Orientation by passerine birds under conflicting magnetic and stellar conditions: no calibration in relation to the magnetic field

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

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

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Introduction

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

However, subsequent independent experiments by me and co-workers found little support for the first two of these claims. Rabøl et al. (2002) found no indication of an inclination compass (statement 1), since the orientation of four samples of migrant passerines was not reversed when the magnetic field was inverted. Rabøl & Thorup (2006) could not confirm statement 2, since the orientation of first-time migrants raised and tested under a starry sky and in a useless magnetic field deviated significantly from due S.

The present paper reports on my experiments in 2001-2002 concerning statements 3 and 4 (the meaning of the concepts *calibration* and *dominance* follows from Figs 1-3). Concerning 3, no indications were found of a magnetic calibration of the stellar compass during sunset/early night when birds were caged in magnetic fields where magnetic N was deflected towards geographical W or E (same intensity and inclination as the Earth's field), and later during the night were tested in funnels in the natural magnetic field. Both caging and testing were carried out under a clear sky. Concerning statement 4, I found that the stellar compass dominated the magnetic compass in most cases. However, sometimes birds which had spent the sunset/early night in a deflected magnetic field and were later tested in the same deflected field under a starry sky displayed reverse orientation in reference to the magnetic compass and seemed to ignore the celestial information, at least for the establishment of a course.

Clearly, there is much need for further replication and further development of the experiments constituting the basis for the generalizations of the Wiltschkos and co-workers, and for designing new ones. Here we should be aware that perhaps it is not possible to generalize too much from experiments carried out under a stationary "16-star-sky". It should also be kept in mind that the birds, in most experiments, were deprived of celestial but not of magnetic information for extended periods when caged, and only had access to celestial information when tested; therefore they might be prone more or less to ignore the celestial cues when establishing the course. Investigators should also consider whether the stellar information presented to the birds was as adequate as the magnetic and sunset information – in most outdoor sunset/early night experiments only few stars were present and only at the very end of the testing period. Finally, there is a clear need of more night (star) experiments to balance the generalizations based on the much more common sunset/early night experiments, and in particular a need for experiments involving long-duration conflicts between magnetic and celestial information; such a procedure would be a logical extension of the less "natural" standard short-term, pulse procedure for answering questions about compass dominance and/or calibration.

Material and methods

The experiments are based on the fact that symmetrical deflections towards E and W (preferably same number of tests in the two constellations) are a very strong tool for detecting calibration and dominance of one or another of the two compasses (geographic/stellar versus magnetic). Fig. 1 shows, by means of three examples, how it will be manifested if the magnetic compass at sunset/early night do calibrate the stellar compass for the rest of the night (total dominance). The compass with no influence will reveal itself by a bimodal pattern, with 180° between the peaks at right angles to the mean direction of the unimodal distribution relative to the dominant compass. Manifestation of a partial dominance of the stellar or magnetic compass is illustrated in Figs 2-3.

The birds were caged and tested outdoors in a glade in a forest, all the time exposed to the sky and – if not overcast – able to see the sun and stars. Results of Muheim et al. (2006a, 2006b) suggest that it is important that the birds can see (some of) the sky all the way down to the horizon. This is not possible in a forest glade, but the horizontal screening towards N did not exceed 12-14°. Towards W (and the sunset) there was an almost unobstructed view down to the horizon, and in the other directions down to 8-10°.

The controls were caged in the undisturbed magnetic field whereas the experimentals were caged in a magnetic field where resultant magnetic N was deflected from geographical N towards geographical W or E. The resultant inclination

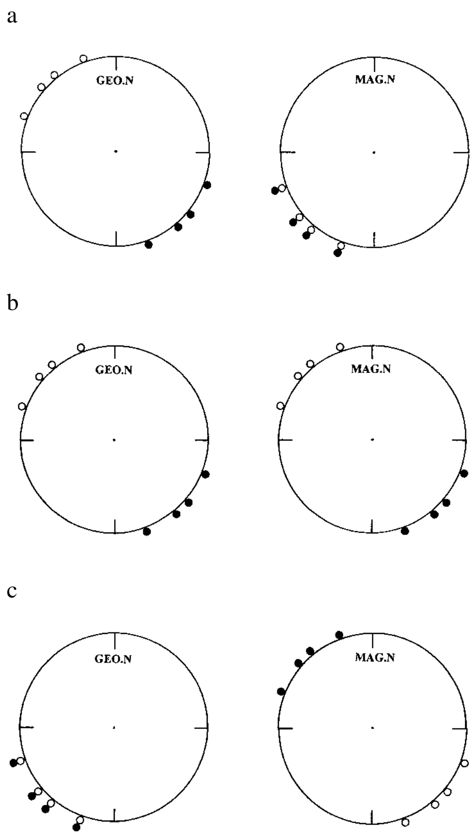

Fig. 1. Constructed examples of the outcome of a test of the hypothesis that the migratory direction is established in reference to magnetic N, and that the magnetic compass calibrates the stellar compass in the sunset/early night phase. After the calibration, the stellar compass is in charge of maintaining the migratory direction for the rest of the night. The dots represent tested birds, and magnetic N is deflected towards geographical E (white dots) or W (black dots). The standard direction is SW (225°), and for the sake of reality some directional variation is introduced (200°, 220°, 230° and 250°, sample mean vector 225° - 0.951 (n = 8)). a) The orientation of the experimental birds relative to geographic and magnetic N during the calibration phase (magnetic compass active). b) Orientation of the same birds during night (calibrated stellar compass active); tested in the normal magnetic field. c) As b), but control birds, calibrated in the normal magnetic field and tested in the deflected fields.

Konstruerede eksempler på forsøgsudfald under den forudsætning, at magnetkompasset ved solnedgang/tidlig nat kalibrerer stjernekompasset, som så bruges resten af natten. Magnet-kompasset bruges altså alene ved kalibreringen. I dette tilfælde er normaltrækretningen SW, og der er en vis variation (fra 200° til 250°) symmetrisk omkring normaltrækretningen. De sorte prikker viser retninger for fugle, for hvilke magnetisk nord under kalibreringen var afbøjet til geografisk vest, de hvide prikker retninger for fugle, for hvilke magnetisk nord under kalibreringen var afbøjet til geografisk øst. a) Forsøgsfuglenes orientering i forhold til henholdsvis geografisk og magnetisk nord i kalibreringsfasen (magnetkompasset aktivt). b) Forsøgsfuglenes orientering senere (stjernekompasset aktivt); fuglene testet i det normale magnetfelt. c) Kontrolfuglenes orientering senere (stjernekompasset aktivt); disse fugle er kalibreret i det normale magnetfelt, men testes i de afbøjede magnetfelter.

and intensity was unchanged compared with the natural values. Before each nightly experiment the resultant direction of magnetic N and the resultant magnetic inclination (+70°) were checked. The homogeneity of the magnetic intensity was not measured, but since only a single cage or funnel was placed in the centre of each pair of coils the variation was probably even lower than the 0-1% reported by Rabøl et al. (2002) for the same setup (with inverted magnetic inclinations).

The deflected magnetic fields were produced by eight Helmholtz coil sets (quadratic 80×80 cm with 45 cm between the two coils). Magnetic N of the coil field was directed towards SW (four sets) or SE (four sets). The applied magnetic vector was horizontal and the intensity $\sqrt{2}$ times the intensity of the horizontal component of the natural magnetic inclination vector. Therefore, resultant magnetic N pointed towards W or E, respectively. However, in 2002 one of the coils had a defect making it impossible to deflect resultant magnetic N towards geographical E (if an unchanged magnetic inclination and intensity had to be retained). In this single case resultant magnetic N was only deflected towards NE. However, the resulting asymmetry only had a slight influence on the directional patterns of the total sample

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

The orientation and amount of activity of the individual birds were estimated as previously described by, e.g., Rabøl (1979, 1993). The patterns of scratches was carefully inspected from above to locate the maxima and minima of activity, and the mean directions were estimated to the nearest 5°. In case of a clear bimodal pattern both peaks were estimated, and the major peak was identified, but sometimes the two peaks were about the same size. The concentration of scratches around the mean direction was estimated as high, medium, low, or disoriented. It was rarely possible to count the scratches, but the amount of activity was estimated as zero, very small, small, medium, large, or very large. The significance of the sample mean vector was found by application of the Rayleigh test, and the confidence interval test and the Watson-Williams test were used for testing the difference between two dependent and independent samples, respectively (Batschelet 1981). Furthermore, the parametric test for the concentration parameter (Batschelet op.cit.) was applied to test for difference in concentrations of the two samples.

The birds were exposed for the sunset and early night stars in their cages until at least 1½ hours after sunset where the brighter stars – in case of a clear sky – had been visible for at least 45 min. The controls were kept in the normal magnetic field, the experimentals in the fields deflected towards W or E. The birds were transferred to the funnels about two hours after sunset, where no trace of the sunset was visible. The birds were tested in the funnels for about 1½ hours. All birds were tested under moonless conditions, and for this reason the testing sometimes had to be postponed until later in the night.

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

The birds always experienced a clear sunset/early night before the testing, but in two cases (16/9 and 26/9 2001) the tests were carried out with very few visible stars. Very probably, the birds were still able to maintain a course selected in the sunset/early night phase in relation to these few stars, but almost certainly they were not able to establish a course in relation to stellar rotational N during these nights.

Experimental birds were sometimes tested in the natural magnetic field and thus spent 2-3 hours outside the deflected field, and since the birds were caged two by two even the cage-mates of these birds spent the same time outside the deflected field (always without access to the sight of the stars). With this single exception, the experimental birds spent all their time within the deflected fields, meaning that the procedure was

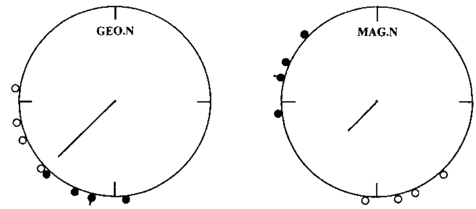

Fig. 2. Constructed example showing the influence of a dominating stellar compass: the vectorial influence of stellar N is twice the influence of magnetic N. The birds – which could be controls or experimentals – are tested in a deflected magnetic field during night, and there is no calibration in the sunset/early night phase. As an example, the marked black dot shows the orientation of a bird with a resultant direction between a vector pointing towards 220° in relations to stellar N and a vector half the size pointing towards 220° in relation to magnetic N. The resultant direction is 194° relative to stellar N and -77° (283°) relative to magnetic N. The sample mean vector of the eight birds in relation to stellar N is 225° - 0.851, and in relation to magnetic N 225° - 0.426. The latter concentration is half the size of the former, and in general an influence ratio of x/1 of the vectors produces a sample concentration ratio of x/1.
Man forestiller sig her, at fuglene – når de testes under stjernehimlen i et mod vest eller øst afbøjet magnetfelt – orienterer sig i en retning, der er et kompromis mellem retningerne indikeret af henholdsvis magnet- og stjernekompasset, og at sidstnævntes indflydelse er dobbelt så stor som førstnævntes. Den sorte plet markeret med en streg viser således en fugl, der søger at orientere sig mod 220° i forhold til begge kompasser. Kompromis-vektorens retning bliver 194° i forhold til geografisk nord og 283° i forhold til magnetisk nord. Gennemsnitsvektoren for de otte fugle er rettet mod SV (225°) i forhold til begge kompasser, men koncentrationen i forhold til magnetisk nord bliver kun halvt så stor som koncentrationen i forhold til geografisk nord.

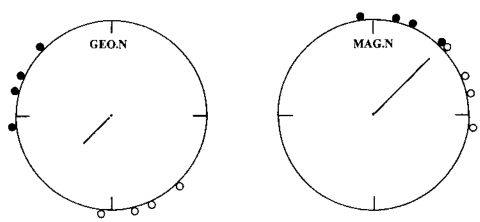

Fig. 3. Constructed example showing the influence of a dominating magnetic compass in the reverse (NE) direction. The vectorial influence of the stellar compass (SW) is half the influence of the magnetic compass. The birds are tested in a deflected field during night, with no calibration at sunset/early night.
Som Fig. 2, men med magnetkompassets indflydelse dobbelt så stor som stjernekompassets, og med fugle, der udviser omvendt orientering i forhold til magnetkompasset.

different from the normal short-term treatment where the birds are tested within the deflected (or inverted) field but otherwise are caged in the normal magnetic field (e.g. many papers by the Wiltschkos; however, see Beck 1984, Beck & Wiltschko 1988).

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

The first group consisted of 40 first-year Pied Flycatchers *Ficedula hypoleuca* trapped 19-20 August 2001. They were caged on Christiansø until 29 August and then in Copenhagen until 3 September before transported to Endelave. From trapping until 6 September, when they were placed outdoors, the birds never saw the starry sky but sometimes the sun; from 6/9 until the first experiments on the night of 11/9 the birds had a free view of the day and night sky, but only a single night (8/9) was starry. After that the birds often experienced the stars. The tests were carried out on seven moonless and starry nights between 11/9 and 26/9. Only 28 of the birds (12 controls and 16 experimentals) were included in the study.

The second group consisted of 14 Pied Flycatchers and 9 Redstarts *Phoenicurus phoenicurus* (all first-years), trapped 28/8–5/9 2002 on Christiansø and 6/9 transported to Endelave. The birds never experienced the sunset or starry sky between capture and arrival on Endelave, where they were placed outdoors. Experiments took place on 8-9/9 where the sky was clear during both day and night. The birds were divided into 16 experimentals and 7 controls (cf. Appendix).

The third group consisted of 15 Pied Flycatchers and 15 Redstarts, all first-years except for three 2nd-year or older Redstarts. They were trapped 6-9/9 2002 and transported from Christiansø to Endelave on 11/9, arriving in the morning of 12/9. Before that they were exposed to the clear sunset and early night sky on 10/9, and on arrival they were immediately placed outdoors under clear day and night conditions before being tested on the clear nights of 12-14/9. They were divided into 16 experimentals and 14 controls, as equal as possible according to species, age and trapping date.

Results

In the following, mean vectors are given in the format "α – r", where α is the direction measured in degrees and r the concentration ($0 \le r \le 1$). Statistical significance is indicated by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). In cases with bimodal orientation, the direction of the major peak – if any – is written in bold types.

All nightly, individual orientations are given in Appendix. The results are shown in Figs 4-5 and in Table 1.

1) Controls were tested in the natural magnetic field on eight nights. The orientation total of all controls in the natural field is shown in Fig. 4a. The mean sample vector is highly significant (166° – 0.463***, n = 81); nevertheless, the distribution looks bimodal with peaks at about 125° and 215°.

Although both concentration and activity of most of the single birds were rather high on the first three nights in 2001, their directions varied so much that, as a sample, they were more or less disoriented. For the three nights lumped together a bimodal pattern with peaks at E-ESE and SSW-SW was fairly obvious; the total sample mean vector was statistically insignificant (148° – 0.286, n = 34, $0.05 < P < 0.10$). On 26 September 2001 the same controls were clearly oriented, approximately in the standard direction (206° – 0.864***, n = 12). On 8 and 9 September 2002 the mean vectors of the second control sample were 171° – 0.540 (n = 12) and 203° – 0.935* (n = 5), respectively. The mean vectors of the third control sample on 12 and 13 September 2002 were 151° – 0.657* (n = 10) and 129° – 0.631** (n = 14), respectively. The mean orientation on each of these eight nights, and the grand mean vector (164° – 0.893**, n = 8), are shown in Fig. 5a.

2) Experimentals were tested in the natural magnetic field on five nights. On three nights the orientation was close to standard; on one – 26 September 2001 – it was significantly bimodal **200**°/20° – 0.509* (n = 16); and on 14 September 2002 it was SSE (163° – 0.871***, n = 16).

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

Fig. 5c shows the nightly mean directions of the experimentals in the natural magnetic field. The grand mean vector is 203° – 0.930** (n = 5).

On 16 and 26 September 2001 the sunset/early night sky (seen by birds in their baskets) was clear, but later (when birds were tested in funnels) only a few stars were occasionally visible. The sample mean vector on 16 September of the (formerly) W-deflected birds was 239° - 0.802* (n = 7), and of the E-deflected birds 218° - 0.774** (n = 8). On 26 September both samples were axially oriented, **190°**/10° - 0.761** (n = 8) and 40°/220° - 0.409 (n = 8), respectively. Thus, there seems to be no difference in orientation between the W- and E-deflected experimentals.

3) Controls were tested in the deflected magnetic fields on three nights, and in particular on the first two nights the orientation was in the standard direction in reference to geographical N, just as in the contemporary experiments carried out with the experimentals in the natural magnetic field (see below).

The total of all controls in the deflected fields is shown in Fig. 4c. The sample mean vector in relation to magnetic N is 92° – 0.255 (n = 21), and in relation to geographical N 222° – 0.508** (n = 21).

Fig. 5b shows the nightly mean directions of the controls in the deflected magnetic fields. The grand mean vector in relation to geographical N is 220° – 0.805 (n = 3).

On 16 September (cf. 2)) the orientation of the controls in reference to geographical N was 241° - 0.823** (n = 8), whereas two separate peaks were apparent in reference to magnetic N: The birds in the W-deflected magnetic field were oriented towards "N" (between 330° and 30°) and the E-deflected birds towards "SE" (between 115° and 195°). On 26 September the orientation was more dispersed, and two birds out of eight were axially oriented. However, the sample mean vector of the six birds showing unimodal activities was 245° - 0.793* in reference to geographical N. In reference to magnetic N the same six birds were oriented towards "NW" (between 285° and 35°; W-deflected birds) and "SE" (125° to 150°; E-deflected birds).

4) Experimentals were tested in the deflected magnetic fields on nine nights. On the first three

Table 1. Experimentals and controls tested in the deflected field: mean vectors from all birds showing significant orientation, irrespective of whether they were tested in a W or E deflected field. The last column shows the proportion between the concentrations of the vectors in the second and third columns, a measure of the influence of the magnetic compass relative to the influence of the geographical (stellar) compass. A negative sign in the concentration-ratio means a reverse magnetic sample mean vector, i.e. a sample mean direction more or less reverse to the standard direction (SSW-SW).

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

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

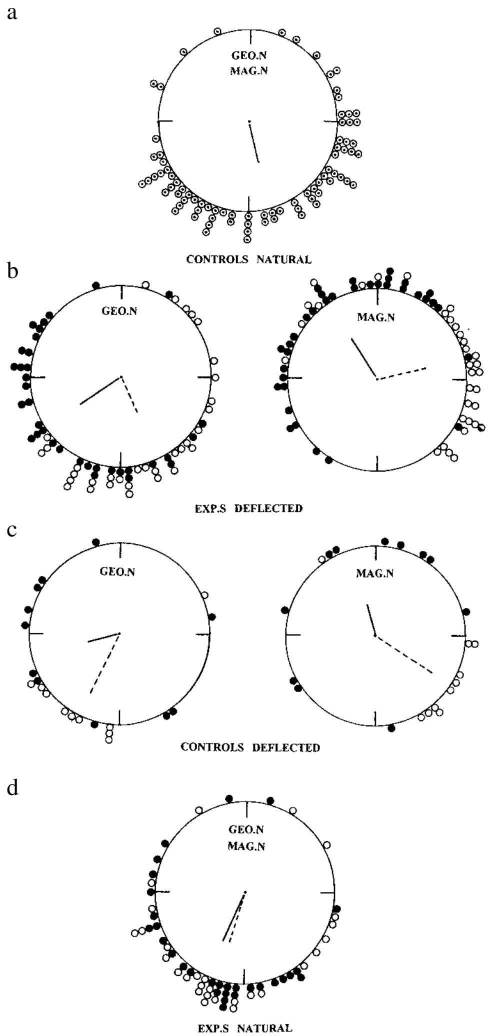

Fig. 4. a) The orientation of the controls tested in the natural magnetic field (magnetic N = geographic (stellar) N). Sample mean vector 166º – 0.463*** (n = 81).

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

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

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

*Fire kombinationer af kontroller (controls) og forsøgsfugle (exp.s) tragt-testede i henholdsvis det naturlige (natural) og de afbøjede (deflected) magnetfelter. a) og d) viser kontroller og forsøgsfugle testede i det naturlige magnetfelt, hvor der jo er sammenfald mellem geografisk og magnetisk N. b) og c) viser orienteringen af forsøgsfugle og kontroller i de afbøjede felter. De sorte og prikkede streger, der udgår fra cirklernes centrum, viser gennemsnitsvektorerne for henholdsvis de vest- og øst-afbøjede fugle. Bemærk at orienteringen i forhold til magnetisk nord er omtrent modsat normaltrækretningen. Gennemsnitsvektorerne i forhold til geografisk nord udviser ikke de store forskelle (fra oven og ned: 166° – 0,463***, 196° – 0,431***, 222° – 0,508**, og 201° – 0,577***).*

nights in 2001 the sample mean vector in relation to magnetic N was 19º – 0.564*** (n = 24), and in relation to geographical (stellar) N 214º – 0.241 (n = 24), i.e., the orientation was about the reverse of the standard direction in reference to the magnetic compass (cf. Table 1). On the fourth night (15 September), the sample mean vector in relation to geographical N was 156º – 0.854** (n = 8), whereas the pattern in relation to magnetic N was bimodal with peaks at 61º (the E-birds) and 251º (the W-birds), and an insignificant sample mean vector (300º – 0.090, n = 8).

On the remaining five nights – and compared with the corresponding orientations of the controls and experimentals in the natural magnetic field – the orientation is clearly reverse in reference to magnetic N on 12 September 2002, but standard in relation to geographical N on 23 September 2001, 8 September 2002, and 13 September 2002 (the abrupt shift in the significant compass reference from 12 to 13 Sep. 2002 is noteworthy, Table 1). On 9 September 2002 the orientation is reverse (36º – 0.621, n = 5) in reference to magnetic N and standard (237º – 0.562, n = 5) in relation to geographical N, i.e. the two tendencies are more or less opposite and obscure each other.

The total of all experimentals in the deflected fields is shown in Fig. 4b. The sample mean vector in relation to magnetic N is 20° – 0.324*** (n = 68), in relation to geographical N 196° – 0.431*** (n = 68).

Fig. 5d shows the nightly mean directions of the experimentals in the deflected magnetic fields. The grand mean vector in relation to geographical N is 207° – 0.797** (n = 9).

I tested the difference between the controls and experimentals in natural magnetic fields. The angular difference between the grand mean vectors for the whole material (Fig. 5) is 39° (0.02 < P < 0.05, Watson-Williams two-sample test). Considering the sample mean vectors based on all

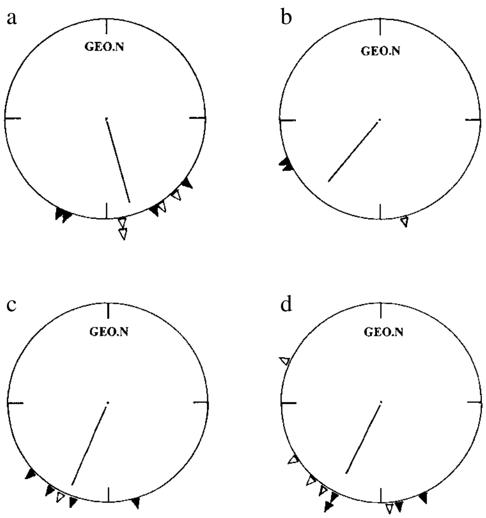

Fig. 5. Nightly mean vectors for a) controls tested in the natural magnetic field, b) controls tested in deflected magnetic fields, c) experimentals tested in the natural field, and d) experimentals tested in deflected fields. Black triangles refer to directions of statistically significant nightly mean vectors (P < 0.05, Rayleigh test), the white triangles to directions of mean vectors which were not significant. The four grand mean vectors are 164° – 0.893** (a), 220° – 0.805 (b), 203° – 0.930** (c), and 207° – 0.797** (d).
Denne figur viser i princippet det samme som Fig. 4 i relation til geografisk N, men der er her set på retningerne (trekanter) af de natlige gennemsnitvektorer. a) og c) er henholdsvis kontroller og forsøgsfugle i det naturlige magnetfelt, mens b) og c) er henholdsvis kontroller og forsøgsfugle i de afbøjede magnetfelter. Igen er der ikke den store forskel på retningerne, mens koncentrationerne som forventet er noget større end i forhold til Fig. 4.

nightly individual mean directions (Fig. 4) – 166° – 0.463***, n = 81 (controls) and 201° – 0.577***, n = 58 (experimentals) – the difference is highly significant (P < 0.001). However, if the latter comparison is restricted to the two nights (8 and 9 September 2002) with contemporary experiments, with sample mean vectors 190° – 0.692**, n = 11 (controls) and 211° – 0.666**, n = 13 (experimentals), the difference is not significant (0.30 < P < 0.40).

I also tested for the difference in reference to geographical N between the W- and E-deflected experimentals and controls in (cf. Fig. 4b and 4c). Both differences were significant (P < 0.01, Mardia-Watson-Wheeler two sample test). Furthermore, the difference between the E-deflected experimentals and controls was significant (P < 0.05), whereas the difference between the corresponding W-deflected sub-samples was not (0.10 < P < 0.20).

Finally I tested the homogeneity (Watson-Williams multi-sample test) between all four sample mean vectors in Fig. 4, and between the four grand mean vectors of Fig. 5 (in both, geographical N was used as the compass reference in the deflected magnetic fields). Both tests showed significance (P < 0.01), the heterogeneity primarily caused by a tendency towards a south-easterly orientation of the controls in the natural magnetic field (confirmed by testing the remaining three samples for homogeneity: P > 0.05 both when considering the sample mean vectors based on all nights (Fig. 4) and the grand mean vectors (Fig. 5)).

Table 1 gives the sample mean vectors in reference to geographical (stellar) N and magnetic N, respectively, on each of the 12 nights where birds were tested in deflected fields. The last column shows the proportion between the sample concentrations based on two compasses (a negative sign indicates a sample mean direction more or less reverse to the standard direction (SSW–SW)).

Discussion

The inspiration for the experiments here reported was the paper by Sandberg et al. (2000) where the authors concluded that the magnetic compass in the sunset/early night phase calibrated the stellar compass for the rest of the night, on basis of nightly departure directions of birds spending the sunset/early night in a deflected magnetic field. However, when I applied a rather similar procedure, I obtained different results. 1) In all cases where experimentals were tested in the natural magnetic field (Figs 4-5), the orientation was more or less in the standard direction. However, if the magnetic compass at sunset/early night calibrates the stellar compass, the orientation when tested in the funnels during night should be bimodal with the two peaks at about right angles to the standard direction (Fig. 1). 2) Likewise, when the experimentals were tested in the deflected magnetic fields (Figs 4-5), the results diverged from the predicted outcome if a magnetic calibration takes place in the sunset/early night phase (Fig. 1). So only the controls tested in the deflected magnetic fields (Figs 4-5) were compatible with the sunset/early night magnetic calibration hypothesis. However, an alternative explanation here is that the birds – during night – make use of the stellar sky as the dominating compass reference, and considered in concert with 1) and 2) above this alternative explanation seems to be the best one.

Furthermore, by reasoning along similar lines it will be seen that the results give no indication of a sunset and/or stellar compass calibrating the magnetic compass during sunset/early night. If for example a sunset compass calibrated the magnetic compass the formerly W-deflected experimentals should be oriented about NW and the E-deflected about SE, but as seen in Fig. 4d there is no difference between the orientation of these two groups when tested during night in the natural magnetic field. This could have something to do with the presence of stars on the night sky, but the same pattern was apparent on the two almost star-less nights 16 and 26 September 2001 (see 2) and 3) under Results).

However, the results from one of the four constellations did suggest that something was going on in the sunset/early night phase: for experimentals tested in the deflected fields there was a strong indication that the magnetic compass dominated in four of the nights (Table 1), suggesting that extended exposure to a deflected magnetic field well into the night sometimes will lead to dominance of the magnetic compass. However, this magnetic influence manifested itself as a reverse orientation, whereas stellar influence – apparently dominating in four other series – lead to standard or south-easterly (right angle) orientation.

A similar but weaker effect was apparent when the controls were tested in the deflected fields.

Clearly, the interplay between the stellar and magnetic compasses is not well understood, and one should even consider the possibility that the magnetic compass is not of the inclination type. I will return to that question later.

The orientation of the controls under the starry sky and in the natural magnetic field was often east of south, suggesting influence of right angle orientation rather than standard orientation (SSW-SW). Such a reaction could be compensatory to the western displacement (similar patterns was observed in two other batches displaced in the autumn of 2004; own unpubl. data). Another possibility is that the SE orientation was a kind of basic reaction or nonsense orientation – i.e. some kind of forerunner to standard orientation (cf. Rabøl 1997).

Sandberg et al. (2000)

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

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

When the controls and deflected birds were released in the undisturbed magnetic field under a starry sky, the formerly deflected vireos and waterthrushes in 1997-98 were oriented 104° and 113° clockwise to the release orientation of the controls. No such difference in release orientation of controls and deflected vireos was reported from 1992.

Summing up, there is evidence of a significant co-influence and after-effect of the magnetic compass. However, the early night starry phase in the cages should have been longer – at least about one hour. That would have given time for a natural development of the interplay between the magnetic compass and one or both of the stellar compasses (i.e. celestial rotation/rotational-N or stellar-S in the terminology of Rabøl (1998a)). In the cage-tests and releases of Sandberg & Moore (1996) and Sandberg et al. (2000), conditions were probably too poor (in the funnels) or time before releases too short for rotational-N to act as an establishing compass (a compass in reference to which a course is established; later on the course may be maintained in reference to another compass).

R. and W. Wiltschko, and Bingman

According to R. and W. Wiltschko (e.g., Wiltschko & Wiltschko 1999, 2003) the magnetic compass is dominating and/or calibrates the sunset and stellar (pattern) compasses, at least after some delay. This should hold true for birds grown up in the wild under natural conditions, and captured on migration. In hand-raised migrants, celestial rotation in the pre-migratory period sets and calibrates all other compasses, including the magnetic. However, celestial rotation should only yield N/S-information, whereas the magnetic compass in some way (not explained in operational terms) provides E/W-information. As an example, the initial SW standard direction of German Garden Warblers *Sylvia borin* is supposedly established by a pre-migratory interplay (setting) between celestial rotation and the magnetic field (Weindler et al. 1996, Weindler et al. 1998); if existing at all, the evidence for this hypothesis is slim.

A long time ago R. and W. Wiltschko and coworkers performed cue-conflict experiments involving the magnetic compass and the natural starry sky, and experiments of this type, using European chats and warblers, remain rather few. Among them, in particular the results and interpretations of Wiltschko & Wiltschko (1975a,b) and Bingman (1987) have been generalized and today constitute the main foundation for the claim that the magnetic compass is superior to other compasses. The Garden Warbler and Robin *Erithacus rubecula* experiments of Wiltschko & Wiltschko (op.cit.) were carried out using the octagonal Frankfurt-cage and with the view of the starry sky much restricted, and in all probability not including the rotational point (*Polaris*). Furthermore, the birds were only allowed to see the stellar sky during the tests and not in the much longer intervening periods of caging. The Robin experiments of Bingman (op.cit.) were carried out with the proclaimed intention to improve the possibilities of getting directional cues from the stars, mainly by using Emlen-funnels and low shielding, allowing an almost unrestricted view of the stellar sky. However, again the birds were caged indoors and only exposed for the starry sky when tested in the funnels. Such shortcomings of the experimental design make it difficult to generalize the results of these studies, and the arguments why a magnetic compass should take over in the course of the autumn are not convincing.

Prinz & Wiltschko (1992) reported results resembling the reverse magnetic orientation reported in the present paper. Pied Flycatchers grew up outdoors with view to the day and night sky. Magnetic N was deflected to 120° in one group and 240° in another. Later, the birds were tested in the natural magnetic field without access to celestial cues. The sample mean vector of the latter group was 356° – 0.57*** (n = 110), compared with 237° – 0.51*** (n = 41) for the controls, which strongly suggests that the magnetic compass was calibrated by celestial rotation. However, the orientation of the first group (magnetic N at 120°) was not about 120°, as expected if the magnetic compass was calibrated by celestial rotation; the sample mean vector was 12° – 0.19* (n = 87), and "It is unclear whether the barely significant mean really represents a diffuse directional tendency or whether the distribution should rather be looked upon as random behaviour." The authors end up presenting an "explanation" involving true asymmetry of behaviour following clockwise and counter-clockwise shift of magnetic N, but miss the more parsimonious explanation, that the birds in both groups orient towards N (i.e., reverse) in reference to magnetic N as an after-effect of the conflict between celestial N and magnetic N. Such an interpretation becomes more obvious if the grand mean vectors instead of the sample mean vectors are considered. The grand mean vectors of the 240° group and the 120° group are calculated as 358° – 0.86** (n = 8), and 9° – 0.69* (n = 7), respectively.

Able & Able

Able & Able (1996) continued the Savannah Sparrow *Passerculus sandwichensis* experiments initiated by Frank Moore, and performed many ingenious experiments with both hand-raised birds and migrants trapped in the wild. According to them, celestial rotation calibrates all the other compasses in both juvenile and adults birds, not just in the pre-migratory period (Able & Able 1995). In their view, a stellar-pattern compass ranks low and may be dominated and calibrated by the magnetic compass (and the sunset compasses). They consider stellar patterns just like landmarks, as references for the maintenance of migratory orientation established on the basis of other cues. However, in the terminology of these authors, celestial rotation (rotational-N in my terminology) is something different from, and superior to a stellar (pattern) compass, and therefore – in this latter sense of a stellar compass – they may agree with the Wiltschkos that the magnetic compass calibrates the stellar compass.

Åkesson et al. (2002)

Åkesson et al. (2001, 2002) and Muheim & Åkesson (2002) reports on funnel experiments carried out during sunset/early night close to the magnetic north pole, where magnetic inclinations are very steep. The results indicates that the two species of sparrows investigated make use of both a magnetic compass and a sun(set) compass, but not of a stellar compass – and no wonder, because very few stars were visible during the tests. The magnetic compass had the primary role whereas the sun(set) compass apparently was used only for maintaining a course established in reference to the magnetic compass. The results thus support the findings and conclusions of Sandberg et al. (2000) and might lead to the idea that the magnetic compass dominates and calibrates the celestial compasses.

There are, however, a few problems with these findings of Åkesson et al.: the orientation (in reference to geographical N; the declination was +33°) of the juvenile control birds during sunset was E (86°), which is a significant deviation both from the expected rhumbline (SSE-SE) and from the great-circle (SE) standard directions.

A group of sparrows experienced a 90° counter-clockwise outdoor deflection of magnetic N for one hour in the afternoon, starting 2-4 hours before sunset. Later, during sunset, the birds were tested in the natural magnetic field. These birds – as another group of birds deflected 90° counter-clockwise in the test-phase – changed their orientation about 90° counter-clockwise compared with the controls. It thus appears that the magnetic compass in the afternoon-phase calibrated the sunset compass used in the sunset/early night phase, where the magnetic compass reference was ignored. This result is remarkable and its deeper significance was not appreciated by the authors, because there is no "conventional" logic in the observation. The afternoon calibration-phase was well before the sunset/early night phase which is usually thought to be the sensitive calibration period. Furthermore, the birds were not supposed to be motivated for initiating migration during the afternoon. Perhaps the reaction is a spurious outcome of the treatment and therefore irrelevant for normal orientation.

Cochran et al. (2004)

Cochran et al. (2004) investigated the orientation of released, radio-equipped thrushes in Illinois in spring. The birds were tracked on their nightly migration under a starry sky and in the natural magnetic field after spending the sunset/early night phase in a cage where magnetic N was deflected towards geographical E. Controls were heading N (Gray-cheeked Thrush *Catharus minimus*) or NW-NNW (Swainson's Thrush *Catharus ustulatus*), whereas test birds on the first night following treatment were deflected 80°-90° counter-clockwise. It certainly looks as if the deflected magnetic compass in the sunset/early night phase is responsible for this outcome, and the interpretation of the authors was that the twilight (i.e., sunset) compass calibrated the magnetic compass which later, during the night, acted as the compass in relation to which the orientation was maintained. This compass calibration lasted for the entire night, but according to the authors the compass was back to normal in the following nights; it appears, however, that the orientation of at least the Swainson's Thrushes had shifted significantly to a little E of N ($P < 0.05$, Watson-Williams test), compared with the controls. The interpretation of mine would be that this latter orientation is compensatory (compensating for a too westerly orientation during the first night).

Muheim et al. (2006a,b)

Muheim et al. (2006a) reviewed "cue-conflict experiments where the magnetic field was shifted in alignment relative to natural celestial cue." They concluded that if the full sunset/sunrise sky down to the horizon was not in view then, as an aftereffect, the magnetic compass was not the calibrating compass but was itself being calibrated by some other compass. The main conclusion was that "we envision a cue hierarchy in which celestial cues available at sunset/sunrise (presumably polarized patterns from the region of sky near the horizon) provide the primary reference system for calibration of the magnetic compass, while the magnetic compass in turn is used to calibrate the star compasses, as well as zenith polarized light patterns".

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

Discrepancies

The experiments summarised above, together with mine, draws a confusing picture. Sandberg et al. (2000) concluded that the magnetic compass calibrates the stellar compass in the sunset/early night phase, Åkesson et al. (2002) that the magnetic compass calibrates the sunset compass in the afternoon, and Cochran et al. and Muheim et al. that a sunset/sunrise-based compass calibrates the magnetic compass (which perhaps later on calibrates the stellar compass). And from my own investigation it appears that there is no (long-lasting) calibration between the celestial and magnetic compasses, but that the stellar compass normally dominates the magnetic compass (occasionally the latter may dominate, but then the orientation is reversed). Some of my findings lie close to the ideas of the Able & Able (1995, 1996). Some reasons for these discrepancies are discussed in the next section.

The compasses at sunset/early night

When people make sunset/early night orientation experiments, the magnetic, the sunset and the stellar compasses are implicitly considered to compete at an equal footing. It should be kept in mind, however, that if the birds display directed activity before the stars appear on the sky, the stellar compass is irrelevant. The same holds true for the sunset compass if the experiments are carried so far into the night that the sunset is no longer visible.

According to my own experience, the brighter stars become visible between 40 and 80 minutes after sunset. 80 minutes after sunset is about the time where most researchers finish their sunset/early night tests.

In the clear sky experiments of mine all three compasses were available at the sunset/early night exposure, whereas only the stellar and magnetic compasses were available during the testing phase in the funnels. As already mentioned the sunset/early night phase of my experiments was generally half an hour to one hour longer than is normally the case, implicating that the stellar compass was here given a better chance in the "competition" with the magnetic compass.

Most people consider the twilight period (= the sunset/early night phase) the most important time for the three "kinds" of compasses to couple together, and during which a stellar-pattern compass is calibrated by the magnetic and/or the sunset compass. The hypothetical scenario comprises 1) a narrow calibration stage, closely associated to 2) the simple clock-&-compass hypothesis and the perception of 3) a single establishment of direction per migratory step.

My perception is a little different: When the twilight activity starts in the cages or funnels – or when real departures takes place – the stars are not yet visible on the sky to a degree sufficient for stellar-compass orientation or stellar navigation (Rabøl 1997, 1998a). Only the magnetic and sun/sunset compasses are available for use. Only later do the stellar compasses gradually come into function, and compass calibrations – and in all probability also navigatory checks – are carried out several times in the course of the night.

Reverse orientation

The sometimes very prominent component of reverse orientation in reference to magnetic N of the experimentals tested in the E- or W-deflected fields is a remarkable new result. It calls for an explanation – and it could potentially be a bomb under the magnetic inclination compass hypothesis.

Reverse orientation, i.e. orientation in approximately the opposite direction of the standard direction, is a common phenomenon. Reverse orientation is found in connection with low fat reserves of the migrants, with low plasma corticosterone levels, with an overcast and/or rainy sky, an overshoot in the migratory progress, or in case of headwinds – and in cases of inversions of the magnetic inclination (e.g. Rabøl 1967, 1983, 1985, 1994, 1995; Martin & Meier 1973; Geil et al. 1974; Lindström & Alerstam 1986; Wiltschko & Wiltschko 1995; Åkesson et al. 1996; Sandberg 2003; Giunchi & Baldaccini 2004).

Rabøl (1998b) distinguished between receptor- and motivation-mediated orientation, and when the Wiltschkos in one or another of their experiments inverted the magnetic field, and the orientation of the birds shifted c. 180°, it was interpreted as a receptor-mediated response: the receptor registered the inversion as a 180° shift in the compass reference. From this naturally follows the idea that birds are endowed with an inclination compass.

Another distinction could be between a rigid and a flexible response. In the present context the first means that the (intended) orientation is always in the standard direction, whereas the outcome of a flexible system depends on the circumstances and may be standard, reverse, or right angle orientation, or a combination. In the scenario of the Wiltschkos the reaction to an inversion of the inclination is a rigid response; the bird still performs standard orientation (or believes it does). Apparently, it never occurred to the Wiltschkos – or others – that perhaps the bird performed a motivation-mediated reverse response in reference to a magnetic polarity compass. But this scenario should not be dismissed as a serious alternative.

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

Short-term contra long-term magnetic deflections

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

Now, in almost all experiments the magnetic deflection was added as an about one-hour (short-term) "pulse" in a presumed sensitive period, or when tested during night or sunset/early night. After the funnel-testing the birds are returned to their cages in the natural magnetic field, i.e. magnetic N = geographical N. However, as far as I can see this is not the best way to do it; the optimal procedure in compass conflict experiments should be more nuanced, as the one presented here, where the experimentals are caged (and tested) all the time in the deflected magnetic field.

In my own magnetic pulse experiments (controls tested in deflected magnetic fields, and experimentals tested in the natural magnetic field) no influence of the magnetic compass was observed. Perhaps the strong effects of the pulse experiments by other people have something to do with their standard procedure; the birds are caged inside without exposure to celestial cues except when tested, or briefly just before the tests. In the experiments of ours the birds are caged outdoors all the time.

Some warnings and conclusions

In the present paper I play the popular game that migratory orientation in juvenile migrants is only a matter about compass orientation.

Migratory orientation may sometimes be best – and (almost) sufficiently – described within the complex of concepts known as compass orientation. In other cases it is best understood and described in terms of gradient navigation. Perhaps the reverse orientation in reference to magnetic N is best considered as a sort of navigatory response released by the discrepancy between the geographical and magnetic compasses (Table 1). And perhaps there is no active, reverse orientation in reference to magnetic N. An alternative scenario could be that the active compass is geographic/stellar N, and the orientation observed is a mixture between standard and right-angle orientation (to the right when magnetic N is deflected towards geographical W, and to the left when magnetic N is deflected towards geographical E). However, this scenario seems less parsimonious than the one of reverse orientation in reference to magnetic N.

It is also conceivable that the dominant geographic/stellar compass, claimed in connection with Fig. 4d and Fig. 5d, is an illusion, and the outcome is founded in stellar gradient navigation.

Part of the compass game is also that the concepts of calibration and dominance are legal and meaningful. In the first section of Material and methods and in Figs 1-3 is sketched and exemplified how outcomes of calibration and dominance will look like and manifest themselves.

The most powerful demonstration of compass calibration of the stellar compass by the magnetic compass would be as shown in Fig.1b, experimentals tested in the normal magnetic field during night. And here the results, shown in Fig. 4d and Fig. 5d clearly fail to support the hypothesis. Further, looking at the examples in Figs 2-3 it appears that a simple comparison between the sample mean vectors of the orientation in reference to geographic/stellar N and to magnetic N makes sense: The ratio between the concentrations mirrors the relative influences of the two compasses. Furthermore, the ratio could be signed positive or negative depending on the influential direction – standard or reverse. In the terminology of Table 1, the ratio in Fig. 2 is 1/2 and in Fig. 3 -2/1. Of course, these ratios should not be considered all too accurate. They are burdened with noise and just show rough and not necessarily significant tendencies.

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Resumé

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

Trækfugleforskerne tror på, at unge trækfugle har en normaltrækretning nedlagt i generne. Det må i så fald være i forhold til en ydre kompasreference, for en retning er ikke noget, der svæver frit i luften.

Hvilke kompasreferencer står til rådighed? Magnetkompasset en oplagt mulighed, og det samme gælder stjernekompasset: stjernehimlens rotations-punkt tæt ved Nordstjernen står hele tiden i N og er dermed en simpel kompasreference. En tredje mulighed er solen, der dog er noget kompliceret at bruge, da den bevæger sig med 15° i timen. Alligevel bruger mange dyr solen som kompas, således er den en vigtig kompasreference i brevduens navigationssystem. Solnedgangen og -opgangen er også mulige kompasreferencer – og især et gennemsnit af dem, fordi et sådant uanset årstid og breddegrad udstikker den geografiske N/S-akse.

Ved at udelukke muligheden for at bruge en eller flere af de nævnte kompasreferencer har man fundet ud af, at trækfugle kan bruge dem alle i fravær af de andre. Fugle, der vokser op uden at se solen og stjernerne, er således orienterede i normaltrækretningen, og denne kurs kan vises at være fastlagt i forhold til et magnetkompas. Nyere forsøg foretaget med Tornsangere *Sylvia communis* på Endelave tyder også på, at fugle, der vokser op i et ubrugeligt magnetfelt, har genetisk fastlagt deres trækretning i forhold til solen og/eller stjernerne (Rabøl & Thorup 2006).

Hvilket kompas er det primære i udviklingsforløbet og/eller det dominerende i den aktuelle situation? I mange år mente man – og især de tyske orienteringsforskere Roswitha og Wolfgang Wiltschko – at magnetkompasset var det primære, medfødte kompas, der så senere kalibrerede de andre kompasser (se Fig. 1). Senere resultater tydede imidlertid på, at stjernehimlens rotationspunkt var en mere primær kompasreference end magnetkompasset, og siden har Wiltschkoerne arbejdet hårdt på at få sidestillet magnetkompasset med stjernerotationskompasset, som de hævder kun giver N/S-information, mens magnetkompasset skulle være nødvendigt for at kunne følge en trækkurs afvigende fra stik S eller N. Ovennævnte Tornsanger-forsøg tyder dog ikke på, at den idé er holdbar.

Vi ved endnu ikke, hvordan fugle sanser magnetismen, men meget tyder på, at det sker gennem øjet.
Med hensyn til solnedgangen og solopgangen er det tilsyneladende ikke den lysende V- eller Ø-himmel i sig selv, der virker som kompasreference. Men især omkring solopgang og solnedgang er himlens lys polariseret, og kan man – som fuglene – se det, strækker der sig på disse tidspunkter et lysbånd fra N til S gennem zenit. Dette bånd kan bruges som kompasreference (selv om det ikke skelner mellem geografisk N og S).

Konfliktforsøg

For at forstå hvilket kompas, der er det kalibrerende/dominerende, er det oplagt at lave konfliktforsøg. Det er således nemt gennem kunstige magnetfelter at ændre på det magnetfelt, som fuglene sanser, og f.eks. dreje magnetisk N om i geografisk V. I planetarier har man mulighed for at dreje stjernehimlens rotationspunkt i forhold til magnetisk N, og gennem polarisationsfiltre kan man dreje solnedgangshimlens bånd af polariseret lys, så det ændrer retning i forhold til geografisk og magnetisk N/S.

Spørgsmålet er så, hvordan fuglene opfatter og reagerer på sådanne konflikter, der sædvanligvis i diverse forsøg har været unaturligt store (60° til 120°). I naturen skal vi til områder med kraftige magnetiske anomalier, eller tæt på den magnetiske nordpol, for at opleve meget store retningsforskelle mellem magnetisk og geografisk N. Ved unaturligt store kompaskonflikter vil fuglene evt. følge et af kompasserne og ignorere de andre, eller de kan lave et simpelt kompromis, men måske sker der noget helt tredje, f.eks. omvendt orientering i forhold til det ene af kompasserne.

Mine – og Sandbergs – forsøg

I efterårene 2001 og 2002 lavede jeg tragtorienteringsforsøg med unge Brogede Fluesnappere *Ficedula hypoleuca* og Rødstjerter *Phoenicurus phoenicurus.* Fuglene var fanget som trækgæster på Christiansø og derfra transporteret til Endelave. De blev anbragt i bure eller tragte udendørs i en skovlysning. Kontrolfuglene stod i det uforstyrrede, naturlige magnetfelt, mens forsøgsfuglene sad i bure anbragt i kunstige magnetfelter,

Fugle kan bruge forskellige kompasreferencer, f.eks. under trækket: Solen, stjernehimmelen, jordens magnetfelt, m.v. Flere forskere anser magnetfeltet som den primære reference, der kalibrerer de øvrige. Denne opfattelse kunne imidlertid ikke bekræftes under forsøg med fugle i afbøjede magnetfelter. Foto: Carl Erik Mabeck.

hvor den resulterende magnetiske vektor havde samme styrke og inklination (+70°) som i det naturlige jordfelt, men hvor magnetisk N vendte mod Ø (fire felter) eller V (andre fire felter). Fuglene havde normalt adgang til at se Solen og stjernehimlen både i burene og i tragtene, hvor de blev testet en ad gangen.

Formålet med forsøgene var især at eftergøre et forsøg af Sandberg et al. (2000), der for amerikanske nattrækkere, især Rødøjet Vireo *Vireo olivaceus*, konkluderede, at magnetkompasset ved solnedgang/tidlig nat kalibrerede stjernekompasset, der så var det kompas, fuglene tog kurs efter under det senere nattræk. Sandberg og medarbejdere tragt-testede først fuglene inden for de drejede magnetfelter, og senere samme nat slap de fuglene løs med et lysmærke i halen og noterede bortflyvningsretningerne. Fuglene i tragtene, hvor magnetfeltet ved solnedgang og tidlig nat var drejet Ø eller V, havde en henholdsvis højre- eller venstredrejet aktivitet i forhold til kontrollerne, der opholdt sig i det naturlige magnetfelt. Denne drejede orientering gik igen i bortflyvningsretningerne om natten (i det naturlige magnetfelt), og den rimelige konklusion var, at stjernekompasset i tragtene ved solnedgang/tidlig nat var blevet kalibreret af det drejede magnetfelt (via et drejet magnetkompas hos fuglen), og at den drejede orientering senere på natten blev fastholdt i forhold til stjernekompasset, mens informationerne fra magnetkompasset nu blev ignoreret.

Jeg gentog disse forsøg, dog således, at fuglene blev testede i tragte om natten efter at have tilbragt solnedgang/tidlig nat i deres bure, så jeg kender faktisk ikke deres orientering i denne første fase. Kontrolfuglene blev normalt (otte gange) tragttestede i det naturlige magnetfelt, men jeg undersøgte også tre gange deres orientering i de Ø- eller V-drejede magnetfelter. Forsøgsfuglene blev normalt (ni gange) tragttestede i de Ø- eller V-drejede felter, men også (fem gange) i det naturlige magnetfelt. Specielt den sidste konstellation er interessant, fordi den i princippet svarer til, hvad Sandberg gjorde, og på Fig. 1 er vist, hvordan natorienteringen i mine forsøg burde falde ud efter en magnetisk kalibrering solnedgang/tidlig nat. Jeg fandt dog ingen spor af en sådan kalibrering (Fig. 4).

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

I forsøgene ses dog dominans af et magnetkompas i fire nætter ud af de ni, hvor forsøgsfuglene blev tragttestede i de Ø- eller V-drejede magnetfelter (se Tabel 1). I alle disse tilfælde – og i øvrigt generelt for testene i et Ø- eller V-drejet magnetfelt – er orienteringen imidlertid omvendt i forhold til normaltrækretningen. Dette resultat var højst uventet. Men omvendt træk/orientering optræder ganske ofte, især under bestemte omstændigheder såsom udtømte fedtdepoter hos fuglene, overskyet himmel, efter forlænget forårstræk, i forbindelse med modvindstræk, samt efter invertering af magnetfeltets hældning (inklination). Omvendt træk menes i de fleste tilfælde at have overlevelsesværdi i den pågældende situation, dog er omvendt orientering i forbindelse med en invertering af inklinationen blevet opfattet som en effekt af den måde, fuglene sanser magnetfeltet på.

Forskellige stjernekompasser

En nøjere granskning af resultaterne tyder på, at et eller flere stjernekompasser bruges til at fastlægge og/eller fastholde kursen. Det vigtigste – og det der formentlig fastlægger kursen – er stjernehimlens rotationspunkt (også kaldt rotational N, celestial (stellar) rotation eller Nordstjernen (*Polaris*)). Et andet, som man f.eks. kunne kalde sydhimmelkompasset, er baseret på sydhimlens stjerner; disse bevæger sig fra øst over syd mod vest, så fuglene skal huske at korrigere med 15° i timen. Jeg har kaldt et sådan kompas for et "time-compensated stellar S compass" og gætter på, at det bruges almindeligt af trækfugle om efteråret, når de har kursen rettet mere eller mindre mod stjernen på sydhimlen. En gang imellem bliver det formentlig så kalibreret af Nordstjernekompasset.

Det kalibrerende solnedgangskompas

Cochran et al. (2004) lavede forsøg med amerikanske skovdrosler *Catharus* spp., der udstyret med radiosendere blev sluppet fri om natten efter at have tilbragt solnedgang/tidlig nat i et bur, der befandt sig i et magnetfelt, der var drejet 90°. Forsøget lignede altså meget det af Sandberg et al. (2000), men resultatet var ganske anderledes: der var klare tegn på, at nattrækket blev styret af et magnetkompas, der forudgående var blevet kalibreret af et solnedgangskompas. På linje med Cochran et al. har Muheim et al. (2006a,b) fundet, at det ikke er magnetkompasset, der i solnedgang/tidlig nat fasen kalibrerer solnedgangs- og eller stjernekompasset, men derimod et gennemsnit mellem solopgangs- og solnedgangskompasset, der kalibrerer magnetkompasset (og stjernekompasset). Muheim et al. (2006a,b) hævder, at det er essentielt for den styrende kalibrering fra solnedgangs/opgangskompasset, at der har været frit syn fra bure/tragte ned til horisonten. Den af Wiltschkoerne og andre (herunder Muheim og Åkesson) fundne styrende kalibrering fra magnetkompasset skulle ifølge denne opfattelse være et forsøgsartefakt forårsaget af horisontafskærmning af bure eller tragte i solnedgangs/tidlig nat-fasen.

Sidste nyt fra Christiansø og konklusion

Sidste nyt er forsøg af mig på Christiansø i efterårene 2006, 2007 og 2008, hvor der i lighed med forsøgene på Endelave 2001-2002 ikke kunne påvises kalibrering fra hverken magnet- eller solnedgangskompasset, heller ikke efter uhindret udsyn ned til horisonten ved solnedgang/tidlig nat. Fuglene, der alle var fanget samme eller foregående dag, tog åbenbart kurs efter stjernerne uden forudgående kalibrering fra andre kompasser.

Man skulle tro, at det var nemt at finde ud af hvilke kompasser, der dominerer og/eller kalibrerer de andre kompasser. Men det er det ikke; forskellige forskere får forskellige resultater, og det er derfor umuligt at generalisere og sige, at nattrækkende småfugle gør sådan og sådan. Problemet er endvidere, at fuglene ofte laver noget andet og mere end den rene og simple kompasorientering. Efter min opfattelse forsøger de også at navigere, dvs. at målrette deres kurs. Endelig behandler og tester forskerne deres fugle forskelligt og ofte – omend ubevidst – på en måde, så deres forventninger til, hvad der skal ske, opfyldes i størst mulig grad.

Hvad der kan siges med sikkerhed, er, at feltets ledende forskere (Wiltschkoerne, Muheim, Åkesson) har været for tidligt ude med deres generaliseringer, samt at både magnetfeltets og solnedgangens indflydelse er overvurderet. Men det er jo sådan set bare den sædvanlige historie indenfor forskningsverdenen, beskrevet så udmærket af Platt (1964): paradigmeholderne bliver så forelskede (det skriver han faktisk) i deres yndlingshypoteser, at de er blinde og døve over for alternative og mere nuancerede fortolkningsmuligheder.

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Appendix on p. 102

Appendix

Complete list of vector directions of each of the birds (degrees, with N = 360º; degree symbols º are omitted). Sometimes a major peak was found in a bi- or tri-modal pattern, shown as e.g. 245/(45), and sometimes two almost equal-sized peaks occurred, e.g. 180/320. DIS means dis-orientation, zero means no activity, - means no experiment; W and E mean magnetic N deflected towards W and E, respectively, during the funnel-testing. Where magnetic N was deflected, the given angles should be transformed when depicted in relation to magnetic N (by adding (E) or subtracting (W) 45º) or in relation to geographical (stellar) N (by adding (E) or subtracting 135º (W)).

As an example, control-bird **16B** oriented towards 70º on 11 September 2001, towards 120º on 13 September, towards 240º on 14 September, and towards 180º on 23 September; on 26 September the bird was tested within a magnetic field where magnetic N of the resultant field was deflected towards geographical W; here the orientation was 35º (80º-45º) in reference to magnetic N and -55º (=305º; 80º-135º) in reference to geographical N. The bird was not tested on 15 or 16 September.

Species tested were Pied Flycatcher *Ficedula hypoleuca* (all birds in 2001, and all birds in 2002 with F as the first letter of the identifier) and Redstart *Phoenicurus phoenicurus* (all birds in 2002 with R as the first letter of the identifier). Birds RB11, R11, and R12 were adults, all other were juveniles.

2001 (11, 13, 14, 15, 16, 23 and 26 September)

Controls

16B: 70, 120, 240, - , - , 180, W 80, **16**: 30, 260, 120, - , W 20, 195, W 330, **18B**: 220, 150, 20, - , - , 180, - , **18**: 160, 190, 215, - , W 15, 230, - , **19B**: 60, 315, 200, - , W 75, 250, W 60, **19**: 245/(45), 90, 100, - , W 50, 165, W 300/105, **2B**: 250, 220, 205, - , E 75, 230, - , **2**: 240, 120, 75, - , E 50/(250), 240, - , **5B**: 105, 60, 85, - , E 70, 165, E 75/260, **5**: 225, 290, DIS, - , - , 240, E 100, **15B**: DIS, 120, 150, - , - , 180, E 80, **15**: 125, 340, 105, - , E 95, 220, E 105.

Experimentals

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

2002 A (8 and 9 September)

In birds **F17** (8 Sep) and **R17** (9 Sep), 75º has to be added instead of 45º, and 120º instead of 135º (because within this coil field the resultant magnetic N was only deflected towards geographical NE).

Controls

FB15: 200, 235, **F15**: 210, 170, **FB16**: 140, 200, **F16**: 360/190, 210, **RB20**: 105, DIS, **R20**: 135, DIS, **R19**: 290, 200.

Experimentals

RB3: W 285, 100, **R3**: 170/(360), W 60, **FB12**: W 75, 255, **F12**: 250, W 10, **FB14**: W 50, 270, **F14**: 280, W 60, **F11**: W 330, 200, **R11**: DIS, W DIS, **RB10**: E 50, zero, **R10**: zero, E DIS, **F17**: E 60, 220, **R17**: 120, E 5, **FB8**: E 70, 200, **F8**: 215, E 70, **FB18**: E 70, 205, **F18**: 195, E DIS.

2002 B (12, 13 and 14 September)

In birds **FB5** (12 Sep) and **F5** (13 Sep), 75º has to be added instead of 45º, and 120º instead of 135º.

Controls

FB1: 120, 45, W 120, **F1**: 190, 105, W 215, **FB2**: 85, 85, E 290, **F2**: 130, 180, E 65, **FB7**: 230, 210, W 280, **F7**: 240, 110, W 285, **RB11**: 135, 90, - , **R11**: 170, 140, - , **RB12**: - , 100, - , **R12**: - , 100, - , **RRG**: 90, 225/(60), E 50, **RG**: 150, 220, E 50, **R18**: - , 125, - , **F18**: - , 140, - .

Experimentals

FB19: W 45, - , 195, **F19**: - , W 315, 190, **FB6**: W 15, - , 145, **F6**: - , W 310, 150, **RB13**: W 10, - , 185, **R13**: - , W 285, 145, **RR15**: W 80, - , 160, **R15**: - , W 330, 155, **RB20**: E 260, - , 110, **R20**: - , E 240, 105, **FB5**: E 350, - , 130, **F5**: - , E 40, 185, **FB4**: E 360, - , 170, **F4**: - , E 360, 175, **RB8**: DIS, - , 200/(35), **R8**: - , E 90, 205.