

Night and sunset/early night experiments in magnetic fields where magnetic N was shifted towards geographical E or W. Conflicts between the magnetic compass and the sunset- and star compasses

Introduction

The purpose was a repetition of the 2006 experiments on Christiansø (Rabøl 2006, doc.Dron06b www.jorgenrabol.dk). In the 2006 experiments we found no signs of compass calibrations in the sunset/early night phase. Furthermore, in most cases a stellar compass apparently dominated the magnetic during night.

Material and methods

In order to avoid directional influence from one control funnel to the nearest neighbor we abandoned the use of eight funnels per board, and only four funnels were used per board (Fig.1). The nearest distance from one funnel to a neighbor was about 50 cm (edge to edge), or about 80 cm (center from one funnel to center of neighbor funnel). Now, no directional influence was found between the funnels. On the board (60 cm times 240 cm) the four funnels (diameter 30 cm) are seen from above.

As also reported in Rabøl (2006) the tree-frames of the magnetic coil fields in particular influenced the sunset/early night orientation in such a way that the long axis of the frame acted as a kind of “leading line”. As shown on Fig.2 an **additional tree-frame** was added to the tree-frame of the coil field changing the bilateral symmetry as seen from the sight of the bird in the funnel to radial symmetry, and as reported below the spurious directional influence of the frame-system was outfoxed by applying this corrective frame. On the additional tree-frame was mounted 37 cm long “legs” hanging down in each of the four corners – in order to outfox the four “legs” of the coil frame. The dimensions of the frames are 45 cm times 80 cm. The example shown is one of the coil fields where magnetic N of the resultant field was pointing W. However, corrective tree-frames were first added during the last two sunset/early-night experiments on 21 and 22 Sep.

On five nights/sunset (16 Sep., 18 through 22 Sep.) collars of a non-magnetic metal were placed on tops of the funnels (Fig.3). The diameter of the collars was a little more than the funnel diameter (30 cm), and the height 8 cm cutting about 30° of the lower sky as seen by a bird high up in the middle of the funnel. If the bird’s eyes are situated close to the outer edge and high up in the funnel only the lower about 20° of the (opposite) sky is screened away.

Otherwise, the procedure was as described by Rabøl (2006).

Results

On 10 night/sunsets we performed these conflict experiments involving a total of 160 birds.

The experiments fall in some natural groups depending on the treatment, time (night or sunset), cloudiness, and application of collar or not. A short discussion of the results is given in each section.

Night experiments

On the four **nights** of 9, 12, 16 and 18 Sep. experiments were carried out with Robins *Erithacus rubecula* under a clear **starry** sky. The controls were tested in the undisturbed magnetic field, and the exp.s under the deflected sky. On the last two nights collars were applied in half of the birds (both controls and exp.s – two for magnetic N deflected towards W, and another two for magnetic N deflected towards E). The results are shown at Fig.4: The orientation of the **controls** are denoted on Fig.4A: The sample mean vector is $201^\circ - 0.591^{***}$ ($n = 27$). The orientation of the **exp.s** in reference to paper N (Fig.4B) is $345^\circ - 0.205$ ($n = 24$), or after doubling the angles $95^\circ/275^\circ - 0.338^*$ ($n = 28$), i.e. it looks like the frame has some “leading line” effect on the pattern. The orientation of the exp.s in reference to **geographical N** is significant (Fig.4C): The sample mean vector is $146^\circ - 0.487^{**}$ ($n = 24$). On the contrary, the orientation of the exp.s in reference to **magnetic N** (Fig.4D) is not significant: The sample mean vector is $159^\circ - 0.198$ ($n = 24$). In conclusion, **geographical N seems to be the compass reference in charge**. However, the directions of the sample mean vectors (Fig.4A contra Fig.4C) differ significantly (M-W-W test, Chi-square = 6.52, $P < 0.02$). The reason for the discrepancy is probably not (only) spurious influence of the frames, but has something to do with the compass conflict leading a more basic response than stereotype orientation in the standard direction (and/or involvement of an escape response on right angles to the standard direction).

The effect of the **collars** on the **night** orientation of Robins was studied on the two **starry** nights of 16 and 18 Sep.(Fig.5). The sample orientation of the **non-collar controls** was $212^\circ - 0.973^{***}$ ($n = 8$), whereas the **collar controls** (Fig.5A) were insignificantly oriented though in about the same direction ($196^\circ - 0.436$, $n = 7$).

The orientation of the **exp.s** was – apparently, because all mean vectors were non-significant – 1) steered by a celestial (probably stellar) compass (Fig.5B compared with Fig.5C), and addition of collars elicited a right angle response (Fig.5B, upper distribution compared with lower distribution). The sample mean vectors of Fig.5B were: Non-collars $189^\circ - 0.549$ ($n = 6$), and collars $98^\circ - 0.679$ ($n = 6$), and of Fig.5C: Non-collars $310^\circ/130^\circ - 0.466$ ($n = 7$), and collars $157^\circ/337^\circ - 0.149$ ($n = 6$).

Collars apparently increase the directional scatter (and perhaps leads to a right angle response, B) but there seems to be no shift towards more influence of the magnetic compass.

On 13 Sep. we performed a single **cross experiment**, i.e. the exp.s spending the sunset/early night in the cages within the deflected magnetic fields were transferred to and tested in the funnels in the normal magnetic field during **night**, whereas the opposite treatment was used in case of the controls. The sunset/night **was** clear/starry. The orientations are denoted on Fig.6.

The exp.s tested in the normal magnetic field showed standard orientation, although the pattern is slightly bimodal (Fig.6A: $203^{\circ}/23^{\circ} - 0.768^*$, $n = 7$). Clearly, there was no calibration by the magnetic compass in the sunset/early night phase. If so the pattern should be bimodal with the peak of the W-exp.s in SE and of the E-exp.s in NW.

In the controls tested in the deflected fields there seems to be no or only slight spurious directional influence of the frames (Fig.6B: $244^{\circ}/64^{\circ} - 0.510$, $n = 6$). The orientation of the controls is not easily deduced: it might be standard/reverse in reference to geographical N (Fig.6C: $218^{\circ}/38^{\circ} - 0.493$, $n = 6$), i.e. steered by a celestial probably stellar compass), or a right angle response steered by the magnetic compass (Fig.6D: $140^{\circ} - 0.814^*$, $n = 6$).

Two further night experiments were carried out, both under an **overcast night sky**. As the directional patterns looked different the two nights are considered separately.

11 Sep., the sunset/early night was only partly covered, i.e. both sunset and part of the starry sky were available. However, during tests in the funnels the sky was totally covered. The orientation of the controls seems slight bimodal but most are in about the standard direction (Fig.7A: $218^{\circ}/38^{\circ} - 0.498$, $n = 4$). Fig.7B and 7C show the orientation of the exp.s in reference to geographical N and magnetic N, respectively. The sample mean vectors are $150^{\circ} - 0.636$ ($n = 7$) and $160^{\circ} - 0.612$ ($n = 7$), respectively. It is not easy to deduce which of the compasses are most influential. Anyway, there is an insignificant deflection towards E in both compared with the controls (as described above in other conflicting constellations).

18 Sep., both sunset/early night and night were totally overcast. The orientation of the controls were in about the standard direction, and possibly somewhat co-influenced of a positive photo-taxis towards the light from the lighthouse (Fig.8A, $272^{\circ} - 0.778^*$, $n = 6$). The orientation of the exp.s was probably under the influence of a phototaxis established in reference to geographical N (Fig.8B: $307^{\circ} - 0.892$, $n = 6$), compared with Fig.8C: $43^{\circ}/223^{\circ} - 0.677$, $n = 6$). The difference between the controls and the exp.s in reference to geographical N is not quite significant on the 0.05 level applying the M-W-W test (Chi-square = 5.16 (however, an W-W test should be tried as the strict condition for using this test seems present, both r above 0.75). Nevertheless, the photo-taxis seems stronger in case of the compass conflict, probably adding up to the general observation of a departure from normality during conflicting/inferior conditions.

Sunset/early night experiments

21 and 22 Sep. **sunset/early night** experiments were carried out under **clear sky** conditions and under application of compensatory tree-frames (Fig.2). As collars (Fig.3) was also applied in half of the birds the results (Fig.9) are rather detailed. Fig.9A shows the orientation of the controls: Both distributions look slightly bimodal, and in fact

doubling the angles describes better for the non-collar distribution: $249^\circ/69^\circ - 0.371$ ($n = 6$). In the collar distribution doubling the angles lead to a slightly smaller concentration, and the sample mean vector is $233^\circ - 0.387$ ($n = 8$). If the two distributions are combined doubling the angles leads to the higher concentration: $242^\circ/62^\circ - 0.333$ ($n = 14$). Summing up, the controls seem to be oriented on about the standard/reverse axis with most orientations in the standard direction (which in the Robins involved should be about 215° according to recoveries of migrants banded on Christiansø).

Fig.9B shows the orientation of the exp.s in reference to paper N, and the conclusion of mine is that the spurious influence of the tree-frames disappears – or at least the “westerly” peak does. The sample mean vectors are: $60^\circ/240^\circ - 0.609^*$ ($n = 8$) for the non-collar birds, and $104^\circ - 0.431$ ($n = 8$) for the collar birds.

Fig.9C shows the orientation of the exp.s in reference to geographical N, and the sample mean vector of the non-collar birds is $275^\circ - 0.464$ ($n = 7$), and of the collar birds $288^\circ - 0.578$ ($n = 8$). Obviously there seems to be no difference and summing the two distributions leads to $283^\circ - 0.522^*$ ($n = 15$).

Fig.9D shows the orientation of the exp.s in reference to magnetic N, and the sample mean vector of the non-collar birds is $180^\circ/0^\circ - 0.363$ ($n = 8$), and of the collar birds $40^\circ/220^\circ - 0.293$ ($n = 8$). Summing the two samples leads to $17^\circ/197^\circ - 0.258$ ($n = 16$).

Finally, Fig.9E denotes the orientation of the exp.s in reference to geographical N if distinguishing between birds where magnetic N was deflected towards W or E, respectively. Clearly, there seems to be no difference: The sample mean vector of the W-birds is $292^\circ - 0.573$ ($n = 7$), and of the E-birds $274^\circ - 0.489$ ($n = 8$).

Considering Figs.9A, C, D and E together geographical N seems to be the compass reference in charge.

Finally, Fig.10 shows the **sunset/early night** orientation under the **overcast** condition of 20 Sep. The orientation of the controls (Fig.10A) looks a little bimodal. However, doubling the angles leads to a slightly smaller concentration ($295^\circ/115^\circ - 0.514$, $n = 6$), compared with the untransformed calculation: $246^\circ - 0.539$ ($n = 6$). Fig.10B indicates that the rectangular tree-frame (which was not compensated on this occasion) had a spurious directional effect. The sample mean vector is $280^\circ/100^\circ - 0.580$ ($n = 8$). Fig.10C and 10D show the orientation of the exp.s in reference to geographical N ($110^\circ - 0.258$, $n = 7$) and magnetic N ($173^\circ - 0.300$, $n = 7$), respectively. Clearly the orientations look random and it is difficult to say anything about the compass reference in charge. We should expect magnetic N to be the one, but clearly the resemblance to Fig.10A is not good.

Discussion

The general observations/conclusions are that

1) geographical N under both starry night and clear sunset/early night conditions seems to be the compass reference in charge (compared with magnetic N). This (probably) means that a stellar compass or a sunset compass, respectively, is dominant compared with a magnetic compass.

2) There is no calibration of the stellar compass by the magnetic compass in the sunset/early night phase.

3) Collars probably increase the directional scatter during starry nights but not during clear sunsets.

4) As found in autumn 2006 (doc. Sunset in www.jorgenrabol.dk) the rectangular tree-frames forces a strong directional pressure (bimodal/axial, along the long axis of the rectangle) on the sunset/early night orientation, whereas the influence on the night orientation is lacking or at least much less obvious. Application of a rectangular tree-frame at right angles to the coil frame (Fig.2) results in a disappearance of this spurious orientation.

Other papers on conflict between celestial and magnetic compasses

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

With supporting online material

www.sciencemag.org/cgi/content/full/313/5788/837/DC1

We show that migratory Savannah Sparrows used polarized light cues from the region of sky near the horizon to recalibrate the magnetic compass at both sunrise and sunset. We suggest that skylight polarization patterns are used to derive an absolute (i.e., geographic) directional system that provides the primary calibration reference for all of the compasses of migratory songbirds

The paper was much discussed in animal-forum-owner@rin.org.uk in August-Sept. 2006; in particular there was an at times rather heated discussion between William W. Cochran and John B. Phillips.

Cochran objected that the conclusions of the paper were not met by the results. In particular, he found no evidence for averaging SS and SR was the primary compass reference in all birds, and not even in the Savannah Sparrows.

The general conclusion of mine is that there is a crude indication that polarized light cues calibrate the magnetic compass – under the circumstances and in the species investigated. How this finding relates to the natural/free-flying condition is not easy to know. Influence from the stellar sky was not investigated, and the authors play the usual game, that only a compass orientation system is involved. However, true navigation is probably also involved in the migratory progress of the birds. As almost always I wonder about authors of a (so called) scientific paper who present and modify their data to the maximal degree of fitting their favorite hypothesis – instead of trying to understand what is going out there in the real and natural world.

I wonder about why the authors are not testing the difference between the two bimodal distributions in Fig.1E (in particular, because they tested the difference between the two Fig.1D samples). The axial difference is only 9° and certainly far from significant (I tried several relevant tests). I also wonder about (Fig.1E) the "*triangles outside circles (which) give predicted responses for a +/-90° shift in BMP relative to the natural SR and SS position*". It is impossible to understand Fig.1E, and the authors do not understand it

themselves. It is just some kind of witchcraft. There too many implicit unclear assumptions.

I have some comments on Table S1.

Following doubling the angles the concentration **at sunset** is 0.61 and not 0.58.

I am not too happy about the procedure focusing on birds only with an initial orientation of $135^\circ \pm 90^\circ$. The problem is obvious in the sunset experiments where 16 out of 36 birds are omitted, and the sample concentration of the 36 birds must had been close to zero. Furthermore, we do not know the within and between individual variation. The implicit message in the way of treatment is, that all variation is between-individuals, but if so the variation is all too large for a vector-orientation programme. If on the other hand all the variation is within-individuals then the variation is all too high and we need the means of many initial orientations and many responses after exposures in order to obtain a useful figure for the deviation from the initial response.

I considered the sample distribution of the 14 birds both tested SS and SR. The mean vector is $-2^\circ - 0.58^{**}$. Thus the concentration is surprisingly low compared to the concentrations of SS and SR after doubling the angles (0.61 and 0.54). As we all know doubling the angles reduces the concentration very significantly. So perhaps this is an indication that the polarizing filters in some way strengthens the reactions or make them somewhat spurious.

Instead of focusing on $135^\circ \pm 90^\circ$ it would had been more natural to focus on $135^\circ \pm 45^\circ$, and $315^\circ \pm 45^\circ$ as bimodal patterns along the standard/reverse axis is to be expected (and is also found in Fig.1E).

Furthermore, in Table S2 data are given for 6 individuals tested without access to visual cues near the horizon. Here all initial directions are in use, but only a single is within the demands of Table S1, i.e. $135^\circ \pm 45^\circ$. As the conclusions reached on the basis of tables S1 and S2 is far-reaching this is simply bad and insufficient "science". Furthermore, if considering the last initial response in Tab.S1 compared with the initial response in Tab.S2 there is no connection (the subtractions are -35° , 85° , -100° , -70° , -130° , and 150°). The mean vector is not significant. How can these initial directions be used when not consistent?

I have some more general points.

I can understand that averaging the polarized light patterns at SR and SS is a possible way to find true geographical N, but it seems much easier to me to take a look at the starry sky and make use of Polaris. It seems very easy to calibrate the magnetic compass by means of Polaris. But I know people are mostly interested in polarized light patterns and the magnetic field, not in the starry sky, which is almost never given a fair chance of directional establishment in their experiments.

I also wonder about why the authors have not shifted the magnetic field instead of the polarized light patterns. In this way the natural, undisturbed sky could be used, and we should expect unimodal instead of bimodal orientations in the experiments. I also wonder about whether the quadratic boxes in some spurious way enforced the bimodality at right angles.

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. DOI 10.1007/s 10336-07-0187-4

More or less the same as already reported/discussed by Muheim et al. (2006).

I tested a suspicion that the procedure with the selection of orientations in the half circle between NE over E and S to SW produced a spurious “E/W”-response if the directional differences were plotted. Apparently, no such spurious pattern (but a random distribution) occurs.

When inspecting Fig.1 it is clear, that the selection of the orientations in the half circle (A, upper left) is an invalid procedure – unless the **between** individual variation is very much higher than the **within** individual variation. And the large variation in “Magnetic orientation after exposure” and the small (bimodal) variation in “Deviations from initial response” are compatible with such a scenario. However, I have problems with this scenario – recall that 16 out 36 initial orientations were selected against because they were situated in the opposite half circle – this is an all too high natural between individual variation.

I have some further comments: 1) Referring to Weindler et al. (1996, 1997) Muheim et al. apparently buy the remarkable proposal that “ - - *the star compass by itself only seems to contain information about the geographic north-south axis, requiring magnetic compass information to establish the population-specific migratory direction*”. This hypothesis tested by Rabøl & Thorup (2006) under the natural starry sky (Weindler et al. used the artificial (and in the test-phase, stationary “16-dots-starry-sky”) could not be confirmed. 2) Muheim et al. used **rectangular** instead of quadratic card board boxes adding to the possibilities of spurious responses induced by the artificial polarized pattern of the lower part of the sunset sky.

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

Rabøl, J. & K. Thorup 2006: Migratory direction established in inexperienced bird migrants in the absence of magnetic field references in their pre-migratory period and during testing. – Ethol Ecol Evol 18: 43-51.

Weindler, P., Wiltschko, R. & Wiltschko, W. 1996: Magnetic information affects the stellar orientation of young bird migrants. – Nature 383, 158-160.

Weindler, P., Baumetz, M. & Wiltschko, W. 1997: The direction of celestial rotation influences the development of stellar orientation in young Garden warblers (*Sylvia borin*). – J. Exp. Biol. 200, 2107 – 2113.

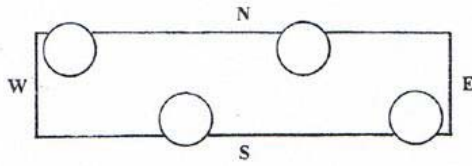


Fig.1: A control table (60 times 240 cm) seen from above with four funnels.

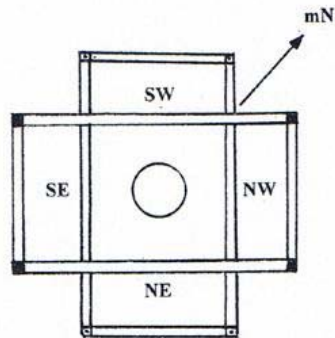


Fig.2: A tree-frame (45 times 80 cm, long axis SE/NW) with magnetic coils as seen from above with a funnel in the middle. The four small black quadrates symbolize the 80 cm long “legs” directed downwards (into the paper) for connecting with the lower part of the tree-frame resting on the table. An additional tree-frame (without coils, long axis SW/NE) was fitted into the coil tree-frame as shown. The dotted crosses symbolize four “legs” (37.5 cm) directed downwards (into the paper). These arrangement turns a bilateral symmetry as seen by a bird in a funnel into radial symmetry.

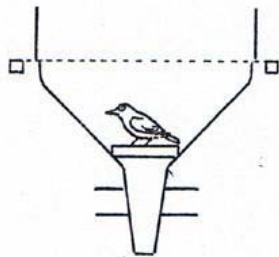


Fig.3: A funnel with 8 cm high collar screening for a horizontal view of the sky.

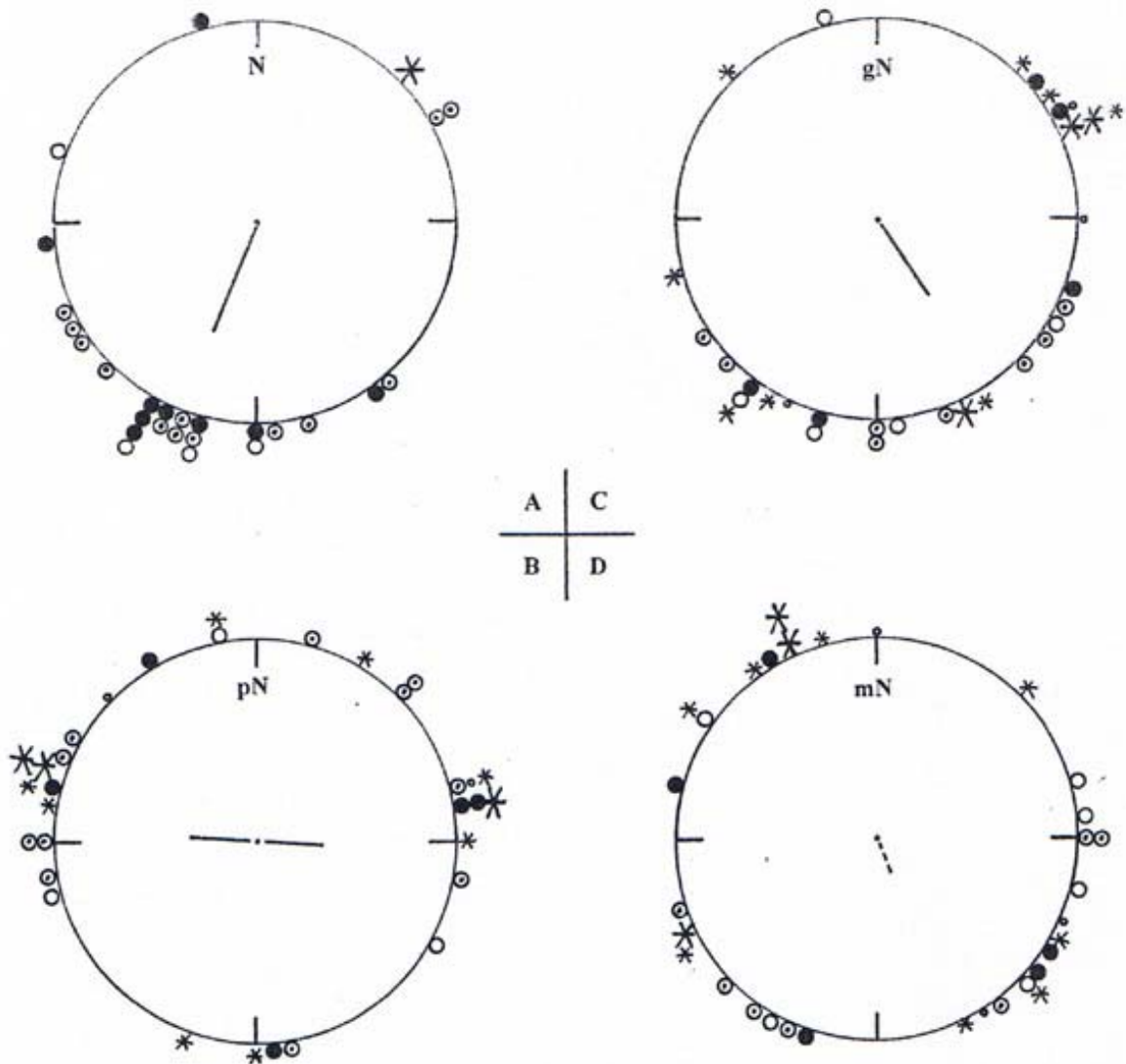


Fig.4: On 9, 12, 16 and 18 September experiments were carried out in under a clear **starry** night sky. The controls were tested in the undisturbed magnetic field, and the exp.s in the deflected magnetic fields. The orientation of the **controls** are denoted on Fig.4A: The sample mean vector is $201^\circ - 0.591^{***}$ ($n = 27$). The orientation of the **exp.s** in reference to **paper N** (Fig.4B) is $345^\circ - 0.205$ ($n = 24$), or after doubling the angles $95^\circ/275^\circ - 0.338^*$ ($n = 28$). The orientation of the exp.s in reference to **geographical N** is significant (Fig.4C): The sample mean vector is $146^\circ - 0.487^{**}$ ($n = 24$). The orientation of the exp.s in reference to **magnetic N** (Fig.4D) is not significant: The sample mean vector is $159^\circ - 0,198$ ($n = 24$).

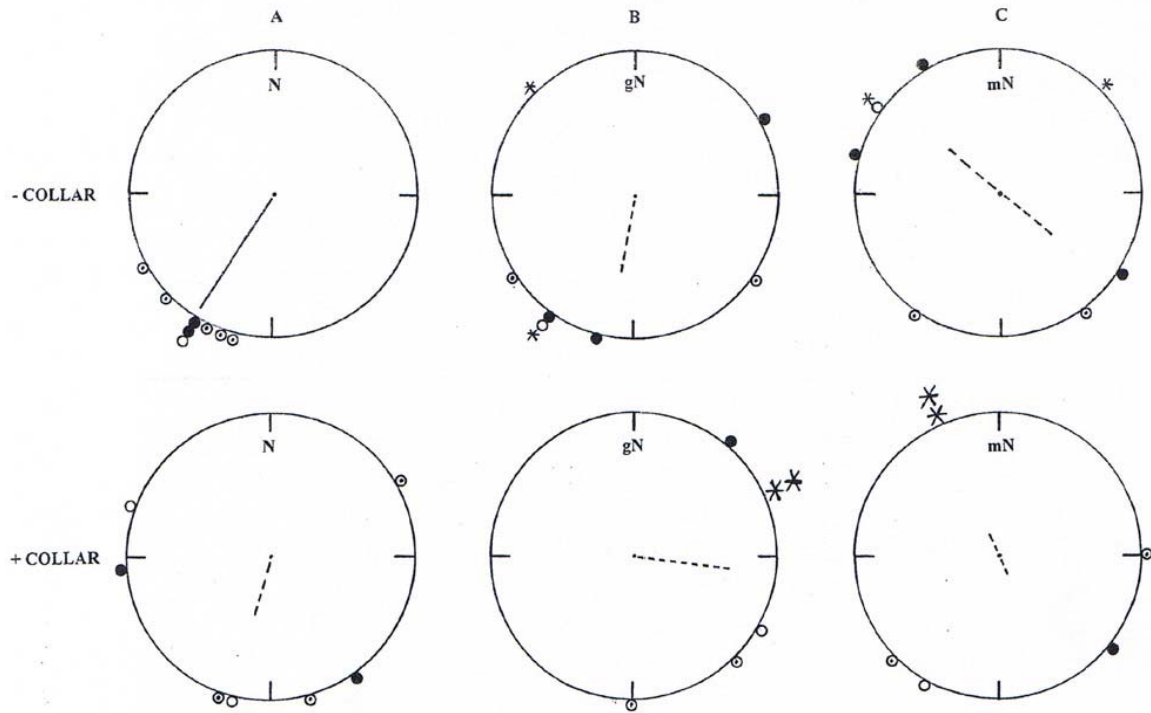


Fig.5: The effect of collars on the two starry nights of 16 and 18 September. The sample orientation of non-collar controls was $212^\circ - 0.973^{***}$ ($n = 8$), whereas collar controls (A) were insignificantly oriented: $196^\circ - 0.436$ ($n = 7$). The sample mean vectors of the exp.s were: B (in reference to geographical N = gN) Non-collars $189^\circ - 0.549$ ($n = 6$), and collars $98^\circ - 0.679$ ($n = 6$), and C (in reference to magnetic N = mN) Non-collars $310^\circ/130^\circ - 0.466$ ($n = 7$), and collars $157^\circ/337^\circ - 0.149$ ($n = 6$).

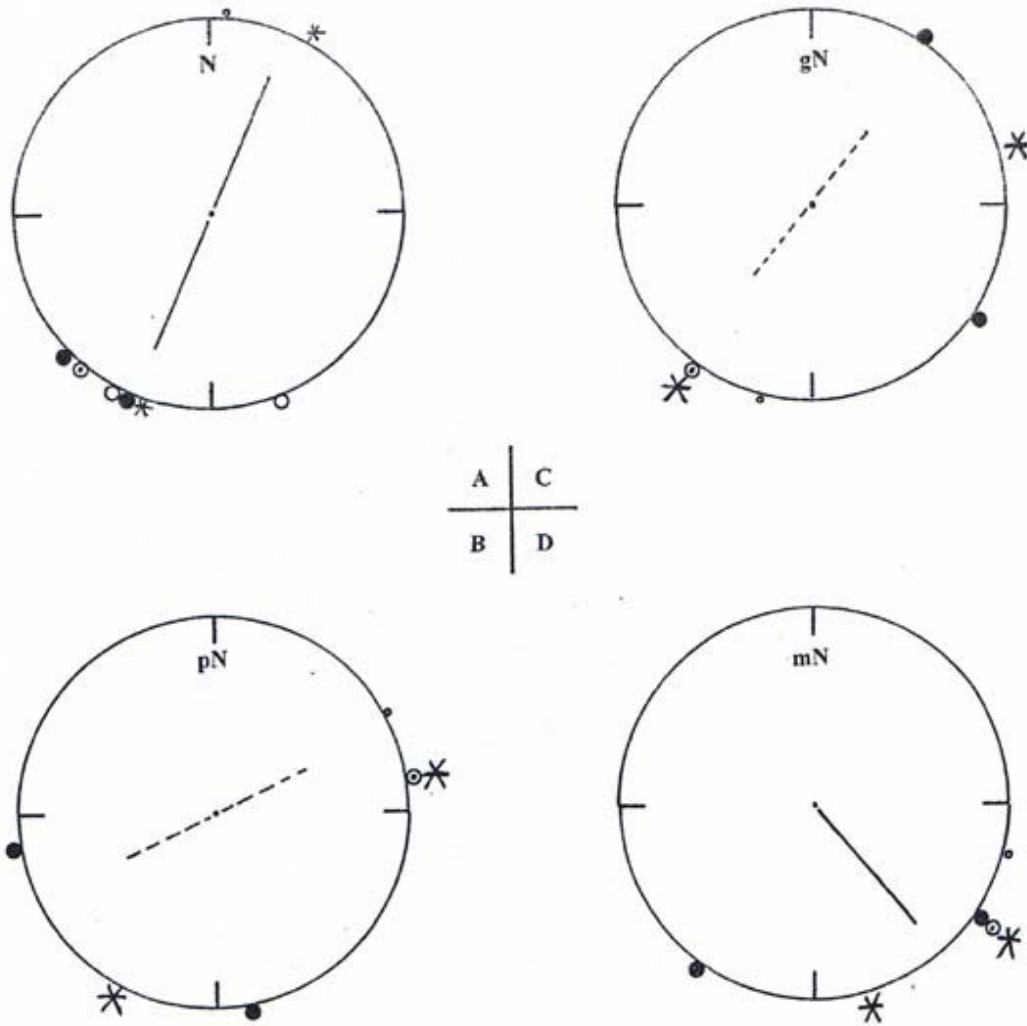


Fig.6: The cross experiment on 13 September. The exp.s tested in the normal magnetic field showed standard orientation, although the pattern is slightly bimodal (A: $203^\circ/23^\circ - 0.768^*$, $n = 7$). Concerning the controls tested in the deflected magnetic fields there seems to be no or only slight spurious directional influence of the frames (B: $244^\circ/64^\circ - 0.510$, $n = 6$). The orientation of the controls in reference to geographical N is shown in C: $218^\circ/38^\circ - 0.493$, $n = 6$, and in reference to the magnetic compass in D: $140^\circ - 0.814^*$, $n = 6$.

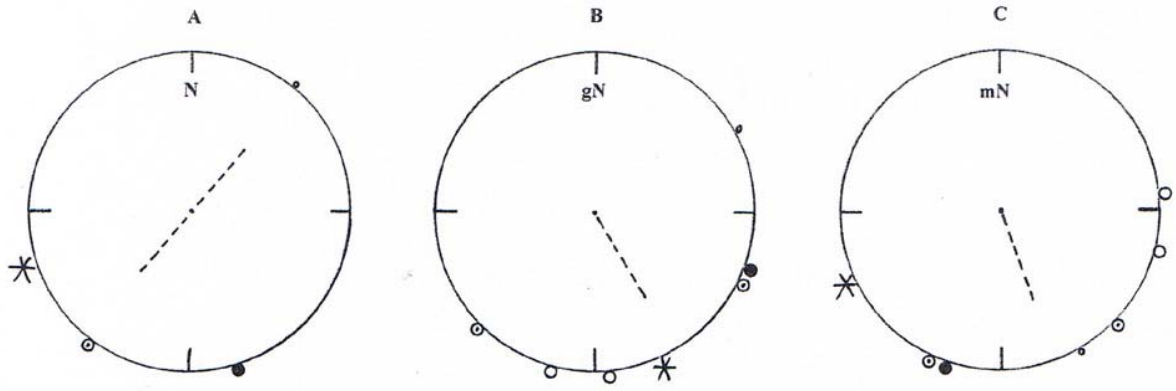


Fig.7: The night orientation on 11 September. The sunset/early night sky was partly covered, During night-tests in the funnels the sky was totally covered. The orientation of the controls is shown in A: $218^{\circ}/38^{\circ} - 0.498$, $n = 4$. B and C show the orientation of the exp.s in reference to geographical N and magnetic N, respectively. The sample mean vectors are $150^{\circ} - 0.636$ ($n = 7$) and $160^{\circ} - 0.612$ ($n = 7$), respectively.

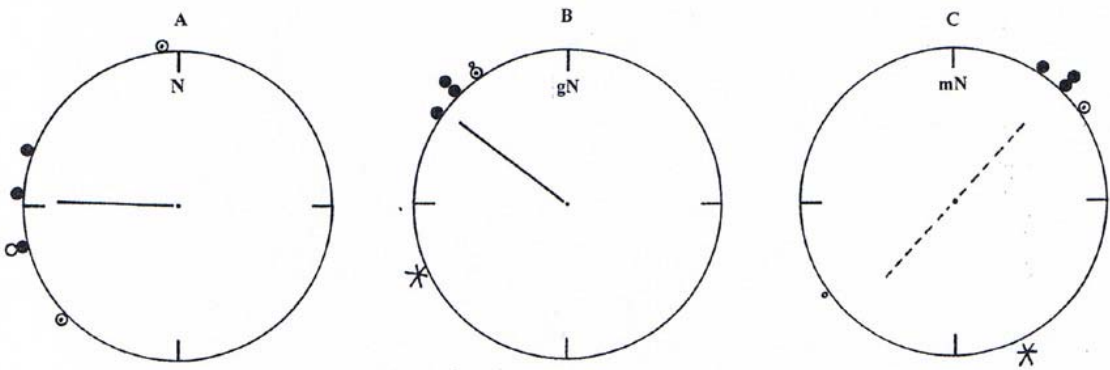


Fig.8: The night orientation on 18 September. Both sunset/early night and night were totally overcast. The orientation of the controls is shown in A: $272^{\circ} - 0.778^*$, $n = 6$. The orientation of the exp.s is shown in B in reference to geographical N: $307^{\circ} - 0.892$, $n = 6$, and in C in reference to magnetic N: $43^{\circ}/223^{\circ} - 0.677$, $n = 6$.

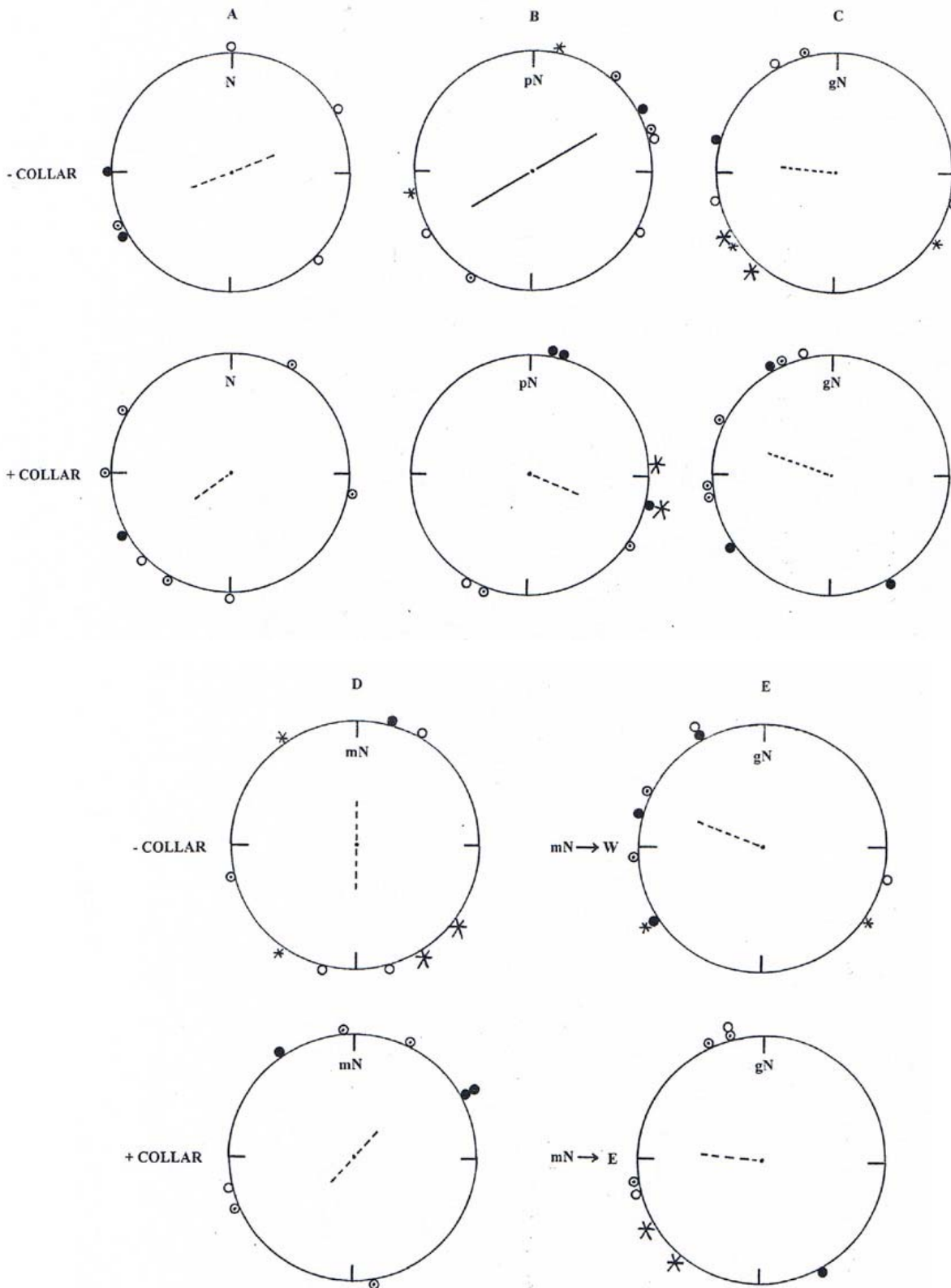


Fig.9 The sunset/early night orientation on 21 and 22 September, clear sky and with compensatory tree-frames (Fig.2). Collars (Fig.3) also applied in half of the bird.

A shows the orientation of the controls. Non-collar birds: **249°/69°** - 0.371 (n = 6), and collar birds: 233° - 0.387 (n = 8).

B shows the orientation of the exp.s in reference to paper N. The sample mean vectors are: **60°/240°** - 0.609* (n = 8) for the non-collar birds, and 104° - 0.431 (n = 8) for the collar birds.

C shows the orientation of the exp.s in reference to geographical N. Non-collar birds: 275° - 0.464 (n = 7), and collar birds: 288° - 0.578 (n = 8).

D shows the orientation of the exp.s in reference to magnetic N. Non-collar birds: **180°/0°** - 0.363 (n = 8), and collar birds: **40°/220°** - 0.293 (n = 8).

E denotes the orientation of the exp.s in reference to geographical N if distinguishing between birds where magnetic N was deflected towards W or E, respectively. The sample mean vector of the W-birds is 292° - 0.573 (n = 7), and of the E-birds 274° - 0.489 (n = 8).

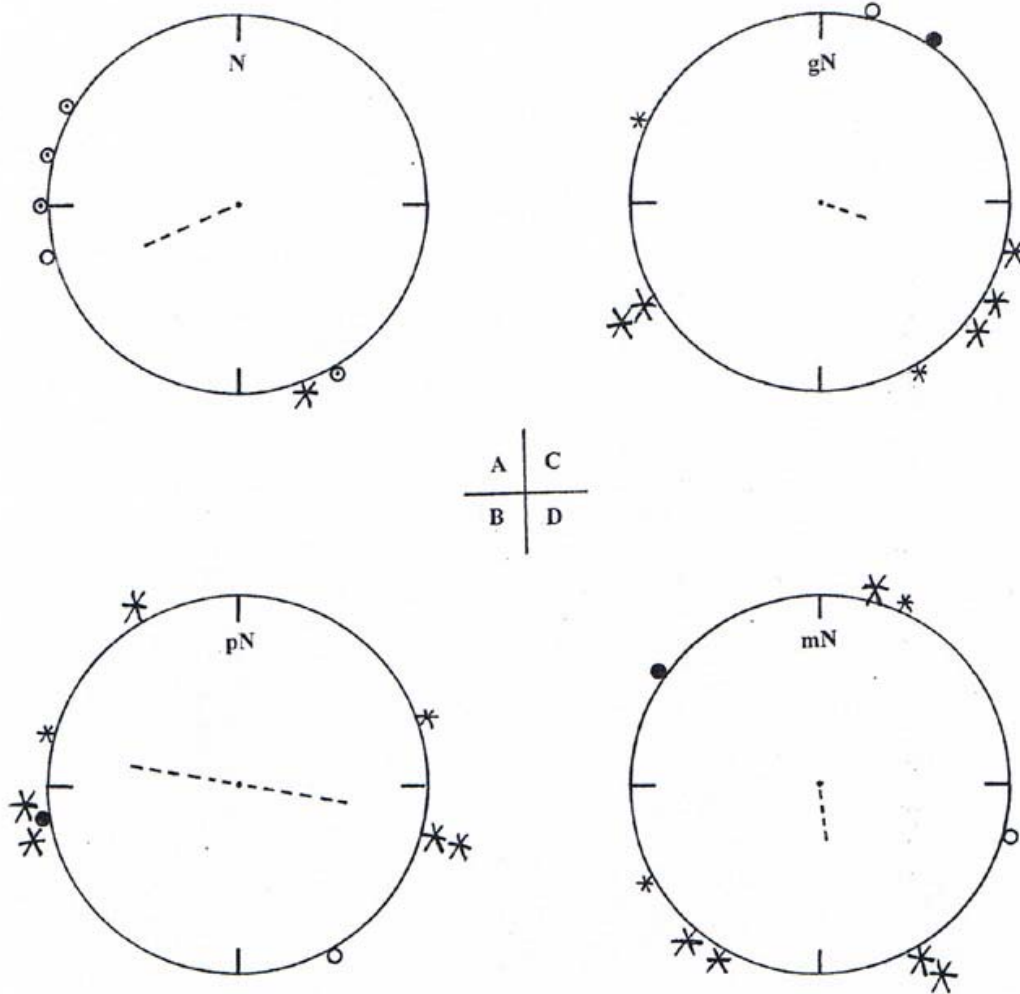


Fig.10: The sunset/early night orientation under overcast 20 September. The orientation of the controls (A): $246^\circ - 0.539$ ($n = 6$). The orientation of the exp.s in reference to paper N indicates that the rectangular tree-frame (which was not compensated on this occasion) had a spurious directional effect. The sample mean vector is $280^\circ/100^\circ - 0.580$ ($n = 8$). C and D show the orientation of the exp.s in reference to geographical N ($110^\circ - 0.258$, $n = 7$) and magnetic N ($173^\circ - 0.300$, $n = 7$), respectively.