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Orientation of night-migrating passerines kept and tested in an inverted magnetic field

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ABSTRACT

From 1992 to1999 more than 500 funnel experiments were carried out with robins, redstarts, whitethroats, and pied flycatchers. The purpose was to elucidate the orientation of birds caged and tested for a prolonged time in an inverted magnetic field, i.e. a field where the vertical component was reversed (pointed upwards). Contrary to expectations, the results did not suggest that orientation was governed by a magnetic inclination compass; generally no differences were found between birds tested in the inverted field and those tested in the natural one. However, occasional patterns of (bimodal) orientation at right angles appeared, probably elicited by the inverted field, and contradictions between stellar and magnetic information. Possibly, the significance and kind of magnetic orientation in passerine birds is less well understood than is normally supposed.

KEY WORDS: Night-migrating passerines - Magnetic inclination compass - Magnetic polarity compass - Stellar compass - Compass hierarchy.

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INTRODUCTION

Juvenile migrant passerine birds on their first autumn migration are steered by one or several orientational or navigational systems (cf., Rabøl, 1980; Berthold, 1988). If clock-and-compass orientation (vector navigation) is the only operative orientation system, then the kind of compasses used and their hierarchical relationships become the main targets of interest.

According to Wiltschko & Wiltschko (1996) and Wiltschko *et al.* (1997, 1998), migrant birds use magnetic and celestial compasses, the latter being divided into stellar and sun/sunset ones. The magnetic compass is of the inclination type, whereas stellar ones are primarily based on stellar rotation. In the pre-migratory period, the latter type calibrates (the sign of) the magnetic inclination compass (cf., Emlen, 1967; Able & Able, 1990; Weindler *et al.*, 1996, 1997; Weindler, 1997). Moreover, according to Wiltschko *et al.* (1998), the magnetic compass gradually assumes dominance over the celestial ones during a bird's first autumn. Wiltschko *et al.* (1994), Wiltschko & Wiltschko (1995), and Munro *et al.* (1997a, b) advanced the possibility of magnetic 'maps', and hence seemed to consider magnetic orientation and navigation the primary explanation of the hitherto mysterious orientation of migratory birds ("the solution of a mystery?", cf. Baker, 1984).

The experiments presented here connect logically with those findings and interpretations. Four species of migrant passerines were caged and tested permanently for weeks in inverted magnetic fields; i.e. inclination = -70°, magnetic N = geographical S (in terms of a magnetic inclination compass). The first experiment was carried out inside a house and the three others outdoors; in moonless periods, the birds were tested under overcast or starry skies. The species were juvenile pied flycatchers *Ficedula hypoleuca* Pallas, 1764 trapped as migrants in late August on Christiansø in the Baltic Sea; locally bred juvenile whitethroats *Sylvia communis* Latham, 1787 trapped in late July and transferred to the inverted magnetic field in the pre-migratory season; robins *Erithacus rubecula* Linnaeus, 1758 trapped as migrants in early October at Blåvand, the westernmost point of Jutland; redstarts *Phoenicurus phoenicurus* Linnaeus, 1758 trapped as migrants in early May at Blåvand. The robin is a medium-distance migrant; the other three species are long-distance migrants. The first experiment was carried out indoors at Strødam north of Copenhagen, and the three others outdoors on the island of Endelave in Kattegat, north of Funen.

The general expectation was that the control birds (not exposed to the inverted magnetic field) would be oriented in the standard direction, and the experimental birds in the reverse direction in indoor and outdoor experiments, at least on overcast nights. The underlying research-hypothesis was that migrant birds have an inclination compass which dominates other compasses, whereas the corresponding null-hypothesis is that there is no (dominating influence of an) inclination compass.

To our knowledge, these are the first conflicting experiments between the stellar compass and the magnetic inclination compass where the birds are caged and tested for weeks in an inverted magnetic field.

As we report on four different experimental series, it is important not to lose sight of the main questions and expectations. These points are stressed in the section above and two further related questions on a different level are: are the results indicative of a magnetic inclination compass at work, and (if not); are the results indicative of a magnetic polarity compass at work?

MATERIALS AND METHODS

Experimental groups

Pied flycatchers

Sixteen first-year of life pied flycatchers were trapped on Christiansø, 25 August 1992. The birds were transported to Strødam the next day, and divided into two groups (10 and 6 birds, respectively). The experiments in the first group were initiated on 27 August with the birds, until 2 September, being caged and tested (on six nights) in the natural magnetic field (inclination = +70°). In the evening of 3 September (night 0), the birds were transferred to, and tested in, an inverted magnetic field (inclination = -70°). Thereafter they were caged and tested (nights 1, 3, 5) in the inverted field. The last tests (night 5) were carried out on 8 September. The six birds in the second group were caged in the natural magnetic field, and the experiments were initiated on 3 September with the birds, until 8 September, being tested (on four nights) in the natural magnetic field. In the evening of 9 September (night 0), the birds were transferred to, and tested in, an inverted magnetic field. Thereafter they were caged and tested (nights 1, 3, 5) in the inverted magnetic field. The last tests (night 5) were carried out on 14 September.

The birds were caged and tested indoors. They were never allowed to see the sun or stars, and the same bird was almost always tested in the same funnel and position. The birds were tested singly for two hours before midnight in plastic funnels covered with a translucent, but not transparent, plastic sheet. Ten centimetres above the centre of each funnel, a side-shielded light bulb (1.5 V, 0.2 amp) produced a very weak light so that the illumination within the funnel was not biased in any direction.

The purpose of the experiments was to find out whether the magnetic compass perhaps shifted from an inclination type to a polarity type after some days and nights in the inverted magnetic field. Initially, we had no doubt that at least on night 0 the magnetic compass would be of the inclination type, as reported by all other Authors.

Whitethroats

Twenty local juvenile whitethroats were trapped on July 28 and 29, 1996, on Endelave. Autumn migration had not started and during the first week of August, no activity, or very little, was observed in the cages from sunset until midnight. The majority of the Endelave birds departed from the island around August 9-12 and the last whitethroat on the island was observed on 15 September (pers. obs.).

On August 3, eight experimentals were placed in the coil fields, where they were kept until September 19. The remaining twelve birds were used as controls. On August 3 through 6, both controls and experimentals were exposed to the sunset and the stars until midnight thus enabling them to observe, compare, and calibrate the three compasses.

On every test night, the birds were exposed to the sunset/starry sky for at least one hour before and half an hour after the tests.

On nine clear and starry nights, August 17-21 (4), September 3--5 (3) and September 16-17 (2), a total of 76 and 36 tests were carried out with controls and experimentals, respectively, while on four 'overcast' nights, September 8, 9, 14, and 15, 31 and 16 tests were carried out with controls and experimentals, respectively.

On September 7, four controls were exposed to the sunset and the first stars, and later tested in the inverted inclination, whereas the eight experimentals were exposed and tested in the Earth's magnetic field. Both groups were tested under the starry sky. After the tests, the controls were returned to the Earth's magnetic field and the experimentals to the inverted fields. On September 18, this procedure was slightly changed: both groups were exposed to the sunset and early stars in their usual magnetic fields, but the controls were then shifted to, and tested in, the inverted fields, and the experimentals in the Earth's magnetic field. Then tests were carried out under an 'overcast' sky.

Robins

Nineteen robins were trapped on October 2, 1996, at Blåvand; probably of Norwegian origin on a direct over-sea-immigration. The birds were taken the next day to Endelave, where eight of them were placed in the four cages within coil-fields, and the remaining eleven in crate-cages. Most birds were rather lean but increased in weight to fatness within two days. One experimental bird and two controls were adults. The orientation of the adult birds was not outstanding compared with that of the juveniles. Because of overcast sky and rain, the birds were not exposed to the sunset or early night stars until October 6.

On the two starry nights, October 6 and 10, 16 and 8 tests were carried out with controls and experimental, respectively, while on the two overcast nights, October 9 and 12, 16 and 8 tests were carried out with controls and experimentals, respectively. On October 14, the birds were exposed to a clear sunset and the first stars. Later in the funnels, they were tested under an overcast sky without plastic sheets. The eight experimentals were tested in the normal field, and four controls in the inverted field, mirroring the conditions of the whitethroats on September 18.

Redstarts

Ten male redstarts were trapped as migrants at Blåvand, eight birds on 3 May and two on 4 May, 1999, in easterly winds. On 7 May, the birds were transported to Endelave, where tests were carried out the same night (starry sky, previous exposure to the sunset) in the undisturbed magnetic field. Eight birds displayed migratory activity; six were oriented NNE-NE and two SSE-S. This pattern could be interpreted as a major peak of standard/compensatory orientation (due to the wind drifting to Blåvand), and a minor peak of reverse orientation.

The birds were divided into two approximately equal groups: six controls (mean directions 15°, 60°, 60° and 180° plus the two inactive birds from 7 May), and four experimentals (mean directions 340°, 45°, 60° and 165°). Several hours before sunset on 8 May, the experimentals were placed in their baskets inside the inverted magnetic fields, and, from then on, they spent all their time until 18 May (see below) in these inverted fields.

All birds were tested under natural overcast skies on the six nights 8, 9, 11, 12, 13, and 14 May (Fig. 2D), and on the last two nights experienced the sunset (partly covered sky).

On 15, 16 and 17 May, the birds were tested under a starry sky after previous exposure to a clear sunset, while on 18 May they also experienced a clear sunset and early starry night in their usual magnetic fields. However, when tested, the four experimentals were placed in the natural magnetic field (+70° inclination), whereas four controls were placed in the inverted fields (-70° inclination). From then on, until the experiments finished the next night (19 May), these eight birds were caged in their baskets and tested in the funnels in the opposite fields to those they were caged and tested in before.

and only in the first ten minutes or so was a slightly brighter sunset-sky obvious for the human eye, but probably not for the birds in the 'overcast' funnels. Certainly, in case of the robins (Figs 2C, 4B), tested at the night under a natural overcast sky, no sunset taxis could have influenced their orientation, but in particular the bimodal pattern in Figure 4B has much resemblance to the whitethroat-pattern in Figure 2B. Anyway, a magnetic inclination compass in action should produce differences in the 'overcast'/overcast patterns of corresponding controls and experimentals, but no such differences were found. Probably, the prominent peaks of NW-N orientations should be considered as orientation at right angles (and to some extent as reverse orientation). Probably, this has something to do with the 'overcast'/overcast conditions, but why a NW-orientation is prominent for the whitethroats and robins compared with the SE-orientation for the pied flycatchers is not easy to tell. In conclusion, slight influences of various taxes (such as a positive sunset taxis) cannot be excluded. However, on the whole these were considered negligible and clearly could not be totally responsible for all significant orientations under indoor, overcast and 'overcast' conditions.

Considering some unknown, non-magnetic and non-celestial compass reference, Muheim & Åkesson (2002) reported: "We cannot completely exclude the possibility that birds have access to other unknown cues when tested under completely overcast skies or under Plexiglas sheets simulating overcast, but according to current knowledge this is very unlikely".

As pointed out by Wallraff (pers. comm.) we have no direct indication of a magnetic polarity compass in action. However, at least in the case of the indoor orientation of the pied flycatchers (Fig. 2A) and in the more or less unchanged orientation of the whitethroats in Figure 4A compared with Figure 2B, the indirect evidence of a polarity compass is strong. At least, the patterns observed cannot be perceived as steered by a celestial calibrated magnetic inclination compass.

When starting the first (indoor) experiments with the pied flycatchers, we had no doubt about the significance of the magnetic inclination compass; the only question was whether the orientation after several days and nights in the inverted field was still steered by an inclination compass, or whether a polarity compass perhaps took over in the course of time. Surprisingly, there was no indication of an inclination compass in action, not even on the very first night (0). However, because of the unexpected ESE mean orientation (far from the standard direction of ca SSW-SW), we were reluctant to draw any far-reaching conclusions about compass mechanisms in action. On the other hand, our results were not without precedents. Also the Frankfurt-group (e.g., Beck & Wiltschko, 1982; Bingman, 1984) sometimes found 'SE' orientation in pied flycatchers during the first part of the autumn when the standard direction is SW. In experiments with conflict between the magnetic compass and celestial compasses, e.g., Wiltschko *et al.* (1998) revealed that the magnetic (inclination) compass needs some time or a number of tests before achieving dominance over the celestial compasses. However, there is no reason to expect a delay (of more than five nights) under overcast skies; in all earlier inverted inclination experiments, the indoor or overcast orientation was reversed already on the very first night and no delays were reported (Wiltschko & Wiltschko, 1996).

When the whitethroat experiments were planned, we still had no doubt about the significance of a magnetic inclination compass – otherwise the experiments were rather meaningless. If the magnetic compass in the pre-migratory period was calibrated by stellar rotation the expectation was reverse orientation (NNE-NE) under overcast skies, and also a 180° different orientation in both controls and experimentals when tested under inverted field conditions compared with the normal cage field. At least under starry conditions, controls were oriented in the standard direction, whereas experimentals were not reversely oriented. However, the latter were skewed, though not statistically significantly so towards 'SE'. When tested under 'overcast' skies, there was no difference between controls and experimentals; the orientation in both groups appeared as bimodal SW/N. Clearly, the Whitethroat experiments, considered together with the subsequent robin ones, on the whole (and at 'best') were indicative of some influence of the magnetic inversion on the motivational state, but not on the magnetic compass mechanism as such.

In the final redstart experiments, once again there was no indication of a magnetic inclination compass in action.

In conclusion, and in the case of the first three species, the hypothesis of e.g. Wiltschko *et al.* (1998) may apply: that the magnetic compass had not yet gained dominance over the celestial compasses; the birds were still too close to their breeding area, and the magnetic compass might attain more influence with time and further down in the migratory route. However, this is not likely in the case of a spring migration of the redstarts. The magnetic inclination compass should have attained dominance, and it does not seem very likely either that it would have done so, even if we had continued for more starry nights.

Summing up, it was most surprising to find a lack of distinct reverse orientation in the inverted fields: this finding refuted the influence and action of a magnetic inclination compass in our experiments, and could not be explained by heterogeneity in the inverted field. Furthermore, the experimental birds were mostly not disoriented, but oriented either as the controls or at right angles to the standard direction. More experimentation is needed to establish the influence of different inclinations and intensities of the magnetic field, and their temporal and spatial variations. Sandberg & Pettersson (1996) suggested the existence of both kinds of magnetic compasses in birds and wrote, "Access to both inclination and polarity compasses may provide a flexible

Experimental procedure

The birds were tested individually in plastic funnels (upper diameter 30 cm) overlooking an approximately 160° section of sky. They were placed in the funnels about 1.5 h after sunset, and the experiments normally lasted 60 to 90 min, till around midnight. The orientation and amount of activity of the individual birds were estimated by means of the correction-paper method (Rabøl, 1979, 1994, 1998), though individual mean directions based on activities less than one were omitted, as were (the few) bimodal activities based on two equal peaks (however, see Figs 1B, 4B). Furthermore, in bimodal activities with a major and a minor peak, the larger is denoted by a dot as are the unimodal activities. The significance of the sample mean vector was tested with a Rayleigh test, and the probability of coincidence of two sample distributions, with the Watson-Williams or Mardia-Wheeler-Watson test (Batschelet, 1981).

The experimental birds were caged two by two in four baskets, placed centrally inside four Helmholtz-coils, and they stayed constantly in the inverted magnetic field. The coil fields were produced by electrical wires wound onto two square, wooden frames each measuring 80 × 80 cm, and placed 45 cm apart. The coils were oriented horizontally, and the magnetic field intensity was double the vertical component of the Earth's magnetic field at the test site. The coil field was directed vertically upwards, and the resulting field was thus an inverted magnetic field of the same intensity as the Earth's field, but with an inclination of -70°. The field was monitored daily for inclination and intensity. At Strødam, two funnels were placed along the diagonal within each pair of coils. The total magnetic intensity was measured to vary between 0 and 4% inside the funnels (Ole Rasmussen, DMI). In the experiments on Endelave, only one funnel was placed in the centre of each pair of coils, where the variation was only 0-1%, i.e., probably less than those of Wiltschko (1968), Wiltschko & Wiltschko (1972) and of Sandberg *et al.* (1988).

In the outdoor experiments on Endelave, the baskets were placed two by two on wooden tables, each in the middle of a coil field. Apart from 1 h before, 1-1.5 h during, and 0.5 h after the tests, the baskets in the coils were covered by a wooden box (the whitethroats and robins). The roof of each box consisted of an undulating sheet of translucent, but not transparent, plastic, enabling the birds in the baskets to follow the sun (sunrise, sunset), but offering no view of the stars. In the redstart-experiments, a large, netting cage covered the two coil fields/baskets on each table. The roof was covered with translucent plastic so that the greater and central part of the starry sky was blurred when the cage was in use. The cages had no influence on the magnetic fields.

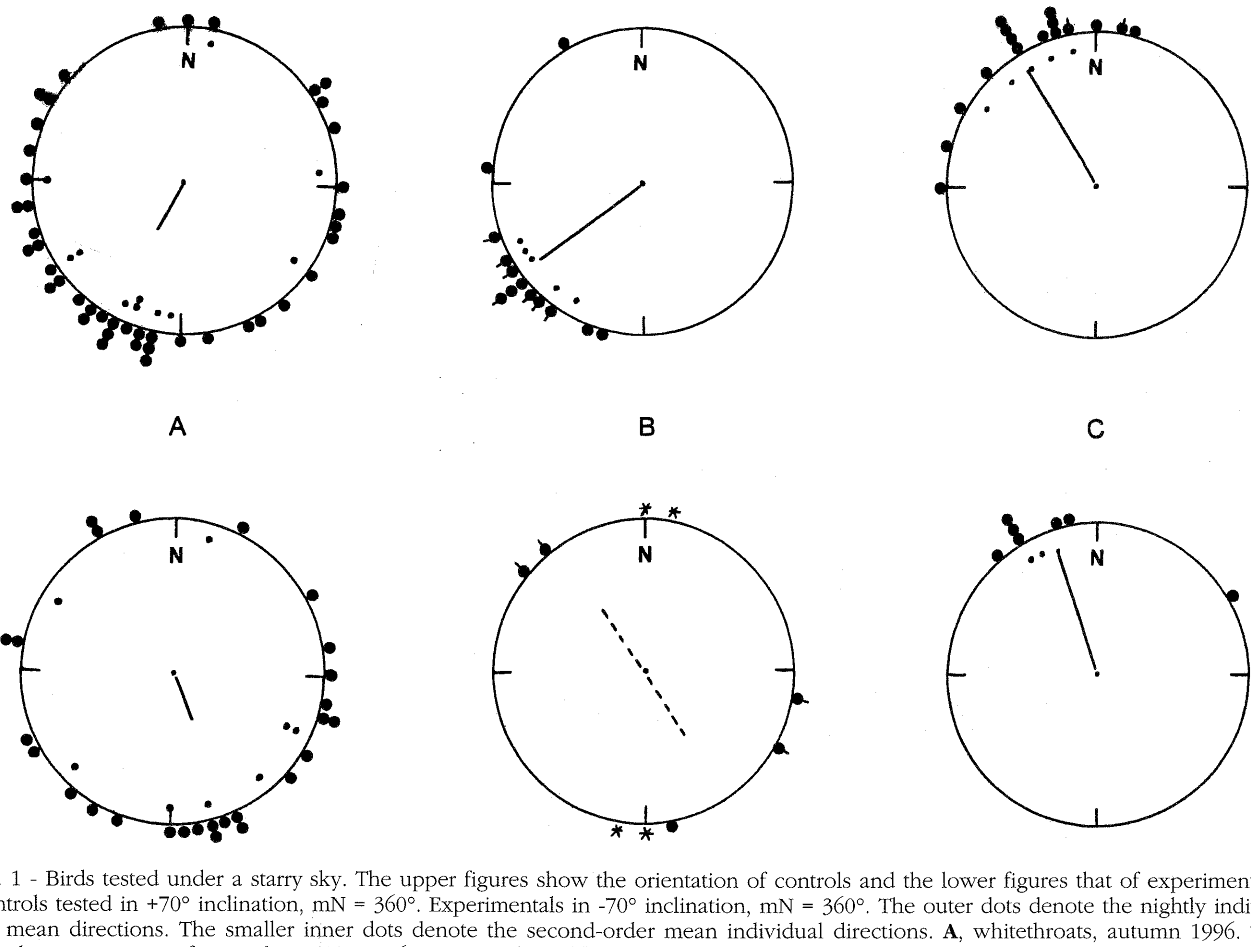

Fig. 1 - Birds tested under a starry sky. The upper figures show the orientation of controls and the lower figures that of experimentals. Controls tested in +70° inclination, mN = 360°. Experimentals in -70° inclination, mN = 360°. The outer dots denote the nightly individual mean directions. The smaller inner dots denote the second-order mean individual directions. **A**, whitethroats, autumn 1996. The sample mean vector of controls is 208°, 0.36, $P < 0.01$ ($n = 44$), and of experimentals 158°, 0.33, $P < 0.05$ ($n = 27$). The grand mean vectors (not shown) are 200°, 0.53, $P < 0.05$ ($n = 11$, controls), and 154°, 0.39, NS ($n = 8$, experimentals). **B**, robins, autumn 1996. The sample mean vector of controls is 234°, 0.85, $P < 0.001$ ($n = 13$), and of experimentals 112°, 0.13, NS ($n = 5$). Doubling the angles of the latter and including the two pairs of bimodal orientations (the crosses) leads to 137°/327°, 0.50, NS ($n = 7$). Only five controls showed consistent and (rather) similar orientation on both nights. The grand mean vector (not shown) is 230°, 0.97, $P < 0.01$. The marks on the dots refer to directions from 10 Oct. **C**, redstarts, spring 1999. The sample mean vector of controls is 329°, 0.89, $P < 0.001$ ($n = 14$), and of experimentals 344°, 0.87, $P < 0.01$ ($n = 7$). The two dots with a mark refer to an individual control bird also tested on 18 and 19 May (not included in the sample mean vector). Seven birds showed consistent orientation from 15 through 17 May. The grand mean vector (not shown) is 330°, 0.97, $P < 0.001$ ($n = 7$).

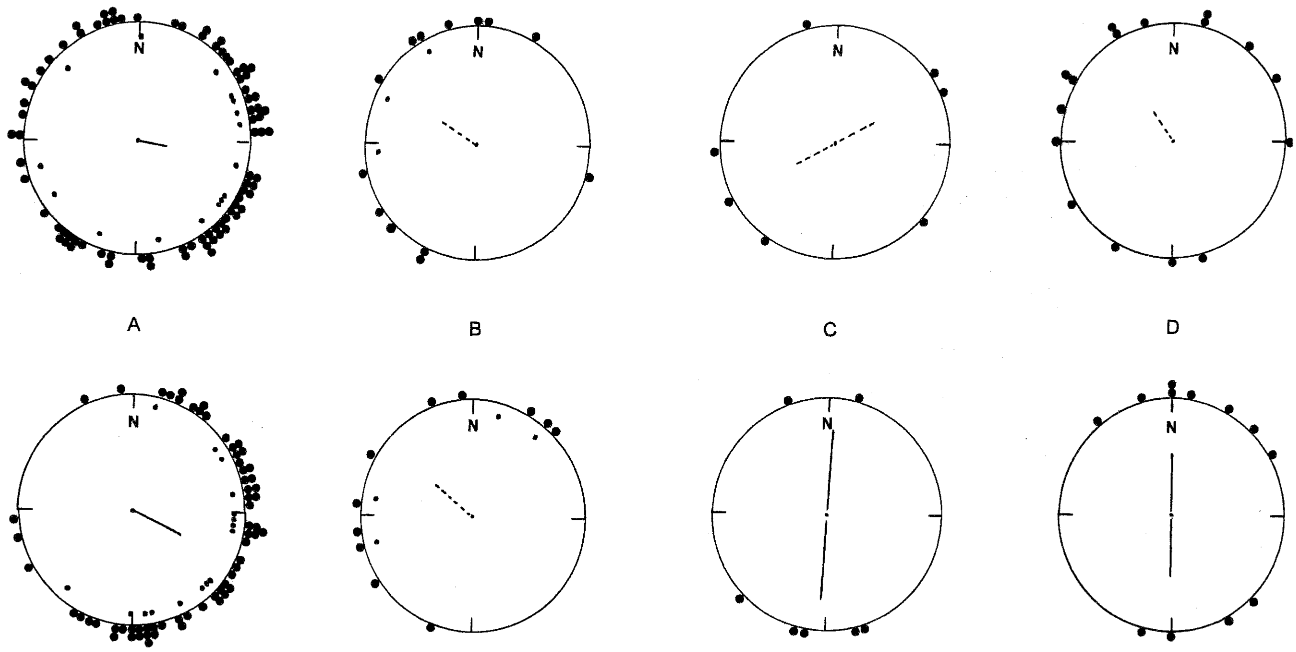

Fig. 2 - Birds tested with no view of the stars. The upper figures show the orientation of controls and the lower figures that of the experimentals. Controls tested in +70° inclination, and experimentals in -70° inclination. The outer dots denote the nightly individual mean directions. The smaller inner dots denote the second-order mean individual directions. **A**, pied flycatchers, autumn 1992. Indoor experiments. Controls tested in +70° inclination, mN = 360°. Experimentals in -70° inclination, mN = 360°. The sample mean vector (denoted) of controls is 100°, 0.254, $P < 0.01$ (n = 84) and the grand mean vector is 107°, 0.380, NS (n = 16). The sample mean vector (denoted) of experimentals is 115°, 0.485, $P < 0.001$ (n = 64) and the grand mean vector is 118°, 0.645, $P < 0.001$. Omitting two individual mean vectors with very low concentration (0.02 and 0.10, respectively with mean directions of 12° and 221°, respectively) resulted in a grand mean vector of 118°, 0.772, $P < 0.001$ (n = 14). **B**, whitethroats, autumn 1996. 'Overcast' sky. The sample mean vector of controls is 301°, 0.36, NS (n = 13), and of experimentals 309°, 0.42, NS (n = 11). The total sample mean vector is 305°, 0.38, $P < 0.05$ (n = 24). Three controls and four experimentals showed significant and rather similar (< 90° different) orientations on at least two nights (the single exception was a control mentioned in Materials and Methods). The grand mean vector of these is 310°, 0.64, $P \approx 0.06$ (n = 7). **C**, robins, autumn 1996. Overcast/'overcast' sky. The sample mean vector of controls is 247°, 0.03, NS (n = 7), or doubling the angles 62°/242°, 0.38, NS. The sample mean vector of experimentals is 193°, 0.39, NS (n = 7), or doubling the angles 183°/3°, 0.73, $P < 0.05$. **D**, redstarts, spring 1999. Overcast sky. The sample mean vector of controls is 322°, 0.31, NS (n = 16), and of experimentals 25°, 0.33, NS (n = 12). Doubling the angles leads to significant orientation in the experimentals (1°/181°, 0.53, $P < 0.05$).

The control birds were placed on the ground in a wooden crate with a free view in all directions between the bars. The top of the crate was covered with a translucent, but not transparent plastic-sheet, which obscured the stars.

Before the field tests, both controls and experimentals were freely exposed to the sunset and later to the stars for one or two hours. The controls were tested on top of the crate, and the experimentals on the tables within the coils. On the test-nights, a varying number of birds was tested, but always four birds in the inverted fields. After the experiments, all birds experienced a full view of the night sky for about half an hour. Apart from the few minutes of transfer before and after the tests, the experimental birds spent all their time within the inverted fields (except for the short times when tested in the natural magnetic field). On some starry nights, artificial overcast ('overcast') sky was produced by covering the funnels with sheets of translucent, but not transparent plastic. For further details on the whitethroats and robins, see Rabøl (1998, unpubl. report, Univ. of Copenhagen).

During recent years, use of second-order individual mean directions and grand mean vectors (based on these individual mean directions) have been common practise. From a statistical standpoint, the sample size should be the number of birds and not the number of bird-nights, i.e. 'pseudo-pooling' should be avoided, if that is convenient and possible under the circumstances. The problem is that this procedure tends to obscure and distort more basic and significant responses and reduce complicated patterns with important information into simple summary-patterns which may then easily be interpreted as the outcome of simple clock-and-compass orientation (Rabøl, 1994). In the categories investigated, the number of tests per bird was often low, and the individual orientations often seemed bimodal: a control whitethroat tested on four occasions under an 'overcast' sky oriented 300°, 225°, 325°/(100°) and 205° (cf. Fig. 2B). In such a case the mean direction of 263° is not very representative of the orientation of the individual. Therefore, in the present context, second-order individual mean directions were only considered in some cases, always based on at least two nightly directions not separated by more than 90° (with the single exception mentioned above).

RESULTS

The results of controls tested in the natural magnetic field (+70° inclination) and experimentals in the inverted magnetic field (-70°) under a starry sky are shown in Figure 1.

In the experiments with the whitethroats, controls were significantly oriented SSW-SW and experimentals SSE (Fig. 1A). The difference was not statistically significant ($0.10 < P < 0.20$, Mardia-Wheeler-Watson test). For the robins, controls were significantly oriented

SW-WSW, whereas a bimodal SE/NW pattern was rather apparent in experimentals (Fig. 1B).

For the redstarts, controls and experimentals were significantly oriented NW-NNW and NNW, respectively (Fig. 1C). The difference was not significant (0.20 < P < 0.30, Watson-Williams test).

The results of the controls tested in the natural magnetic field and experimentals in the inverted magnetic field under an overcast/'overcast' sky are shown in Figure 2.

In the experiments with the pied flycatchers, controls and experimentals were significantly oriented E-ESE and ESE, respectively (Fig. 2A). The difference was not significant (P = 0.10, Mardia-Wheeler-Watson test). For each individual, means of nightly mean directions under +70° and -70° inclination were calculated. Nine birds contributed significantly, and expressing the -70° orientation as a function of the +70° orientation led to no significant pattern (-14°, 0.22, NS, n = 9), i.e., no shift was observed. We also investigated the night 0 orientation in -70° inclination as a function of the preceding night's +70° inclination orientation. Considering the mean directions of the individual birds, a possible pattern emerged (+58°, 0.33, 0.05 < P < 0.10, n = 16), but clearly the orientation was not reversed.

For the whitethroats, both controls and experimentals were oriented ca WNW-NW (Fig. 2B), but statistical significance was not attained except for the combined sample mean vector. The pattern seemed bimodal with SW and N modes, and, using the method of Holmquist & Sandberg (1991) with k = 1.5 led to 355°/235°, 0.65, P < 0.001 (n = 24).

For the robins, controls were disoriented, whereas experimentals were significantly bimodally oriented with a major S peak and a minor N one (Fig. 2C).

For the redstarts, neither of the groups, nor the combined sample, showed any significant unimodal orientation, but the patterns of both groups appeared bimodal with major peaks NNW-N (controls) and N-NNE (experimentals), and minor peaks SSW (controls) and SSE-S (experimentals) (Fig. 2D). Doubling the angles led to significant, bimodal orientation in the experimentals. Compared with the initial orientation on 7 May, the overcast orientation was less concentrated in the controls, and three control orientations (90°, 270°, and 285°, which were all displayed by the same individual bird) cannot be classified as displaying any standard or reverse orientation. Discarding these three orientations, standard/reverse orientation ratios were 6:2 (7 May), 9:4 (controls, 8-14 May) and 8:4 (experimentals, 8-14 May). Obviously, there is no more reverse orientation in the experimentals indicating the influence of an inclination compass.

The results of controls tested in the inverted magnetic field (-70° inclination) and experimentals in the natural magnetic field (+70° inclination) under a starry sky are shown in Figure 3.

In the experiments with the whitethroats, both controls and experimentals oriented SSW (Fig. 3A). Compared with the preceding starry sky orientation in the natural (controls) and inverted (experimentals) magnetic field on 4 and/or 5 September the combined sample was unchanged (+9°, 0.81, P < 0.01, n = 10). See also Fig. 1A.

For the redstarts, controls and experimentals were oriented N and NNW, respectively (Fig. 3B). The difference was not statistically significant (0.10 < P < 0.20, Watson-Williams test). Compared with Figure 1C, there was a slight clockwise shift, but obviously the orientation was not reversed (not even displaying a right angle response). The results of the controls tested in the inverted magnetic field and experimentals in the natural magnetic field under an overcast/'overcast' sky are shown in Figure 4.

In the experiments with the whitethroats, only a single control was active but oriented within the range of the experimentals, which was significantly NW (Fig. 4A), while compared with the 'overcast' orientation from 8 to 15 September (Fig. 2B), the pattern appeared rather unimodal. However, on the whole, the 'overcast' orientation on 18 September was unchanged when individual birds were compared with the 'overcast' orientations on September 14-15 (-37°, 0.33, NS, n = 6).

For the robins, no clear difference was found between controls and experimentals and the pattern of the combined sample appeared bimodal with SSW-SW and

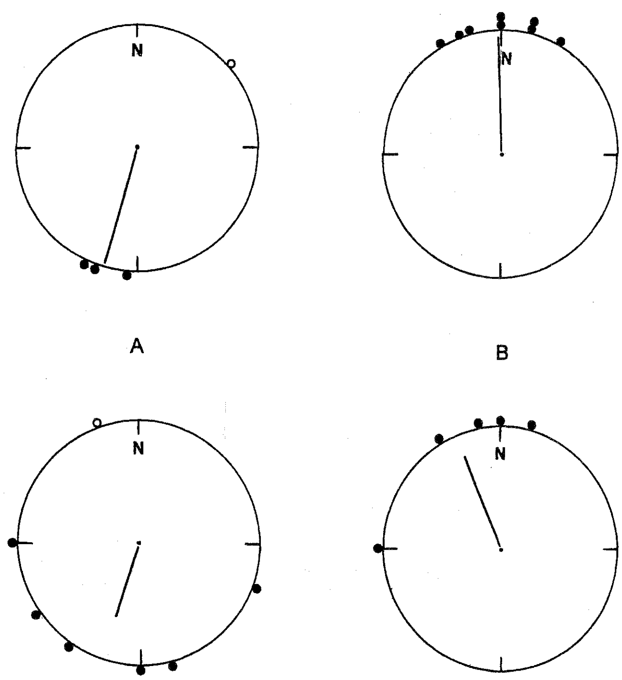

Fig. 3 - Controls tested in -70° inclination, and experimentals in +70° inclination under a starry sky. The upper figures show the orientation of controls and the lower figures that of experimentals. The outer dots denote the nightly individual mean directions. **A**, whitethroats, autumn 1996. The open dots refer to directions based on activities below 1. The sample mean vector of controls is 197°, 0.989, P < 0.05 (n = 3), or including the open dot 182°, 0.550, NS (n = 4). The sample mean vector of the experimentals is 198°, 0.648, P < 0.05 (n = 6), or 209°, 0.451, NS (n = 7). **B**, redstarts, spring 1999. The sample mean vector of controls (upper figure) is 359°, 0.95, P < 0.001 (n = 8), and of experimentals 338°, 0.82, P < 0.05 (n = 5).

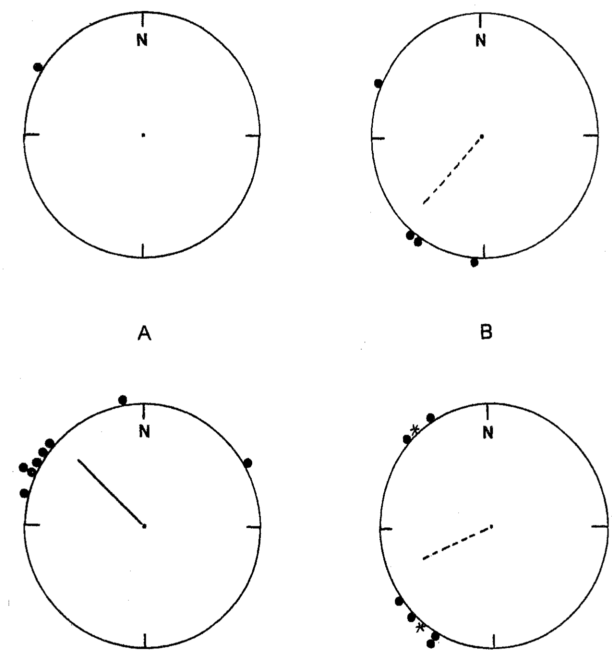

Fig. 4 - Controls tested in -70° inclination, and experimentals in +70° inclination with no view of the stars. The upper figures show the orientation of controls and the lower figures that of the experimentals. The outer dots denote the nightly individual mean directions. **A**, whitethroats, autumn 1996. 'Overcast' sky. The single control bird is orienting at 300°, and the sample mean vector of experimentals is 314°, 0.78, $P < 0.01$ ($n = 8$). The total sample mean vector is 312°, 0.80, $P < 0.01$ ($n = 9$). **B**, robins, autumn 1996. Overcast sky. The sample mean vector of controls is 226°, 0.77, NS ($n = 4$), and of experimentals, 248°, 0.66, NS ($n = 6$). A seventh experimental bird showed bimodal orientation at 225° and 320° (crosses). If the two groups are combined the sample mean vector is 239°, 0.69, $P < 0.01$ ($n = 10$). The distribution appears bimodal with peaks at about SSW-SW and NW. Applying the method of Holmquist and Sandberg (1991) leads to r_{max} = 0.95, $P < 0.01$ for $k = 1.38$.

NW peaks (Fig. 4B). Compared with the starry sky orientation on October 10, the controls were unchanged (-3°, 0.81, $n = 4$), whereas no pattern emerged in the experimentals. Instead, compared with the overcast orientation on October 9 and 12, both groups showed a clockwise deflection, which was significant for the combined sample (+68°, 0.56, $P < 0.05$, $n = 11$).

DISCUSSION

As is obvious from Figures 1 to 4, no general differences resulted between the orientational patterns in +70° and -70° inclination. The only significant difference was in the robins on starry nights (Fig. 1B). However, even here the orientation of the experimentals was not reversed compared with the controls. The conclusion should be that there is no trace of a magnetic inclination compass at work.

On the starry nights (Figs 1 and 3) this could be explained as a dominance of a stellar compass over the magnetic compass, though perhaps this is not the only explanation: the SSE-orientation of the whitethroats (Fig. 1A) and the bimodal SSE/NNW-orientation of the robins (Fig. 1B) in the inverted magnetic fields are probably expressions of a somewhat different motivational state in the experimentals compared with the controls displaying standard orientation. SSE-orientation was also found in two samples of juvenile whitethroats trapped in early July 2000 on Endelave (J. Rabøl, unpubl. data). These birds were kept in outdoor cages from before the pre-migratory season and experienced sunsets and stars. One of the samples was caged and tested in the natural magnetic field; the other sample were caged in a destroyed magnetic field (strong, shifting, approximately horizontal), and tested in a strong, heterogeneous, vertical field. Both samples were significantly oriented SSE in autumn under starry skies. Possibly, orientations approximately, at right angles to the standard direction, as also observed in Figures 2A, 2B, 4A, and 4B, are expressions of some sort of low or basic motivation and conflicting or insufficient directional information (Rabøl, 1983, 1985). Probably, the NNW orientation in the redstarts should not be considered as orientation at right angles to the initial NNE-NE orientation (which, as mentioned, was probably compensatory). The course towards the breeding grounds might well be W of N, and perhaps the NNW-orientation was also slightly influenced by a sunset taxis.

On the overcast nights (Figs 2 and 4), there seemed to be no differences in the orientational patterns of controls and experimentals. Four explanations are possible: 1) the orientation was steered by a magnetic inclination compass which was calibrated by a celestial or non-celestial compass, 2) the orientation was steered by a magnetic polarity compass, 3) the orientation was steered by an unknown non-magnetic (and non-celestial) compass, or 4) the orientation was steered by taxes which may vary between samples.

In the pied flycatchers (Fig. 2A), explanation 1) was not possible, as the birds were not exposed for celestial cues ahead of, or after, translocation to the inverted field. Neither is 4) probable: a pied flycatchers sample was disoriented in the same natural and inverted magnetic fields in the same two rooms in the spring of 1992 (S. Hansen, 1994, unpubl. report, Univ. of Copenhagen). However, several of the individual birds in this spring-sample tested many times were significantly oriented, but in highly different mean directions.

In case of the whitethroats (Figs 2B and 4A) and an 'overcast' sky (i.e., the sight of the starry sky was screened by translucent plastic covering of the funnels) explanation 4), i.e., the influence of a sunset taxis, becomes a serious candidate. However, considering the bimodal pattern in Figure 2B, the direction towards the sunset (ca. WNW) was in between the two peaks, but certainly, the pattern in Figure 4A could be perceived as being influenced by a sunset taxis. However, all tests were initiated one and a half hours after local sunset, geomagnetic orientation system rendering functionality even in the most extreme cue situations". Clearly, more experiments are required to reveal the existence of a magnetic compass of the polarity type.

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