in the funnels under conditions described as standard and cross experiments in the present paper.

In brief, the main difference between the experiments on Endelave 2001-2002 and Christiansø 2006-2012 was the long-term stay within deflected magnetic fields on Endelave, i.e. the experimentals on Endelave were exposed for a much longer time to the conflict between the magnetic and celestial compasses before being tested in the funnels.

The main findings of Rabøl (2010) were 1) no compass calibrations took place and 2) a compass related to gN (probably a stellar compass) was normally dominant, but sometimes a magnetic compass was dominant or had clear co-influence, but in such cases the orientation, in reference to magnetic N (mN), was the reverse of the standard direction. Obviously, the motivation had an influence on whether gN or mN was dominant as the compass reference. Perhaps, mN (for unknown reasons) is used when the birds are motivated to undertake reverse orientation?

Other investigations on compass calibrations

Rabøl (2010) discussed the compass dominance/calibration papers of Sandberg *et al.* (2000, including Sandberg & Moore 1996), Wiltschko & relatives (Wiltschko & Wiltschko 1975a, 1975b, 1999, 2003, Bingman 1987, Prinz & Wiltschko 1992, Weindler *et al.* 1996, 1998), Able & Able (1995a, 1996), Åkesson *et al.* (2001, 2002), Muheim & Åkesson (2002), Cochran *et al.* (2004) and Muheim *et al.* (2006a, 2006b).

Since then several other relevant papers have appeared concerning a) compass conflicts, and b) the nature of the magnetic compass. Short presentations and discussions of the most important contributions follow below.

The findings of Cochran *et al.* (2004) and Muheim *et al.* (2006a, 2006b, followed by the 2007 paper discussed below) were bound to induce strong reactions from Wiltschko & Wiltschko. Muheim *et al.* (2007) is more or less the same as already reported by Muheim *et al.* (2006b). When the polarization pattern of the sunset or sunrise sky was changed +/- 90°, the orientation of Savannah Sparrows *Passerculus sandwichensis* tested the next night indoors in the natural magnetic field also changed about +/- 90°. The interpretation is that a sunset/sunrise compass calibrated the magnetic compass.

Wiltschko *et al.* (2008a) provide a critical reaction including new experiments to the results and interpretations of Muheim *et al.* (2006a, 2006b, 2007). Wiltschko & Wiltschko performed a spring experiment at Armidale, Australia, with Silvereyes *Zosterops lateralis*. The birds were caged outdoors in a magnetic field deflected 90^0 to gW with a view down to the horizon, at least in most directions. When tested indoors at sunset, there was no calibration of the magnetic compass. And both as a combined sample and as individuals (own controls), the experimentals were not different from the controls. In short, I find the procedure, results and discussion convincing.

Muheim *et al.* (2008) claimed that the results of Wiltschko & Wiltschko were influenced by the two weeks stay in an outside aviary in the undisturbed magnetic field before being exposed to sunset and sunrise in the shifted magnetic field. Therefore the birds "may have completed calibration of their compass systems prior to the cue conflict exposures. Previous studies have shown that once calibration of a compass system is completed, updating the calibration (e.g. when the birds are exposed to a new cue conflict) may require several days of exposure." To start with, this is a peculiar argument because the same argument could be used in connection with any previous state of birds flying around in the free before capture. Furthermore, in most studies the cue conflict period has been short as in the studies of the Wiltschko & Wiltschko, and in general researchers agree that recalibration may take place every sunset/early night. In any case, in Rabøl (2010) experimentals held for several days/weeks in deflected magnetic fields and tested in the normal magnetic field showed no calibration. Muheim *et al.* also say that Wiltschko & Wiltschko should have tested if the magnetic compass calibrated the celestial compasses. Wiltschko & Wiltschko believe in such a scenario, and I agree that a test would have strengthened the interpretation of their experiments.

Wiltschko *et al.* (2008b) remark that Muheim *et al.* "originally argue that the magnetic compass would be regularly recalibrated by the polarization pattern, but faced with the discrepancy between findings, now change their argumentation in favour of existing stable calibrations." Clearly this is an ad hoc adaptation by Muheim *et al.,* but perhaps it is sometimes true. Wiltschko & Wiltschko also have problems with the logic in the system of Muheim *et al.* concerning calibration shifts following different polarization patterns in the central and horizontal part of the sky. However, this is a matter of language only. In fact, Muheim *et al.* (2006b) have data (though a low n = 6) showing no shift in magnetic orientation following exposure under a shifted polarization pattern of the central part of the sunset sky.

Muheim *et al.* (2009) continued their calibration experiments using White-throated Sparrows *Zonotrichia albicollis* from Ontario, in both spring and autumn, and at both sunrise and sunset. Magnetic N as well as the polarization pattern were shifted 90°, and when subsequently tested indoors it appeared that the magnetic compass had been calibrated using both setups. The results presented show – convincingly – that the sparrows calibrate their magnetic compass from the sunrise/sunset-compasses, but it was not shown that the view down to the horizon is crucial.

Huttunen (2009) captured Redwings *Turdus iliacus* in eastern Finland in September/October 1999-2001. The birds were tested the same or the next night, and both funnel experiments and releases with a light-stick in the tail (immediately after the funnel experiments) were carried out. The funnel experiments were performed under a clear sky or an overcast sky (sometimes under a translucent but not transparent cover, i.e. the condition "overcast" of my study) in a) the natural magnetic field, or b) a magnetic field deflected 90° counter-clockwise, or c) an inverted magnetic field. Huttunen interpreted the unchanged orientation from the cage to release in the two magnetic treatments as an indication of a calibration of a gN compass by the magnetic compass. This is a possible interpretation. However, a more parsimonious interpretation is one of a dominant gN related compass in both the cage and release experiments.

Gaggini *et al.* (2010) and Giunchi *et al.* (2015) trapped Pied Flycatchers on spring migration on remote islands in the Mediterranean Sea west of the Italian mainland. Only funnel tests were carried out, and the band of maximum polarization (BMP) was changed in some experiments and mN in others. Birds were always tested indoors without access to celestial cues, i.e. in all probability the magnetic compass was the only one available. Exposure was sometimes during sunrise and sometimes at sunset. The Italians found no compass calibrations. Anyway, the magnetic compass was supposed to be in charge. Besides funnel testing, Giunchi *et al.* also recorded subsequent vanishing bearings of free-flying birds under clear starry conditions. Only sunset exposures were investigated. Furthermore, S-oriented birds that were losing weight in the pre-tests were selected out. The magnetic compass was clearly calibrated by the sunset compass, i.e. when changing the BMP +/- 90°.

Åkesson *et al.* (2015) found no evidence of compass calibrations during sunrise and sunset in European Robins, Sedge Warblers *Acrocephalus schoenobaenus* and Dunnocks *Prunella modularis* trapped and tested in South Sweden during autumn.

Chernetsov *et al.* (2011) found no evidence of compass calibrations in Song Thrushes *Turdus philomelos* captured in spring at Rybachi, Russia.

Schmaljohann *et al.* (2013) found no evidence of compass calibrations in Northern Wheatears *Oenanthe oenanthe* trapped in autumn on Helgoland in the North Sea.

The magnetic compass

Wiltschko & Wiltschko published their important book *Magnetic orientation in animals* in 1995, which gave the following two main impressions: 1) the evidence of magnetic compass orientation is broadly and convincingly documented, and 2) there are no clear indications of magnetic navigation. Wiltschko & Wiltschko seemed puzzled about the latter. Nowadays almost all scientists are convinced that magnetic navigation in birds is a fact, and is presumably the most influential kind of navigation above all others. However, this development has been carried too far (Rabøl 2014). Concerning magnetic compass orientation, the accepted scenario is that the magnetic compass in birds always is an inclination compass rooted in the retina. As reported in the present investigation, I had clear problems finding any directional influence and importance of the magnetic field. Furthermore, when I extended and fine-tuned the experiments (autumn 2013), I was not able to demonstrate the action of a magnetic inclination compass. I found no difference in orientation between experimentals tested in an inverted magnetic field and controls, as already reported earlier (Rabøl *et al.* 2002). Finally, I found no influence at all of a magnetic compass (autumn 2014): experimentals where mN was deflected towards gW and gE, respectively, as well as the controls, were all oriented in the standard direction (SSW with reference to geographical N). The 2013 and 2014 investigations were carried out under "overcast" conditions on clear nights without any sign of the setting sun.

In summary

Muheim *et al.* still report compass calibrations by a sunset compass into the magnetic compass. They have even strengthened their former findings by carrying out the compass conflict in two different ways (changing the magnetic field or changing the polarization pattern of the sky). However, the findings of Muheim *et al.* could not be confirmed by the Wiltschko & Wiltschko, Huttunen, Chernetsov *et al.*, Schmaljohann *et al.*, Gaggini *et al.*, Åkesson *et al.*, Rabøl (2010) nor the present paper. However, Giunchi *et al.* supply some confirmation. In both Huttunen and Gaggini *et al.* the importance of the magnetic compass is clearly overrated.

Migrating birds can use different methods to find their way back and forth between breeding and wintering areas. Magnetic clues are one of the methods, but how important is it? Photo: John Larsen; Pied Flycatcher.
Trækfuglene kan benytte flere forskellige metoder, når de skal finde vej under trækket. Magnet-orientering er en af dem, men hvor stor en rolle spiller den? Broget Fluesnapper.

Concluding remarks

In course of the ontogenetic development of the orientation system of a migrant bird, it seems reasonable that there should be some kind of calibration from one kind of compass to another. However, both a magnetic compass (Wiltschko & Wiltschko 1972) and a stellar compass rooted in the rotational point of the stellar sky (Rabøl & Dabelsteen 1983, Bingman 1984, Able & Able 1996) are seemingly inborn. According to Moore (1980) and Able & Able (1995b), the sunrise/sunset compasses also must be considered inherited (because birds growing up without access to the stars and magnetic field orient in approximately the standard direction). At least until recently, people agreed that the sunset/early night period is paramount for compass calibrations and for decisions on which compass should be dominant for the next about 24 hours. I do not believe in this scenario, and the recent contributions of Chernetsov *et al.*, Åkesson *et al.*, and Schmaljohann *et al.* add to this scepticism. I do not know whether compass calibrations are important after some initial or occasional calibrations. For a medium-distance migrant like a Scandinavian Robin – and the same holds by and large true for a long-distance migrant like a Scandinavian Pied Flycatcher – there are only minor differences within their all year home-range between the compass directions of the magnetic and celestial gradients. Nevertheless, I believe it is important that the compasses from time to time are compared and checked out. But there is no logic that such behaviour should be restricted to a short daily period – and there is no need for this to happen once every 24 hours. In short, I am not sure that further studies on compass calibrations are relevant and necessary. Instead, we should direct our efforts to more relevant investigations such as experiments focused on gradient navigation.

Apparently, a magnetic compass does not normally steer migratory orientation in nocturnal migrant passerines when these are tested in funnels a short time – say within 48 hours – after trapping. As the birds (with reference to gN) were oriented also under overcast/"overcast" conditions, a reasonable interpretation is that some kind of inertial orientation (Barlow 1964) is involved. The question remains whether inertial orientation is also the steering mechanism for short-term caged birds tested under a clear starry/"starry" sky. We cannot know based on the 2006-2012 experiments. How do we find out? The compensatory orientation following "displacements" under a planetary "stellar" sky (Rabøl 1998) cannot be used as a direct indication of use of a stellar compass because the birds showed stellar navigation. Furthermore, the birds were long-term caged (from a few days to several weeks). Clearly, we need experiments under the "stellar" sky of a planetarium where the direction of the rotational axis/Polaris with reference to true gN is varied. If the orientation is constant with reference to true gN, this is an indication of an inertial response.

Acknowledgements

I am grateful to an anonymous referee and the editors Steffen Brøgger-Jensen and Hans Meltofte, who all did a fine and time consuming job improving the manuscript. Similarly, Nick Quist Nathaniels improved my English.

Resumé

Kalibrerer trækfuglene deres kompasser før nattens træk?

Spørgsmålet er, hvordan fuglene fastlægger og fastholder deres træk-kurs, og om dette foregår i regi af et system baseret i kompas-orientering eller navigation. De fleste trækfugleforskere mener, at i hvert fald de unge fugle om efteråret bruger et kompas-system, og set derfra forekommer det relevant at undersøge, om trækfuglene kalibrerer deres kompasser før nattens træk.

Trækfugle kan etablere og fastholde en kompas-baseret trækkurs i forhold til Jordens magnetfelt (dvs. magnetisk N = mN), stjernehimlen (dvs. geografisk N = gN), Solen (gN) samt – som afledt af Solen – mønstret af polariseret lys på solnedgangs- og solopgangs-himlen (gN). Omkring solopgang og solnedgang kan fuglene (men ikke vi mennesker) se et "bånd" af polariseret lys, der går gennem zenith og står vinkelret på retningen mod Solen.

Spørgsmålet er så, om der også sker en kompas-kalibrering, dvs. om fuglene fastlægger trækkursen i forhold til én slags kompas og derfra overfører og fastholder den i forhold til en anden type kompas.

For år tilbage sandsynliggjorde Wiltschko & Wiltschko, at magnet-kompasset var medfødt, og at træk-orientering i indendørs forsøg derfra lod sig overføre til en såkaldt '16-stjernehimmel', dvs. et mønster af 16 asymmetrisk fordelte lysprikker, der roterede omkring en akse ned gennem mønstret af lysprikker set indefra en cylinder, som fuglene var anbragt i. Dette blev tolket som et indicium på, at magnet-kompasset i den virkelige verden kalibrerede et stjerne-kompas. Denne fortolkning var rimelig for sin tid, men ville næppe være blevet godtaget i simpel form nu til dags, hvor det har vist sig, at såvel et stjernekompas som et solnedgangs-kompas også synes at være genetisk fastlagte.

Et magnet-kompas er til rådighed hele tiden, så hvis det er mere unøjagtigt end et kompas relateret til geografisk N (gN) er der ingen logisk grund til en overførsel den vej. Så bruger fuglene bare Solen/solnedgangen og stjernerne, når der er mulighed for det, dvs. henholdsvis om dagen/i skumringen og om natten, og når det ikke er for tæt overskyet. Hvis solnedgangs- og stjerne-kompasset er mere nøjagtigt end magnet-kompasset, er der imidlertid grund til at forvente sig en kalibrering den anden vej rundt til brug for orienteringen på overskyede nætter.

Jeg startede med at lave tragt-forsøg i foråret 1967 på Hesselø just efter, at brødrene John og Steve Emlen (Emlen & Emlen 1966) havde introduceret tragt-metoden. I de første år fangede jeg fuglene i morgentimerne og testede dem allerede samme nat i tragtene. Efter fangsten kom fuglen i en hvid plastikspand med sand i bunden og to pinde på tværs i spandens nedre halvdel. Foroven var spanden lukket med et hvidt plastiklåg. Foder i

To the extent that migrants use magnetic clues, do they calibrate the magnetic compass before the onset of the migration? Photo: Albert Steen-Hansen, Common Redstart.
I det omfang trækfuglene bruger magnet-orientering, kalibrerer de så kompasset inden nattens træk? Rødstjert.

form af melorme blev drysset ned i spanden, der stod udendørs i skyggen eller i et rum med vinduer, hvor fuglene ikke direkte kunne se Solen, men hvor der var lys nok til, at fuglene kunne æde og følge det naturlige skift mellem dag og nat. Først på natten blev fuglene taget ud og snart derefter puttet i tragtene.

I efteråret 1978 (Rabøl 1981) ændrede jeg denne procedure: Fuglene – nu anbragt i trådnet-bure med udsyn både opad til himlen og til landskabet på siderne – blev før solnedgang taget udendørs i deres bure og eksponeret frit for himlen og omgivelserne. To timer efter solnedgang blev de flyttet over i tragtene. Årsagen til procedure-skiftet var, at jeg ville maximere fuglenes muligheder for at kunne navigere, dvs. foretage en stedbestemmelse i forhold til et eventuelt mål. Noget sådant antoges at være lettere gennemførligt i bure fremfor spande og i mere lukkede tragte. I efteråret 1978 flyttede jeg Rødhalse *Erithacus rubecula* fra Christiansø til Kanarieøerne, og spørgsmålet var, om fuglene navigerede tilbage mod trækruten i V-Europa og vinterkvarteret i Spanien/NV-Afrika, eller om de "bare" var kompas-orienterede mod SV i normal-trækretningen. På det tidspunkt havde jeg ikke kalibreringer mellem kompasserne inde i tankegang og overvejelser. Trådnet-buret blev også snart (1987) skiftet ud med vasketøjskurve i plastik med udsigt gennem net-struktur i sider og top.

I mange år var jeg mest optaget af forflytningsforsøg for at se, om fuglene kompenserede for forflytningerne. Det gjorde de ofte, hvad der tydede på, at de navigerede. Kompensation sås især med stjerner på himlen, og dette var også tydeligt i mine senere planetarieforsøg, når der blev ændret på 'stjernehimlen' på en måde, der simulerede en geografisk forflytning (Rabøl 1998, Thorup & Rabøl 2007).

Jeg stod imidlertid meget alene med mine forflytningsforsøg, navigations-forventninger og fokus på stjernerne. Af faglig nød og ensomhed besluttede jeg derfor først i 2000-tallet at springe med på kompas-toget. Stort set alle andre fugletræk- og brevdueforskere var nemlig optaget af magnetisme eller dufte, og samspillet mellem magnet- og sol-/solnedgangskompasset. Generaliseringen af Perdeck's (1958) forflytninger af Stære *Sturnus vulgaris* (senest bekræftet af Thorup *et al.* 2007) betød, at man havde lagt sig fast på, at ungfugle var ude af stand til navigere frem i trækruten og mod vinterkvarteret. Det var dem alene muligt at kompas-orientere i normal-trækretningen. Derfor var kompas-orientering så vigtigt og interessant, og det centrale spørgsmål var – og er stadig for de fleste – hvilket kompas, der er medfødt, og hvilke, der er tillærte, afledte og sekundære. Men det er en hypotese, at det forholder sig således. De resultat-fortolkninger, som man når frem til, kan derfor vise sig at være forvrængede eller direkte forkerte.

Rabøl (2010) omhandler mine kompas dominans/kalibrerings-forsøg på Endelave i efterårene 2001 og 2002. Rødstjerte *Phoenicurus phoenicurus* og Brogede Fluesnappere *Ficedula hypoleuca* blev fanget som trækgæster på Christiansø og blev efter flytningen til Endelave holdt i længere tid (flere dage/uger), og de enkelte fugle blev testet flere gange. Proceduren var: 1) Standard forsøg og 2) kryds-forsøg (Tab.1).

I efterårene 2006, 2007, 2008, 2011 og 2012 genoptog jeg disse forsøg på Christiansø og med friskfangede trækfugle testet samme eller næste solnedgangs-periode eller nat efter fangsten i morgentimerne. Jeg brugte stadig standard- og krydsforsøg, men desuden 3) direkte forsøg og 4) halv-kryds forsøg (Tab.1).

I alt lavede jeg 36 forsøg med 659 fugle om natten, og 37 forsøg med 646 fugle i solnedgangs-perioden. Før 2006 havde jeg lavet meget få solnedgangsforsøg, men disse var blevet almindelige, ja faktisk mere almindelige end natforsøg blandt mine med-forskere, så jeg meldte mig lettere skeptisk under fanerne. Skeptisk, for jeg kunne jo se, at solnedgangshimlen i de andres forsøg mestendels påvirkede orienteringen på forstyrrende vis. Meget ofte var middelretningen stort set rettet ind i solnedgangen, hvad der indikerede, at fuglene reagerede på en måde (viste en såkaldt foto-taxi), der ikke direkte eller alene har noget med træk-orientering at gøre. Nedenfor står i korte træk, hvad der kom ud af mine forsøg på Christiansø i 2006 til 2012.

I mine solnedgangs-forsøg på Christiansø så jeg ofte en orientering påvirket af og (delvis) rettet mod solnedgangshimlen, men stort set kun hos kontrollerne og især under en klar solnedgangshimmel. Det sås også indimellem i "overskyet", hvor tragten var dækket foroven med et uigennemsigtigt men lysgennemtrængeligt lag plastik. Resultaterne af solnedgangsforsøgene var, at et kompas relateret til geografisk N – formentlig et solnedgangs-kompas – syntes at være den vigtigste her og nu retningsgiver, medens et magnet-kompas ikke i noget tilfælde kunne påvises at være af dominerende betydning. Et solnedgangs-kompas betyder, at fuglen bruger solnedgangen som et kompas for sin træk-orientering. Den orienterer sig fx mod SV ved at holde en kurs skråt til venstre (68°) for en solnedgang i VNV. Meget ofte – og som nævnt især hos kontrollerne – viser fuglene derimod en direkte orientering mod solnedgangen eller et kompromis mellem retningen mod denne og normal-trækretningen, således i eksemplet mod V som en blanding af SV og VNV. En solnedgang i VNV betyder, at der vinkelret herpå står en "bue" af polariseret lys på himlen spændende fra SSV over Zenith til NNØ. Man mener almindeligvis, at det er denne bue snarere end solnedgangen direkte, der virker som kompas-referencen for træk-orienteringen. Med hensyn til kompas-kalibreringer var der ingen sikre tegn på sådanne.

I mine natforsøg var der ingen sikre tilfælde af kompas-kalibrering, bortset fra nogle enkelte gange, hvor et solnedgangskompas måske kalibrerede et magnet-kompas. Et stjerne-kompas syntes normalt at være det dominerende her og nu-kompas (Fig. 1). I en speciel opstilling, hvor halvdelen af fuglene kunne se frit til siderne fra deres kurve, medens den anden halvdel af fuglene var placeret i små plastikspande, hvor siderne skærmede af for den nedre tredjedel/halvdel af himlen i solnedgangsfasen, var der ikke den forventede effekt på orienteringen i den følgende test i tragtene om natten. I følge Muheim *et al.* skulle man forvente øget indflydelse af magnet-kompasset hos spand-fuglene i den forstand, at magnet-kompasset enten dominerede her og nu eller kalibrerede et stjerne-kompas. Men der var ingen tegn på noget sådant. I så fald skulle V- og Ø-forsøgsfuglene havde været modsat orienterede, men der var ingen forskel. Derimod var spand-fuglene SSØ-orienterede sammenlignet med SV-orienteringen hos kurv-fuglene (Figs 2 og 3). Jeg har ikke nogen forklaring på denne forskel, hvor fuglene blev testet om natten under stjernerne, og hvor spand- og kurv-fuglene i tragt-fasen var udsat for de samme påvirkninger fra omgivelserne. Forskellen – kurve kontra spande – lå alene i forskellene i den forudgående solnedgangsfase.

Ser vi på det historiske forløb af disse kompas-konfliktforsøg, rapporterede forskerne i starten kompas-kalibreringer. Wiltschko & Wiltschko mente, at magnet-kompasset kalibrerede stjerne-kompasset. Senere viste Able & Able, at også det modsatte kunne være tilfældet. Med forsøgene af Sandberg *et al.* lagde et magnet-kompas sig igen kortvarigt i spidsen som det primære, kalibrerende kompas. Så kom Cochran *et al.* og viste det modsatte, fulgt op af Muheim *et al.*, der fandt, at solnedgangs-kompasset kalibrerede magnet-kompasset – i hvert fald (sagde de) hvis der var frit syn til den nedre del af himlen. Giunchi *et al.* fandt det samme – i anden omgang – men i stort set alle de nyeste undersøgelser (inklusive mine) kan der ikke påvises kompas-kalibreringer – i hvert fald ikke hvis sådanne skal opfattes kun til at foregå i en snæver periode omkring solnedgang/solopgang.

Min holdning er p.t., at forskerne bør nedtone relevansen af disse kalibreringsforsøg. Der er vigtigere forskning at beskæftige sig med. Nu er det jo ikke alle, der har råd til at radiospore trækfugle via satellit eller bruge lysloggere, men der er stadig meget at hente gennem tragtforsøg. I efterårene 2013 og 2014 havde jeg således på Christiansø sat mig for at vise, om fuglenes magnet-kompas, som fortolket af Wiltschko & Wiltschko (2003), var af inklinations-typen, og da jeg ikke fik bekræftelse på det, gik jeg videre (2014) og undersøgte det logiske alternativ, at det magnetiske kompas er af den polære type. Det kunne jeg så heller ikke vise al den stund, at både de mod geografisk V og geografisk Ø magnet-drejede forsøgsfugle i tragte dækket med uigennemsigtigt plastik viste den samme SSV-lige standardorientering som også kontrollerne. Denne SSV-orientering lod sig ikke simpelt forklare som en reaktion mod noget (lys, lyde, andet) i omgivelserne. Men hvad var det så? Fuglene kunne jo ikke se stjernerne gennem det uigennemsigtige plastik.

Har trækfuglene så overhovedet et magnet-kompas? Ja – men spørgsmålet er, om de bruger et sådant under normale, fritflyvende omstændigheder? Det er primært det, som mine forsøg sætter spørgsmålstegn ved, for der er mange eksempler på, at trækfugle testet indendørs efter lang tids fangenskab viser orientering i forhold til magnetfeltet. Måske er det en slags basis-reaktion, som fuglene ikke normalt henter frem. I øvrigt er jeg ikke den eneste, der har haft svært ved at vise magnetisk orientering. Svenskerne med Susanne Åkesson i spidsen har således gennem årene haft mere end svare problemer med påvise orientering i normaltrækretningen styret af et magnet-kompas. Wiltschko & Wiltschko m.fl. bruger klart nok fugle og opstillinger, der fremmer tilsynekomsten af magnetisk orientering. Men det er der ikke nødvendigvis noget galt i. Det er ikke snyd, hvis ikke der filtreres "uønskede" data fra. Men det er vigtigt, at vi forstår under hvilke betingelser magnetisk orientering manifesterer sig, og her er både forsøgs-udstyr og (længden af) fangenskabsopholdet inde som betydende og fordrejende faktorer.

References

Able, K.P. & M.A. Able 1995a: Interactions in the flexible orientation system of a migratory bird. – Nature 375: 230-232.

Able, K.P. & M.A. Able 1995b: Manipulations of polarized skylight calibrate magnetic orientation in a migratory bird. – J. Comp. Physiol. A 177: 351-356.

Able, K.P. & M.A. Able 1996: Orientation cues used by migratory birds: A review of cue-conflict experiments. – Trends Ecol. Evol. 8: 367-371.

Åkesson, S., J. Morin, R. Muheim & U. Ottosson 2001: Avian orientation at steep angles of inclination: experiments with migratory white-crowned sparrows at the magnetic North Pole. – Proc. R. Soc. Lond. B 268: 1907-1913.

Åkesson, S., J. Morin, R. Muheim & U. Ottosson 2002: Avian orientation: effects of cue-conflict experiments with young migratory songbirds in the high arctic. – Anim. Beh. 64: 469-475.

Åkesson, S., C. Odin, R. Hegediüs, M. Ilieva, C. Sjöholm *et al.* 2015: Testing avian compass calibration: Comparative experiments with diurnal and nocturnal passerine migrants in South Sweden. – Biology Open 4: 35-47.

Barlow, J.S. 1964: Inertial navigation as a basis for animal navigation. – J. Theor. Biol. 6: 76-117.

Bingman, V.P. 1984: Night sky orientation of migrating pied flycatchers raised in different magnetic fields. – Behav. Ecol. Sociobiol. 15: 77-80.
Bingman, V.P. 1987: Earth´s magnetism and the nocturnal orientation of migratory European Robins. – Auk 104: 523-525.
Chernetsov, N., D. Kishkinev, V. Kosarev & C.V. Bolshakov 2011: Not all songbirds calibrate their magnetic compass from twilight cues: a telemetry study. – J. Exp. Biol. 214: 2540-2543.
Cochran, W.W., H. Mouritsen & M. Wikelski 2004: Migrating songbirds recalibrate their magnetic compass daily from twilight cues. – Science 304: 405-408.
Emlen, J. & S. Emlen 1966: A technique for recording migratory orientation of captive birds. – Auk 83: 361-367.
Gaggini, V., N.E. Baldaccini, F. Spina & D. Giunchi 2010: Orientation of the pied flycatcher *Ficedula hypoleuca*: cue-conflict experiments during spring migration. – Behav. Ecol. Sociobiol. 64: 1333-1342.
Giunchi, D., L. Varni, N.E. Baldaccini, F. Spina & F. Biondi 2015: New cue-conflict experiments suggest a leading role of visual cues in the migratory orientation of Pied Flycatchers *Ficedula hypoleuca*. – J. Ornithol. 156: 113-121.
Huttunen, M.J. 2009: Magnetic and sunset orientation in migratory redwings, Turdus iliacus. – Ital. J. Zool. 76: 133-142.
Moore, F.R. 1980: Solar cues in the migratory orientation of the Savannah Sparrow, *Passerculus sandwichensis*. – Anim. Behav. 28: 684-704.
Muheim, R. & S. Åkesson 2002: Clock-shift experiments with Savannah sparrows, *Passerculus sandwichensis*, at high northern latitudes. – Behav. Ecol. Sociobiol. 51: 394-401.
Muheim, R., F.R. Moore & J.B. 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.
Muheim, R., S. Åkesson & J.B. Phillips 2007: Magnetic compass of migratory Savannah sparrows is calibrated by skylight polarization at sunrise and sunset. – J. Ornithol. 148, Supplement 2: 485-494.
Muheim, R., S. Åkesson & J. Phillips 2008: Response to R. Wiltschko *et al.* (J. Ornithol.): Contradictory results on the role of polarized light in compass calibration in migratory songbirds. – J. Ornithol. 149: 659-662.
Muheim, R., J.B. Phillips & M.E. Deutschlander 2009: White-throated sparrows calibrate their magnetic compass by polarized light cues during both autumn and spring migration. – J. Exp. Biol. 212: 3466-3472.
Perdeck, A.C. 1958: Two types of orientation in migrating Starlings *Sturnus vulgaris* L., and Chaffinches *Fringilla coelebs* L., as revealed by displacement experiments. – Ardea 46: 1-37.
Prinz, K. & W. Wiltschko 1992: Migratory orientation of pied flycatchers: interaction of stellar and magnetic information during ontogeny. – Anim. Behav. 44: 539-545.
Rabøl, J. 1981: The orientations of Robins *Erithacus rubecula* after displacement from Denmark to Canary Islands, autumn 1978. – Ornis Scand. 12: 89-98.
Rabøl, J. 1998: Star navigation in Pied Flycatchers *Ficedula hypoleuca* and Redstarts *Phoenicurus phoenicurus*. – Dansk Orn. Foren. Tidsskr. 92: 283-289.
Rabøl, J. 2010: Orientation by passerine birds under conflicting magnetic and stellar conditions: no calibration in relation to the magnetic field. – Dansk Orn. Foren. Tidsskr. 104: 85-102.
Rabøl, J. 2014: Do migrant European chats and warblers use magnetic gradient navigation? – Dansk Orn. Foren. Tidsskr. 108: 232-250.
Rabøl, J. & T. Dabelsteen 1983: Non-magnetic orientation Pied Flycatchers *Ficedula hypoleuca*. – Dansk Orn. Foren. Tidsskr. 77: 55-56.
Rabøl, J., S. Hansen, L. Bardtrum & K. Thorup 2002: Orientation of night-migrating passerines kept and tested in an inverted magnetic field. – Ital. J. Zool. 69: 313-320.
Sandberg, R. & F.R. Moore 1996: Migratory orientation of red-eyed vireos, *Vireo olivaceus*, in relation to energetic condition and ecological context. – Behav. Ecol. Sociobiol. 39: 1-10.
Sandberg, R., J. Bäckman, F.R. Moore & M. Lohmus 2000: Magnetic information calibrates celestial cues during migration. – Anim. Beh. 60: 453-462.
Schmaljohann, H., T. Rautenberg, R. Muheim, B. Naef-Daenzer & F. Barlein 2013: Response of a free-flying songbird to an experimental shift of the light polarization pattern around sunset. – J. Exp. Biol. 216: 1381-1387.
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.-S. Bisson, M.S. Bowlin, R.A. Holland, J.C. Wingfield *et al.* 2007: Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. – PNAS 104: 18115-18119.
Weindler, P., R. Wiltschko & W. Wiltschko 1996: Magnetic information affects the stellar orientation of young migrant birds. – Nature 383: 158-160.
Weindler, P., V. Liepa & W. Wiltschko 1998: The direction of celestial rotation affects the development of migratory orientation in Pied Flycatchers, *Ficedula hypoleuca*. – Ethology 104: 905-915.
Wiltschko, W. & R. Wiltschko 1972: Magnetic compass of European Robins. – Science 176: 62-64.
Wiltschko, W. & R. Wiltschko 1975a: The interactions of stars and magnetic field in the orientation system of night migrating birds. I. Autumn experiments with European warblers (Gen. *Sylvia*). – Z. Tierpsychol. 37: 337-355.
Wiltschko, W. & R. Wiltschko 1975b: The interactions of stars and magnetic field in the orientation system of night migrating birds. II. Spring experiments with European Robins (*Erithacus rubecula*). – Z. Tierpsychol. 39: 265-282.
Wiltschko, R. & W. Wiltschko 1995: Magnetic orientation in animals. – Springer-Verlag Berlin Heidelberg New York.
Wiltschko, R. & W. Wiltschko 1999: Celestial and magnetic cues in experimental conflict. Pp. 988-1004 in N.J. Adams & R.H. Slotow (eds.): Proc. 22 Int. Ornithol. Congr., Durban.
Wiltschko, R. & W. Wiltschko 2003: Mechanisms of orientation and navigation in migratory birds. Pp. 433-456 in P. Berthold, E. Gwinner & E. Sonnenschein (eds.): Avian Migration. – Springer, Berlin Heidelberg New York.
Wiltschko, R., U. Munro, H. Ford & W. Wiltschko 2008a: Contradictory results on the role of polarized light in compass calibration in migratory songbirds. – J. Ornithol. 149: 607-614.
Wiltschko, R., U. Munro, H. Ford & W. Wiltschko 2008b: Response to the comments by R. Muheim, S. Åkesson, & J.B. Phillips to our paper "Contradictory results on the role of polarized light in compass calibration in songbirds". – J. Ornithol. 149: 663-664.

Appendix 1: http://dof.dk/dof/doft/2019/1.appendix1

Author's address:
Jørgen Rabøl (jrabol@bio.ku.dk)
Biological Institute
University of Copenhagen
Universitetsparken 15
DK-2100 Copenhagen Ø
Denmark