

Compensatory behaviour after displacement in migratory birds

A meta-analysis of cage experiments

Kasper Thorup · Jørgen Rabøl

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Abstract Using a meta-analysis approach we re-analysed orientation cage experiments with displaced migrants found in the literature. A rather large proportion of the orientation experiments showed directional shifts after displacements, indicating ability for birds to detect and react on such displacements. There was a clear difference between overcast and experiments where birds had a view of the starry sky. In experiments under a starry sky, the birds compensated the displacements, whilst under overcast unaltered or reverse orientations were generally displayed. This indicates a role for the stars to be involved in detection of the changes in position. Such a role of celestial cues is further stressed by the results of several studies manipulating a planetarium sky.

Keywords Bird migrants · Orientation system · Compensation · Displacements

Introduction

The system responsible for the spatio-temporal progress of inexperienced, long-distance migrants was a matter of

controversy for many years. Generally, the view has settled that a vector-orientation programme forms the basis of the inherited orientation system (reviews of e.g. Able and Bingman 1987; Wiltschko and Wiltschko 1988; Helbig 1990; Berthold 1990; Wallraff 1990). In a vector-orientation migratory programme (i.e. a ‘clock-and-compass’ strategy), the migratory progress is described as a number of migratory steps with an approximately constant compass course, where the length and number of migratory steps are controlled by an endogenous circannual clock (Berthold 1996). This corresponds to a ‘vector’ with a length and a direction, and the migratory programme may consist of one or more such vectors.

However, migrants in nature are influenced by exogenous factors experienced along the migratory route, such as wind, topographical features, and available orientation cues, and migrants have been shown to respond to at least some of these (e.g. ecological barriers, coastlines, and wind drift; Åkesson 1993; Fortin et al. 1999; Thorup and Rahbek 2004). It has been recognised (e.g. Berthold 1996; Wehner 2001) that migrants combine all sorts of regionally specific geographical cues to ensure arrival at their destination. The capability of coping with such factors could be envisioned as ‘lying on top’ of the vector-orientation programme, allowing a migrant to compensate for different kinds of displacements. Possible mechanisms for such capabilities are, however, largely unknown. The proposed mechanisms range from birds only being able to compensate (partially) for wind drift whilst on migratory flights to birds being able to use navigation on site, the latter approaching the goal area navigation system, which does not imply an underlying vector-orientation programme (Rabøl 1969, 1970, 1985).

The most important distinction between the mechanisms proposed is between those that involve navigational processes, and those that do not. The following hypotheses

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K. Thorup (✉)
Zoological Museum, University of Copenhagen,
Universitetsparken 15,
DK-2100 Copenhagen Ø, Denmark
e-mail: kthorup@snm.ku.dk

J. Rabøl
Biological Institute, University of Copenhagen,
Universitetsparken 15,
DK-2100 Copenhagen Ø, Denmark

can thus be set up for the migratory orientation program in naïve migrants (ranging from the simplest compass orientation to the most advanced navigation capability) (cf. further Rabøl 1994):

- (1) Systems not involving navigational processes. (a_i) Simplest vector-orientation without compensation ('one-direction orientation', Perdeck 1958) and (a_{ii}) Vector orientation with compensation for wind drift during migratory flights. (b) Vector orientation with compensation on site (after drift) using reverse path integration (Wiltschko and Wiltschko 1976).
- (2) Systems involving navigational processes. (a) Vector orientation with compensation using navigation on site (W. Wiltschko in Rabøl 1972, 1994: Fig. 1d) and (b) goal area navigation (Rabøl 1969, 1970).

As navigation involves processes that have not been documented in migratory naïve birds (Berthold 1996; however, see Rabøl 1998), one should not accept such mechanisms before having excluded other possibilities as explanations of observed behaviours. However, failure to reject the simplest hypothesis in a particular experiment might just mean that the birds are unable to express a certain behaviour in a particular experimental setup. Furthermore, it is not unreasonable to assume such an additional orientation system, based on navigation, to be present even in first-time migrants. As we expect experienced birds to be able to navigate, a navigational system is expected to be built up already in the pre-migratory period (from post-fledging) and along the route allowing juvenile migrating birds to compensate at least back toward previously visited sites. This navigational system is unlikely to build on landmark recognition only (e.g. Mouritsen 2003).

One way to test the hypotheses is by testing the behaviour of displaced migrants. Perdeck (1958) performed an impressive displacement experiment involving more than 11,000 starlings of *Sturnus vulgaris*. The unaltered direction shown by the displaced juvenile birds suggested the use of the simplest vector orientation without compensation in first-time migrants, whereas experienced birds tended to orient back toward the previously experienced wintering site. However, the starling is a highly social, diurnal, short-distance migrant. This means that the result could be influenced by social interactions and that it cannot necessarily be generalised to nocturnal, long-distance migrants, where topographical features probably influence the migration routes less and the demands on precise orientation are supposedly much larger (e.g. Thorup and Rabøl 2001). Recent displacement experiments using satellite tracking of White Storks *Ciconia ciconia*, a highly social, diurnal, long-distance migrant, are very difficult to interpret (Chernetsov et al. 2004).

Many displacement experiments have been performed with nocturnal migrants, but the results are generally

considered insufficient for demonstrating a capability for detecting displacements (Berthold 1996; however, see Åkesson et al. 2005). Mouritsen (1999) reviewed many of the displacement experiments described in the literature and in most experiments he concluded that the simplest vector orientation without compensation was sufficient to explain the results. In experiments with wild birds, all factors cannot be controlled. The orientation of migrants often deviates significantly from the expected mean direction (the normal or standard direction) presumably resulting from, e.g. wind drift compensation or temporary reverse migration (e.g. Sandberg et al. 1988; Rabøl 1995; Åkesson et al. 1996; Åkesson 1999; Moore 1990). Therefore, many different experiments with birds transported to many different sites with varying positions in relation to e.g. the coast may be needed to detect compensation.

In this study, we review previous displacement experiments with migratory naïve bird migrants by performing a meta-analysis, i.e. by pooling the experiments contrary to just looking at single experiments. A meta-analysis takes into account the rather large scatter resulting from the varying conditions met by migrants in nature that cannot be controlled later in the laboratory. In the analyses, we included experiments where the orientation was tested after a real or simulated geographical displacement. For comparison with the autumn results, we performed a similar analysis on spring experiments where birds are presumably able to navigate, though the mechanisms are largely unknown (e.g. Mouritsen 2003).

Interpreting orientation reactions after displacements could be confounded by a simple mechanism called 'pseudo-navigation' by Rabøl (1998). In the Northern Hemisphere, stars in the southern sky 'move' more or less like the sun, i.e. their azimuth shifts are about 15° clockwise per hour. Birds using a time-compensated southern sky star compass are thus expected to shift their southerly orientation accordingly when displaced east or west (but not north or south) and perhaps also when their circadian clock has been reset (so-called clock-shift experiments). This shift in orientation will be in the direction expected of a movement compensating for a displacement (a compensatory response), but it is based on compass orientation only.

To distinguish between the different orientation systems, we tested whether the orientation overall differed from unaltered (or standard) orientation under the three conditions of tests (natural starry, overcast and simulated starry sky, respectively), and Table 1 lists the expected outcome of the different hypotheses. To test for differences from unaltered/standard orientation, we used two approaches: (1) binomial tests, where random variation from unaltered/standard orientation is expected to occur equally often to both sides (compensatory and non-compensatory) and (2) circular statistics on the observed directions in relation to unal-

Table 1 Expected directional response in orientation tests with displaced migrants or migrants experiencing a simulated displacement, depending on the orientation system used

Orientation system	Natural starry	Overcast	Planetarium
Vector orientation without compensation	+	Dis/+ ^a	+
Vector orientation with compensation	%	Dis/% ^a	+
Navigation	%	Dis/% ^a	%/+ ^a

We consider whether migrants are expected to show unaltered/standard orientation: ‘+’ indicate that the direction is not significantly different and ‘%’ that it is significantly different.

Dis is disoriented behaviour.

^a Depending on cue use. If the birds use stars for orientation/navigation the first option is expected.

tered/standard. Using the binomial data, we applied logistic regression to test for differences between groups and treatments. The binomial tests were performed considering the combined results of each significant displacement experiment (Table 2). The analyses using circular statistics were also performed on the combined results of each significant displacement experiment (for definition, see “Materials and methods” section), but additionally considering the orientation response of each individual bird.

After having tested whether the observed directions could be considered unaltered, we investigated which alternative fitted the observed orientation best: orientation back toward the start position (full compensation), toward a goal forward in the migration direction, or toward the final goal area (wintering or breeding site). Lastly, we investi-

Table 2 Number of autumn experiments with significant samples (i.e. consisting of four or more individuals and non-random orientation) showing a uni-modal response (or a bimodal response with a major and minor peak)

	<i>N</i>	Compensatory	Non-compensatory	<i>P</i>
All experiments	25	17	8	
Overcast only	5	2	3	
Starry only	20	16	4	0.007
Natural starry sky	13	11	2	0.012
Planetarium starry sky	7	5	2	

Also given is the number of experiments showing compensatory or non-compensatory orientation after displacement. The probability of the observed proportion of directional shifts to the compensatory side when assuming equal probabilities of shifting to both sides is given if the value is below 0.05 (binomial test, $p=q=0.5$). ‘Overcast only’ and ‘starry only’ are subgroups of ‘all experiments’. ‘Natural starry sky’ and ‘planetarium starry sky’ are subgroups of ‘starry only’.

gated whether the observed orientation responses during autumn could be due merely to ‘pseudo-navigation’.

Easy understanding of the meta-analysis requires the use of a consistent terminology; We use the following terminology throughout. An *orientation test* is a funnel test of the direction chosen by an individual bird (a direction). Each case of testing the orientation after a displacement (real or simulated) of a sample of birds of the same (or similar) species from one specific geographic location to another in a short period of time will be considered an *orientation experiment*. The result of an orientation experiment is the combined result (a mean vector) of a number of individual orientation tests. In a *planetarium experiment*, the orientation tests are performed on the same geographical location, with the planetarium starry sky simulating the sky from another geographical location.

Materials and methods

Data

We use experiments testing the orientation of displaced bird migrants in funnels from the literature for our analyses. The principal focus is on the orientation of naïve migrants. In autumn, all birds included in the analyses were juveniles with no previous experience of the migratory route ahead and the wintering area. Spring experiments were included for comparison. During spring, all birds may have been imprinted on previous migratory positions including the breeding/pre-migratory areas. We only included rigorously performed and described experiments, in this study, defined as being experiments where we were at least able to find information on the number of individuals involved and the mean vector (direction and concentration). We excluded the few experiments where the orientation after displacement was tested at or shortly after sunset. Furthermore, we excluded an experiment by Moore (1984) where the birds were moved 2,000 km, presumably directly forward, in the migration direction. In this case, it is not possible to determine the direction of a potential compensatory shift. Furthermore, the relative position of the expected wintering area in relation to the displacement site cannot be determined. The experiments included are listed in the Appendix.

If more than one test was carried out after displacement, we only included the first test. This was done for two reasons: First, we needed to be able to identify individual birds to perform the statistical analyses. Second, a compensatory response may well decrease with time and ‘pseudo-navigation’ is also influenced by time: Depending on direction (E or W), the expected ‘pseudo-navigation’ will advance (displacements to the E) or decrease (to the W) by 1° per day. In the experiments reported by Åkesson et al. 2005 in addition to

those reported in Åkesson et al. (2001), the same individuals were tested at several sites. Because the expectations in these displacements are similar and the same individuals were displaced repeatedly, these experiments do not provide independent samples. Thus, we have included only the first displacements performed under a starry sky and overcast, respectively.

Birds tested under planetarium skies were experiencing a rotating sky. In the experiments performed by JR the sky rotated continuously, but the planetary sky used by Emlen rotated four times and that by Sauer rotated twice every hour. A stationary planetarium sky may be experienced by the birds as a continuous westward displacement. We have included a few experiments involving displacements simulated using stationary planetarium skies (e.g. Mouritsen and Larsen 2001). In the experiments by Mouritsen and Larsen (2001) which lasted throughout the night, we considered the orientation during the first 2 h of ‘displacement’ only. For a thorough discussion about how birds interpret changes in planetarium skies, cf. Wallraff (1960a,b).

For each experiment, expected migration direction (=standard) at the capture site, and wintering and breeding grounds were identified using Zink (1973–1985) or Cramp (1988, 1992) and Cramp and Perrins (1993), except for North American species where the information was found in the original papers. In a few cases, the expected normal direction differed regionally from the overall mean migration direction. This was the case for some of the birds trapped in Jutland, Denmark that presumably were of Norwegian origin with a standard direction E of S (e.g. Rabøl 1969, 1995). Expected normal directions and positions of the goal, wintering, and breeding areas for each experimental group are listed in the ESM S1.

When birds were tested at the site of trapping, we used the observed direction as expected normal/unaltered direction in the analyses. In most cases, there were only minor differences between expected and observed direction, and running the analyses using the expected normal direction instead of the observed direction yielded very similar results.

To control for an effect of bias in the estimated directions, we also ran the analyses replacing estimated directions with values 20° above or below the original estimate and with an overall expected direction of 180°. Very similar results were obtained with these changed estimates.

The analysis is largely based on data compiled by Rabøl and Thorup (2001). Seven new experiments, carried out or published since 2001, are included (#29, #38–39, and #88*–92* in Appendix).

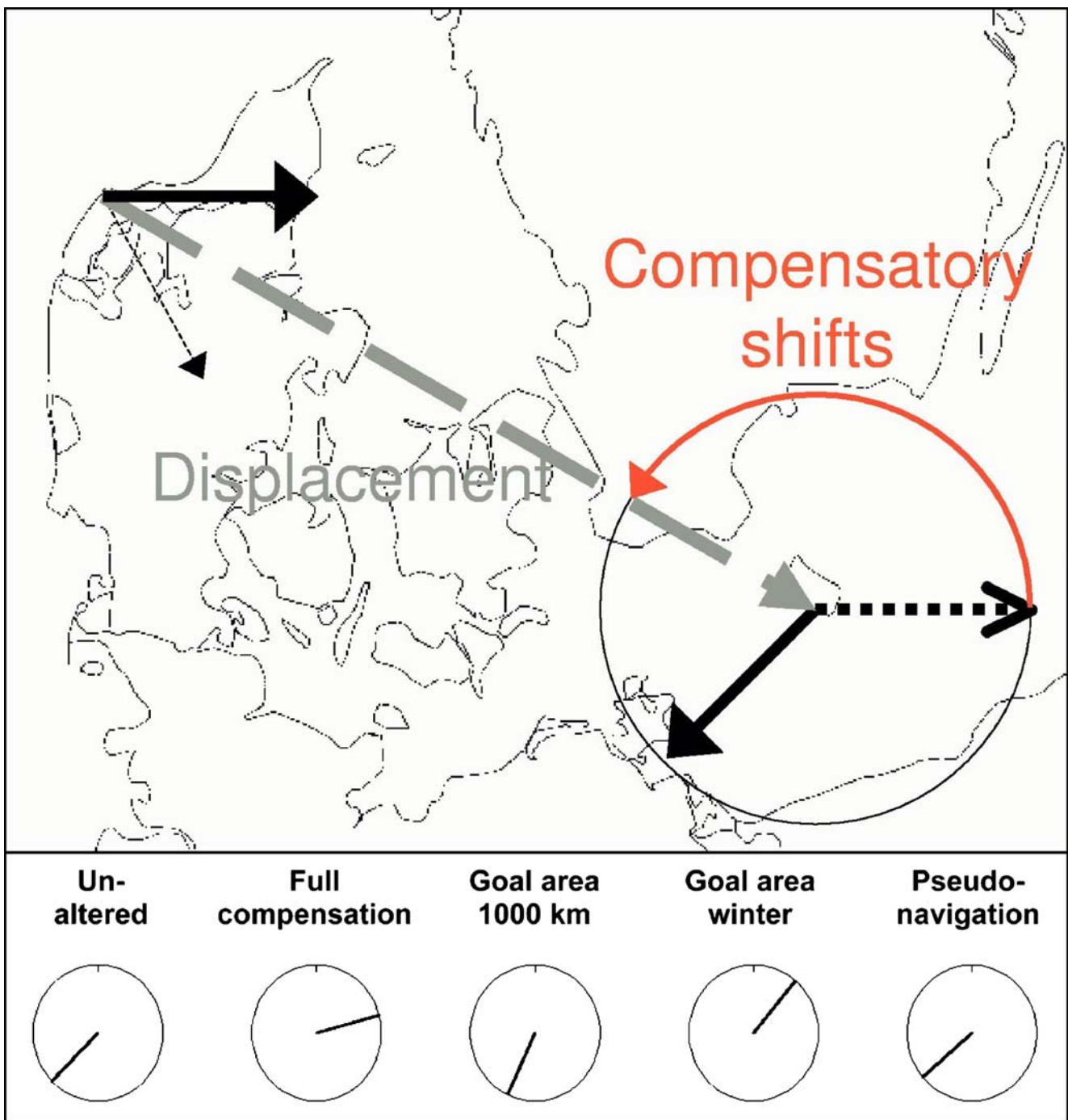
Analysis of circular data

Figure 1 shows the orientation response of a sample of displaced birds. The significance of sample orientations

(mean direction α and concentration r) was tested using the Rayleigh test (Batschelet 1981). Mean vectors are given as e.g. $213^\circ-0.477^{**}$ ($n=25$), where $\alpha=213^\circ$, $r=0.477$, and $n=25$, and significance of r is denoted by $*P<0.05$, $**P<0.01$, or $***P<0.001$. The significance of any observed shift in orientation after displacement for each experiment between the observed and the expected (standard) direction was tested using a confidence interval (CI) test (Batschelet 1981). However, the significance of these differences was not considered for the meta-analyses.

Grand mean vectors of experiments were calculated as the mean vector of the mean direction vectors in separate experiments. When considering experiments, each experiment contributed a unit vector (a direction) irrespective of the directional concentration obtained in the experiment. The orientation responses to displacements in orientation experiments were considered without the inclusion of non-significant ‘sample’ orientations. A ‘sample’ was considered non-significant if less than four individuals were included or the orientation after displacement of the ‘sample’ could not be distinguished from random. When considering individual birds, each bird contributed a unit vector. Because the result of each displacement experiment is the mean vector of individual unit vectors, sample vectors for each displacement experiment can be calculated as n times the sample mean vector. The overall mean vector of individual unit vectors can then be calculated as the sum

Fig. 1 Example of the analysis of a displacement experiment with Garden Warblers displaced from Hanstholm to Dueodde in Denmark (#11 in the Appendix, Rabøl 1970). Geographical N is upwards and the *solid black arrows* show the observed orientations in Hanstholm (E) and at Dueodde (SW), respectively. The *dotted black arrow* shows the direction of unaltered orientation at Dueodde. The *curved arrow* indicates the sector of compensatory orientation. In this case, the orientation is not falling in the compensatory sector, and because the orientation shift is not to the compensatory side [i.e. falls in the half-circle (from W over N to E) of a compensatory orientation shift], the observed change of direction is calculated as negative (−145°) and depicted to the left in Fig. 3, upper left figure. The *small dotted black arrow* shows the expected orientation in Hanstholm (SSE). If the expected orientation had been considered instead, the orientation at Dueodde would, in this experiment, have been considered compensatory, i.e. falling within the compensatory sector (+78°). The *lower pane* shows the observed orientation response calculated in relation to standard orientation, full compensation, a goal 1,000 km ahead, the goal area in winter or ‘pseudo-navigation’. If compensating fully (i.e. back toward the site of trapping) for the displacement toward 118° the birds should orient toward 298°. However, the orientation is directed toward 236°, i.e. 62° clockwise (cf. Fig. 3). The birds’ orientation is approximately the opposite direction than a goal area 1,000 km ahead in the unaltered direction, but is quite similar to the direction expected if the orientation is directed toward the wintering area. The observed change in orientation in relation to the direction toward wintering area is in a compensatory direction, and it is therefore depicted as a clockwise shift. As Dueodde is situated 7° to the east of Hanstholm, the orientation at Dueodde (236°) changes to 229° if corrected for ‘pseudo-navigation’; i.e. in relation to corrected for ‘pseudo-navigation’ it is −138° (Fig. 5). For additional example calculation see ESM S2



of the sample vectors divided by the total number of individuals in all the experiments included.

Meta-analysis

We include published displacement experiments in the analyses. These had a rather similar design, with wild-caught birds tested in orientation cages after a displacement. However, in some other aspects the experiments differed, e.g. by means of transport and possibly means of cues

available during transport between experiments. In general, including various treatments (e.g. means of transport) in a meta-analysis is not problematic as long as they do not introduce bias. Because these will increase scatter, they will make finding consistent patterns more difficult.

The unit when considering the orientation experiments is a significant sample orientation of at least four birds. In the individual analyses, the unit is the orientation of an individual bird. In meta-analysis, it is recommended to weight effect sizes by the inverse of their sampling

distributions (Gurevitch et al. 2001). However, the sampling distributions of the experiments included are not known. Hence, we choose the two extreme forms of weighting (unweighted and each experiment weighted by number of individuals) and included both forms to control for an effect of weighting.

Because we do not know the sampling distributions of the experiments and the statistical properties of these statistics in a combined analysis, we choose to use standard parametrics on the experimental and individual data, respectively, as advocated by Gurevitch and Hedges (1999). Using this procedure will most likely be conservative regarding conclusions as to whether distributions differ from expected ones. If the error variances do not differ substantially between experiments, the type I error rate should be close to the intended value, but the precision, statistical power and type II error rates will be compromised (Gurevitch et al. 2001).

To reveal whether the orientation after displacement was unaltered/standard or compensatory, we used a system-wide test procedure. Because bimodal directional distributions cannot be assigned unambiguously as either compensatory or not, these were omitted from the analyses (#81–82). We used two methods to investigate whether the overall orientation could be considered as compensatory. A binomial test was used to test whether changes in orientation were equally often to the compensatory and the non-compensatory side ($p=q=0.5$). Secondly, we pooled all experiment vectors (individual or sample mean vectors) in a group (starry, planetarium or overcast, respectively) with orientation to the compensatory side calculated as positive (and depicted in figures as clockwise shifts). From this pooled ‘meta’-sample, the grand mean vector was calculated. If the direction of the grand mean vector deviated significantly (clockwise) from 0° (i.e. unaltered/standard) according to a confidence interval test, then the compensatory orientation after the displacement was considered statistically significant.

We used logistic regression to investigate potential effects on the compensatory orientation response in relation to unaltered/standard orientation of different treatments, i.e. cloud cover (starry or overcast), displacement method (by man or planetarium), presence of a control group (no controls, tests using other individuals than those displaced, and true controls using same individuals), season (autumn or spring), and author (Rabøl and co-workers vs other authors). Logistic regressions were performed using SAS v. 8.02 software (proc LOGISTIC).

We considered the orientation after the displacements in relation to (1) unaltered/standard orientation, (2) full compensation with the starting site as a goal, (3) a ‘goal’ 1,000 km (autumn) or 500 km (spring) away from the start site in the direction of unaltered/standard, and (4) the

wintering area (autumn) or breeding area (spring) of the species/population under consideration (see Fig. 1). These predicted directions were all calculated as loxodromes (rhumbline routes) (calculated directions given in S1). In experiments under a starry sky, the capture site was used as the starting site. For some of the planetarium experiments, the planetarium sky start-position was used as starting site. Different goal distances were used for spring and autumn. The distance to a possible ‘goal’ (of maximum survival). In most cases, in spring is probably less than 1,000 km, whereas the distance to the wintering ground in autumn is normally at least 2,000 km, and mostly (in the long-distance migrants) at least 5,000 km.

The observed orientation in relation to these different predicted directions was calculated for each experiment as observed minus predicted direction. To investigate a possible effect of birds being displaced to the right or left of the unaltered/standard direction, we used expected minus observed direction for birds displaced to the right. Thus, compensatory shifts will be positive numbers irrespective of whether the displacement was to the right or left of the unaltered/standard direction. This procedure seems robust in reference to the directional distribution of the displacements.

The overall mean vectors of displacement directions in relation to geographic north in autumn are $213^\circ-0.277$ ($n=25$) and $206^\circ-0.395^{***}$ ($n=459$) for experiments and individuals, respectively. In spring, the mean vectors are $311^\circ-0.534^*$ ($n=10$) and $295^\circ-0.259^{***}$ ($n=164$) for experiments and individuals, respectively. In autumn, the mean directions are rather close to the expected mean/standard direction indicating that most birds were moved forward in the migration direction, with equal numbers of birds displaced to the northwest and the southeast. However, in spring, the mean directions of displacements are different from the expected unaltered/standard direction. The directions of displacements in relation to unaltered/standard directions are shown in Fig. 2 (Table 3). In autumn, starry and overcast displacement directions differed only little from unaltered/standard directions (indicating the equal numbers of birds were displaced to the left and right of the expected mean/standard direction), whereas the differences were somewhat larger in spring. This could introduce some bias in the spring analyses.

Another potential cause of bias in our analysis could be that only experiments providing positive evidence for compensation are being published. However, such an effect is difficult to investigate. At least, regarding the experiments by JR, we could find no such tendency in unpublished experiments performed by JR as the unpublished experiments showed similar results to the published ones.

The orientation after correction for ‘pseudo-navigation’ was calculated as unaltered/standard direction minus degrees of longitude displaced. We calculated these directions for all

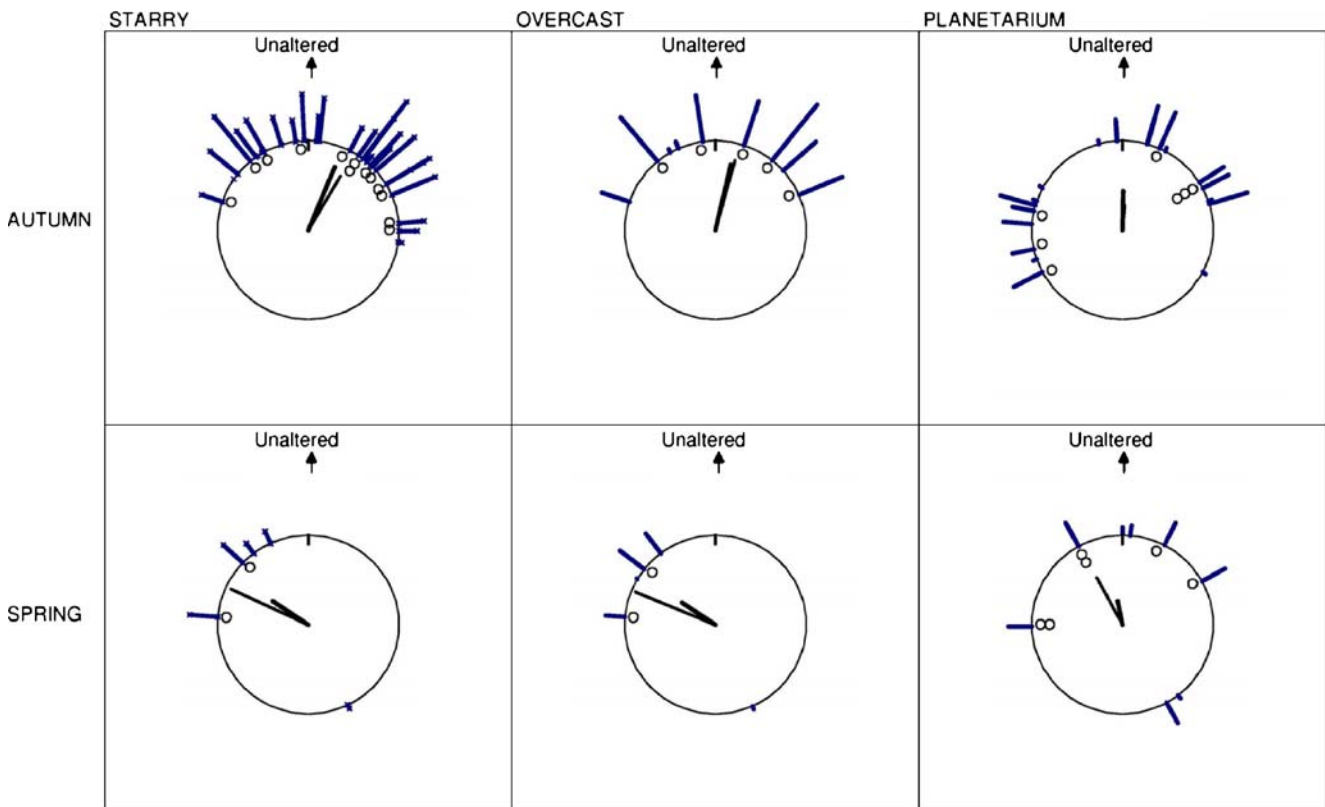


Fig. 2 The directional distribution of displacement directions in relation to standard (expected/observed) directions (upward) for the experiments (small circles inside circle periphery) and individuals (bars outside circle periphery) included in the categories considered in the analysis. If a sample is considered 'insignificant', only the individual orientations are shown (i.e. only the bar and no corresponding circle). The length of each bar showing individual orientations indicates the relative contribution of each experiment to the overall mean. This contribution is dependent on number of

individuals and their mean directional concentration. Grand mean vectors of experiments (thin line) and individuals are shown for each category and season. See Table 3 for summary statistics of the mean vectors. The overall grand mean vectors of displacement directions in relation to standard directions are $23.4^{\circ}-0.59^{**}$ ($n=25$) and $16.9^{\circ}-0.67^{***}$ ($n=459$) for experiments and individuals, respectively, in autumn, and $-47.9^{\circ}-0.70^{*}$ ($n=10$) and $-41.2^{\circ}-0.34^{***}$ ($n=164$) for experiments and individuals, respectively, in spring

autumn experiments under a starry sky and in the planetarium, were birds are presumably most likely to use a time-compensated southern sky star compass. Distinguishing between 'pseudo-navigation' and true compensation becomes difficult over larger distances. Thus, we also calculated these directions in subsamples based on longitudinal displacements between 2.5 and 65° and no more than 30° S (#2, #5–11, #15–18, #22–26, #40–45, #48, #50–52, and #55–56).

'Best' explanation

For each group and theoretical prediction, the experiments were pooled, and the results evaluated using the grand mean vector. The prediction providing the 'best' explanation of the observed directional shifts was investigated using the 'homeward' component, cosine of mean direction multiplied by the concentration ($\cos(\alpha)*r$), where the mean vector is calculated in relation to one of the theoretical predictions (standard direction or direction toward one of the goal areas).

For tests performed in autumn under a starry sky, we made a more detailed investigation of a possible goal area for a more homogenous sub-sample, where birds were displaced only a shorter distance (less than 1,000 km) and tests were performed shortly after the trapping and on one of the first nights after the displacement (#4–16, #17, #22, #22–26, #89*–92*; $n=23$). For tests performed under a planetarium sky, we also considered a more homogenous sub-sample. This consisted of experiments performed in the Tycho Brahe and Steno planetarium in Denmark (#40–50, $n=11$).

Results

In total, we found 80 published experiments testing the orientation of displaced migrants with enough information to be included in our analyses. These are listed in the Appendix.

Table 2 summarises the orientation response in the significant experiments. Overall, the direction of shifts in orientation (either compensatory or non-compensatory)

Table 3 Summary statistics of the mean vectors of displacement directions shown in Fig. 2 in relation to standard (expected/observed) directions

	Starry		Overcast		Planetarium	
	Exp	Ind	Exp	Ind	Exp	Ind
Autumn						
<i>n</i>	13	246	5	98	7	115
<i>r</i>	0.70	0.77	0.81	0.75	0.27	0.43
α	30.5°	22.4°***	15.5°	13.1°***	5.5°	1.1°
$\cos(\alpha)*r$	0.61	0.71	0.78	0.73	0.27	0.43
Spring						
<i>n</i>	2	41	2	43	6	80
<i>r</i>	0.94	0.47	0.95	0.44	0.60	0.26
α	-65.0°	-56.5°***	-67.5°	-56.7°***	-28.6°	-12.0°
$\cos(\alpha)*r$	0.40	0.26	0.36	0.24	0.52	0.26

r values in bold are significant (at least $P < 0.05$) according to the Rayleigh test and α values in bold differ significantly from zero according to the confidence interval test (significance level indicated by * $P < 0.05$, ** $P < 0.01$ or *** $P < 0.001$, respectively).

Exp denotes data for experiments, Ind for individuals, *n* denotes number of experiments (left) or individuals (right), *r* directional concentration of the mean vector, α mean angle, and $\cos(\alpha)*r$ the homeward component.

between trapping and displacement site could be considered random. However, for the starry experiments considered separately, the direction of shifts in orientation could not be considered random, with more shifts to the compensatory side, whereas for overcast experiments the orientation could be considered random (Table 2).

For all experiments with a significant response, logistic regression supported an effect of cloud cover (starry or overcast) on the likelihood of the orientation response to be to the compensatory side (i.e. in the compensatory half-circle; $P = 0.009$) with more compensatory responses under a starry sky. No other variables contributed significantly: in the full logistic regression model the non-significant direction of effects resulting in compensatory responses were autumn, planetarium experiments performed by JR and co-workers.

Autumn experiments

Overall, the orientation observed under a starry sky after displacements in autumn (Fig. 3, left and right columns; Table 4) was turned in a compensatory direction from standard/unaltered orientation (natural and planetarium starry skies, individual and experiments: $P < 0.01$, except individuals under planetarium skies where $P < 0.05$). Under an overcast sky, the sample was not significantly oriented (Fig. 3, middle column; Table 4), which was probably only partly due to small sample size, and the mean directions differed obviously from those observed under a starry sky (Fig. 3, left and right; Table 4).

The compensatory direction observed under starry skies was deviating less from unaltered/standard orientation than expected if birds were oriented toward the trapping site, i.e. full compensation for the displacement (natural starry skies, individual and experiments: $P < 0.01$; planetarium starry skies: $P > 0.05$ and $P < 0.05$, experiments and individuals, respectively). The mean sample direction was not different from the direction to a goal area 1,000 km ahead or the winter area. The 'best' fit (i.e. maximum 'goal'-ward component and α close to 0°) under a starry sky was seen toward the wintering area ($\cos(\alpha)*r = 0.66$ and 0.31, experiments and individuals, respectively) in natural starry experiments and toward a goal area 1,000 km ahead ($\cos(\alpha)*r = 0.68$ and 0.39, experiments and individuals, respectively) in planetarium experiments. For a more homogenous sub-sample of the tests, including short-distance displacements with tests performed shortly after displacements only, the best fit was very similar (toward wintering area: $\cos(\alpha)*r = 0.63$ and 0.32, experiments and individuals, respectively, in natural starry experiments; toward goal area 1,000 km ahead: $\cos(\alpha)*r = 0.85$ and 0.40, experiments and individuals, respectively, in planetarium experiments).

Spring experiments

Much fewer experiments were performed in spring (Fig. 4; Table 5), and considering experiments the orientation was not directed in any cases. The patterns seen under natural starry skies and overcast were rather similar to those seen in autumn (Fig. 3; Table 4). However, the orientations observed under a planetarium starry sky (Fig. 4, right column; Table 5) differed from those observed in autumn. The overall directions were not significantly different from standard/unaltered orientation, and the largest 'homeward' component ($\cos(\alpha)*r = 0.66$ and 0.40, experiments and individuals, respectively) was also found toward standard/unaltered.

Fig. 3 Displacements in autumn tested under a starry sky (left column), overcast sky (middle column) and in planetarium (right column). The orientation of experiments (small circles inside circle periphery) and individuals (bars outside) is depicted in relation to an expected direction (upward): standard/unaltered (top row), the direction toward the starting site (second row from top), the direction toward a goal 1,000 km ahead of the starting site in the standard/unaltered direction (third row) and the direction toward the wintering area of the species/population under consideration (fourth row). See Table 4 for summary statistics of the mean vectors. In relation to unaltered/standard orientation, clockwise shifts can be considered as compensatory. When considering full compensation, anti-clockwise shifts indicate less than full compensation toward trapping site and clockwise shift over-compensation. Considering goal areas, the most important thing is the length of the 'goal-ward' component; clockwise shifts indicate compensation and anti-clockwise shift over-compensation. For further explanation, see Fig. 2

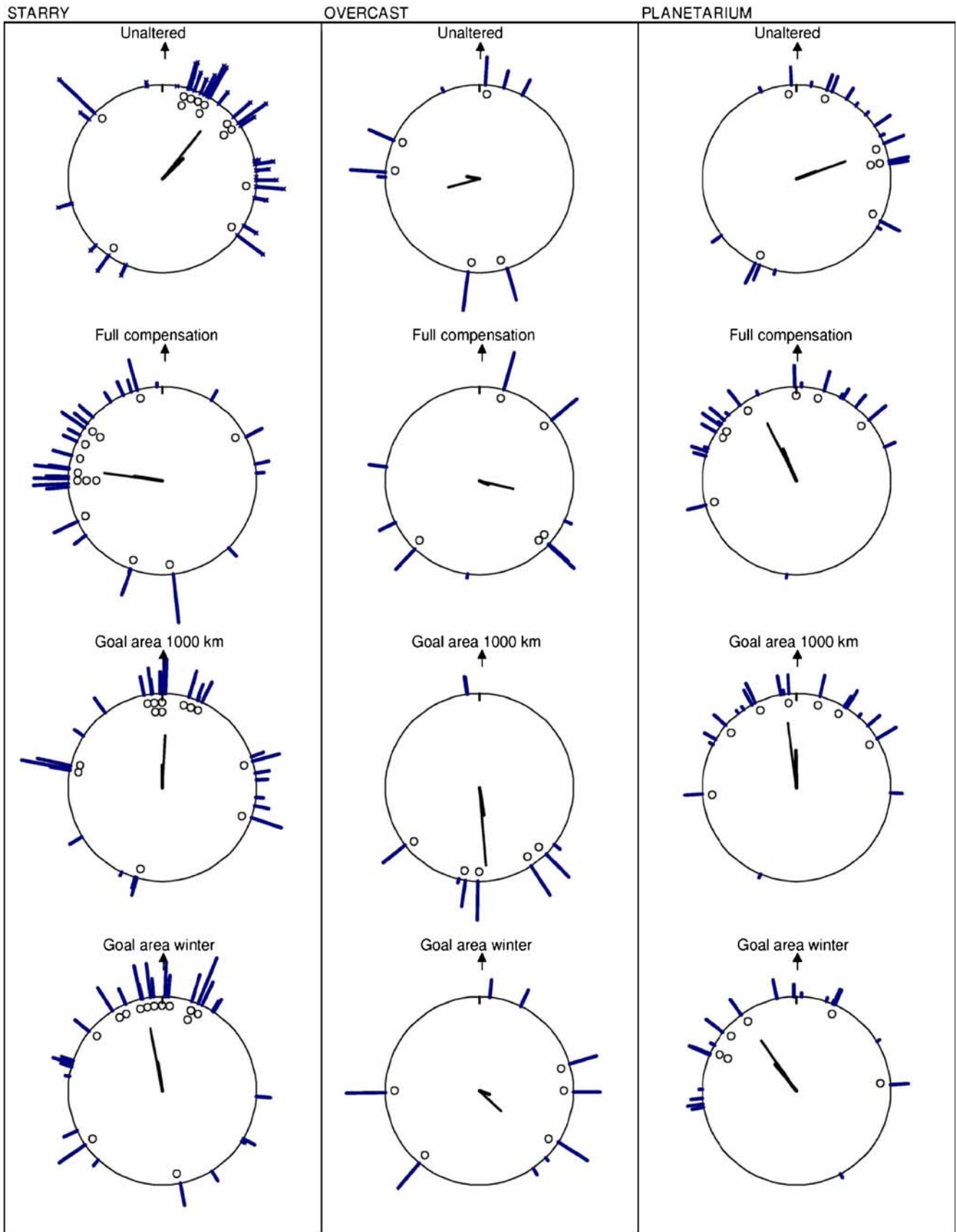


Table 4 Summary statistics of the mean vectors of the autumn displacements shown in Fig. 3

	Starry		Overcast		Planetarium	
	Exp	Ind	Exp	Ind	Exp	Ind
<i>n</i>	13	246	5	98	7	115
Unaltered						
<i>r</i>	0.64	0.31	0.34	0.13	0.55	0.22
α	38.7°*	45.5°***	-105.5°	-81.8°	70.4°***	70.5°*
$\cos(\alpha)*r$	0.50	0.21	-0.09	0.02	0.19	0.07
Full compensation						
<i>r</i>	0.63	0.30	0.37	0.10	0.68	0.36
α	-82.8°***	-80.7°***	104.1°	113.8°	-27.4°	-23.2°*
$\cos(\alpha)*r$	0.08	0.05	-0.09	-0.04	0.61	0.33
Goal area 1,000 km						
<i>r</i>	0.55	0.24	0.83	0.30	0.69	0.39
α	3.0°	0.4°	175.3°	171.4°***	-7.7°	-1.3°
$\cos(\alpha)*r$	0.55	0.24	-0.83	-0.29	0.68	0.39
Goal area winter						
<i>r</i>	0.67	0.31	0.31	0.11	0.65	0.36
α	-10.9°	-9.5°	133.4°	108.4°*	-35.3°	-38.8°
$\cos(\alpha)*r$	0.66	0.31	-0.22	-0.04	0.53	0.28

For further explanation, see Table 3.

Pseudo-navigation

After correction for pseudo-navigation, the observed proportion of directional shifts to the compensatory side was still significantly larger in starry sky experiments (in total 15 of 20 natural and planetarium experiments; $P=0.025$, binomial test, $p=q=0.5$). Correction for pseudo-navigation improved the description of the observed orientations in comparison to standard/unaltered orientation under starry (natural and planetarium) skies (Fig. 5; Table 6). However, under a natural starry sky, the orientation was still turned to the compensatory side ($P<0.01$) for individuals, whereas the shift was not significant when looking at experiments which was also the case under a planetarium starry sky for both individuals and experiments. Still, orientation toward the winter area fitted far better in natural starry experiments and toward a goal area 1,000 km ahead in planetarium experiments (Fig. 3; Table 4).

When looking at the more ideal sample for separating pseudo-navigation from compensation (shorter distance displacements with tests performed shortly after trapping and displacement: #4–16, #17, #22, #22–26, #89*–92*; $n=23$), less improvement resulted from the correction for pseudo-navigation, although the overall pattern was rather similar. Under a natural starry sky, the orientation was turned to the compensatory side ($P<0.01$, CI test; 47.8° – 0.35° ***; $n=154$) for individuals, whereas the shift was only near-significant when looking at experiments ($0.10<P<0.05$; 40.8° – 0.61° **; $n=19$). Similarly, under a planetarium starry sky, the orientation was turned to the compensatory side ($P<0.01$; 36.2° – 0.41° ***; $n=75$) for individuals, but too few shorter-

distance displacements experiments were performed (47.5° – 0.99° **; $n=4$) to test the difference.

Discussion

Overall, the orientations observed in autumn supported the hypothesis that birds can use star navigation to compensate displacements (compensation toward a goal area under both natural and planetarium starry skies and overall disorientation under overcast). This conclusion held whether considering experiments or individuals. In contrast, spring experiments did not show similar compensation under planetarium starry skies, perhaps indicating that the stars are involved in determining a navigational response in autumn but not in spring.

Under the natural starry sky, probably only a part of the observed shift could be explained on basis of pseudo-navigation. For planetarium experiments, pseudo-navigation explained more of these shifts. Because the birds in most displacements were exposed to the sunset/early night stars before the testing or these were carried out several

Fig. 4 Displacements in spring tested under a starry sky (left column), overcast sky (middle column) and in planetarium (right column). The orientation is depicted in relation to an expected direction (upward), standard/unaltered (first row), the transferred direction toward the capture/start site (second row), the transferred direction toward a goal 500 km ahead (third row) and the transferred direction toward the breeding/fledging site of the species/population under consideration (fourth row). See Table 5 for summary statistics of the mean vectors. For further explanation, see Fig. 2

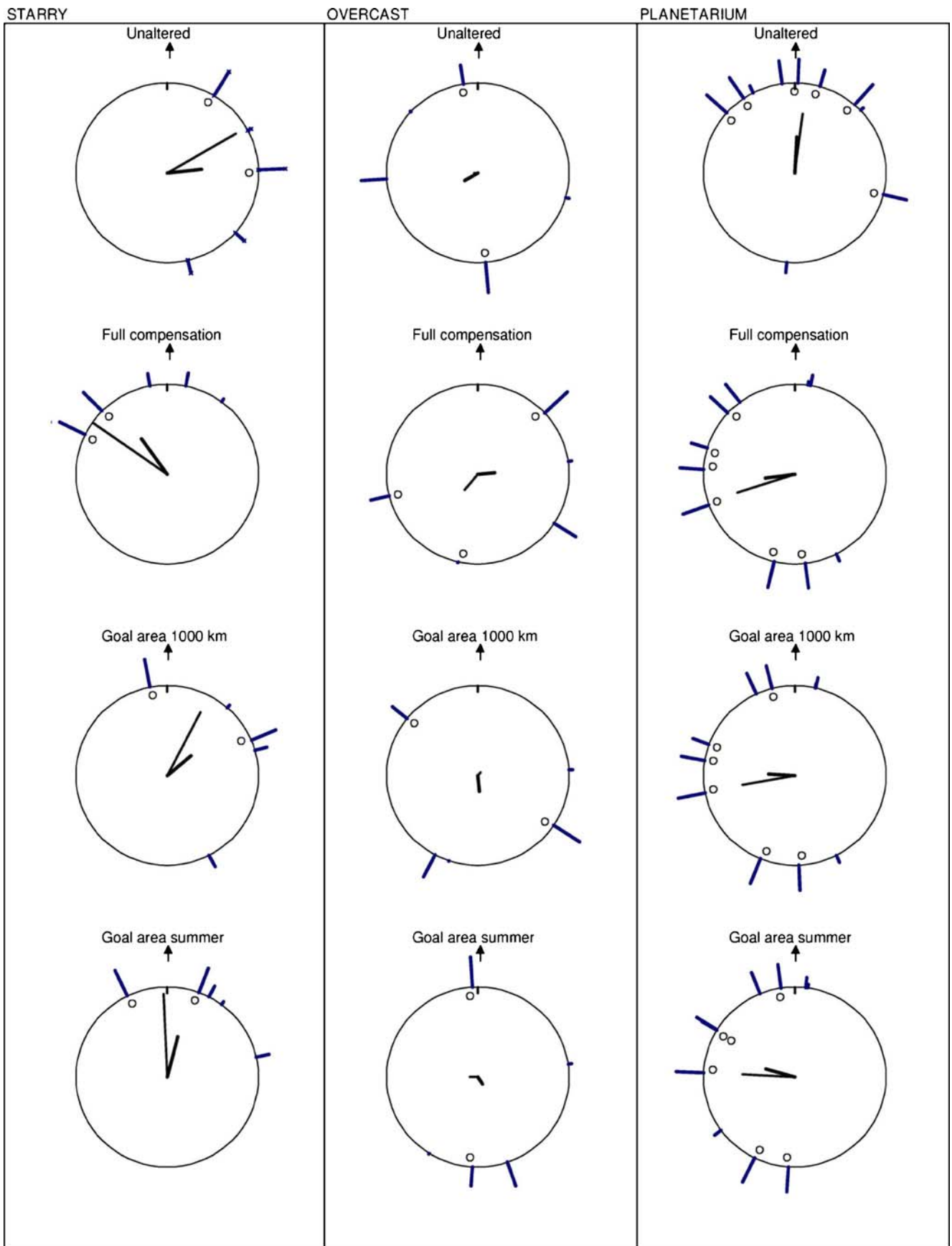


Table 5 Summary statistics of the mean vectors of the spring displacements shown in Fig. 4

	Starry		Overcast		Planetarium	
	Exp	Ind	Exp	Ind	Exp	Ind
<i>n</i>	2	41	2	43	6	80
Unaltered						
<i>r</i>	0.87	0.38	0.04	0.17	0.66	0.40
α	60.0°	83.8°**	-97.5°	-121.7°	7.6°	3.5°*
$\cos(\alpha)*r$	0.43	0.04	-0.01	-0.09	0.66	0.40
Full compensation						
<i>r</i>	0.98	0.48	0.23	0.18	0.66	0.33
α	-55.0°	-35.5°**	-141.1°	85.6°	-108.3°	-98.0°**
$\cos(\alpha)*r$	0.56	0.39	-0.2	0.0	-0.21	-0.05
Goal area 1,000 km						
<i>r</i>	0.79	0.34	0.04	0.18	0.58	0.29
α	27.5°	50.0°*	37.5°	175.1°	-100.4°	-86.8°**
$\cos(\alpha)*r$	0.70	0.22	0.03	-0.18	-0.10	0.02
Goal area winter						
<i>r</i>	0.92	0.46	0.09	0.10	0.57	0.33
α	-2.5°	14.4°	-90.0°	146.2°	-87.2°	-73.7°**
$\cos(\alpha)*r$	0.92	0.45	0.00	-0.08	0.03	0.09

For further explanation see Table 3.

nights and days after the trapping/displacement, we would expect such birds to (re-)calibrate their stellar south compass, and ‘pseudo-navigation’ will not be possible. This indicates that migrants use reverse path integration for compensation or, alternatively, a navigational mechanism.

Furthermore, the displaced migrants generally showed a ‘goal area’ directed orientation after displacement. Because of the large variation in experimental set-ups included in our study, we expect a large variation regarding the distance to a possible goal somewhere along the standard/unaltered direction.

The difference in spring and autumn planetarium experiments indicating that the stars are involved in determining navigation in autumn but not in spring, could be because

spring birds already knowing their goal area from previous experience can accept more drift as predicted by optimal use of variable winds (Alerstam 1979), and thus do not tend to compensate en route. This is also consistent with the general lack of wind compensation in migratory North American thrushes in spring (e.g. Cochran and Kjos 1985; Cochran et al. 2004).

Based largely on large-scale free-flight release experiments with displaced short-distance migrants, first-time migrants are generally considered not to be able to compensate displacements (e.g. Perdeck 1958). Many studies have aimed at testing the possibility that migrants could be able to use the stars to detect displacements also in naïve migrants. Reviewing this issue, Berthold (1996)

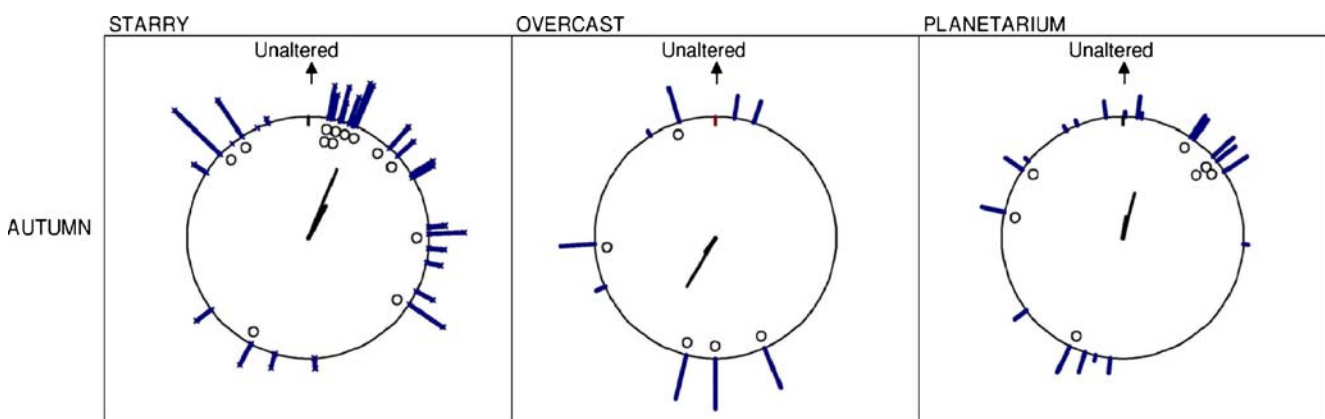


Fig. 5 The unaltered orientation corrected for ‘pseudo-navigation’ (upward). See Table 6 for summary statistics of the mean vectors. Birds using a time-compensated southern sky star compass are expected to shift their southerly orientation in the direction expected

for compensating a displacement based on compass orientation only. This shift was termed ‘pseudo-navigation’ by Rabøl (1998). For further explanation, see Fig. 2

Table 6 Summary statistics of the mean vectors of the unaltered orientation corrected for ‘pseudo-navigation’ shown in Fig. 5

	Starry		Overcast		Planetarium	
	Exp	Ind	Exp	Ind	Exp	Ind
Autumn						
<i>n</i>	13	246	5	98	7	115
<i>r</i>	0.61	0.29	0.47	0.14	0.37	0.16
α	23.0°	30.0°***	-149.8°	-145.0°	15.5°	10.1°
$\cos(\alpha)*r$	0.56	0.25	-0.40	-0.12	0.36	0.16

For further explanation, see Table 3.

concluded: ‘So far, however, there is no convincing evidence for such navigation systems in naïve migrants’. However, Åkesson (2003) discusses the possibility of compensation also in juvenile migrants, and experiments by Åkesson et al. 2005 suggest that both adult and juvenile white-crowned sparrows *Zonotrichia leucophrys gambelii* possess a navigation system based on a combination of celestial and geomagnetic information to correct for longitudinal displacements. Similarly, our results indicate that such navigation systems are found in naïve migrants.

Mouritsen (2003) suggests that experienced birds navigate toward known breeding and wintering sites. Our study suggests that a similar mechanism is working already in first-time migrants. Using stars to detect a displacement from a position experienced previously (full compensation) is not

principally different from homing to familiar breeding or wintering areas as performed by experienced migrants. Observed compensation could be the result of a combination of navigation toward a previous, known position and orientation in the standard direction. Thus, the compensatory behaviour observed in this study does not require that birds be able to navigate toward an unknown goal.

Conclusion

The orientation experiments after a displacement—real or simulated—suggest that migrant birds are able to compensate for a displacement and possibly that some sort of navigational mechanism is involved.

At least some simple form of sign navigation system (Wallraff 1974) seems to be involved in the orientation after the planetarium ‘displacements’ because in these experiments no real transports are carried out and therefore compass based reverse path integration cannot be involved. Furthermore, the lack of compensation under an overcast sky is indicative of a central role of a stellar-based system.

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Appendix

Table 7 Autumn experiments. (ID identifies individual experiments in the ESM S1.)

ID	Species	Trapped at		Displaced to		# birds	Reference
Real displacement: tested under a natural starry sky							
1	Northern Wheatear	Tiksi (Siberia)	RU	Kola (site 6)	RU	20	Åkesson et al. (1995)
2	Bobolink	North Dakota	US	San Francisco	US	1	Hamilton (1962a)
3	Bobolink	New York	US	San Francisco	US	2	Hamilton (1962b)
4	Pied Flycatcher	Christiansø	DK	Czech Rep.	CZ	16	Mouritsen and Larsen (1998)
5	Pied Flycatcher	Christiansø	DK	Klelund	DK	14	Mouritsen and Larsen (1998)
6	Garden Warbler	Blåvand	DK	Ottenby	SE	6*	Rabøl (1969)
7	Lesser Whitethroat	Ottenby	SE	Blåvand	DK	7**	Rabøl (1969)
8	Redbacked Shrike	Ottenby	SE	Blåvand	DK	5**	Rabøl (1969)
9	Willow Warbler	Hanstholm	DK	Dueodde	DK	12**	Rabøl (1970)
10	Willow Warbler	Hanstholm	DK	Dueodde	DK	4**	Rabøl (1970)
11	Garden Warbler	Hanstholm	DK	Dueodde	DK	7*	Rabøl (1970)
12	Redstart/Garden Warbler	Skagen	DK	Langeland	DK	7	Rabøl (1970)
13	Redstart/Garden Warbler	Skagen	DK	Langeland	DK	8**	Rabøl (1970)
14	Garden Warbler/Redstart	Skagen	DK	Tisvilde	DK	13*	Rabøl (1970)
15	Garden Warbler/Redstart	Akerøya	NO	Blåvand	DK	14	Rabøl (1972)
16	Redstart/Whinchat	Akerøya	NO	Christiansø	DK	9	Rabøl (1972)
17	Robin	Christiansø	DK	Blåvand	DK	6**	Rabøl (1975)
18	Robin	Christiansø	DK	Gomera	ES	12	Rabøl (1981)
19	Pied Flycatcher	Christiansø	DK	Kenya	KE	10	Rabøl (1993)
20	Lesser Whitethroat	Christiansø	DK	Kenya	KE	7	Rabøl (1993)
21	Garden Warbler	Christiansø	DK	Kenya	KE	8	Rabøl (1993)
22	Pied Flycatcher	Christiansø	DK	Skallingen	DK	8	Rabøl (1994)
23	Pied Flycatcher	Christiansø	DK	Skallingen	DK	14	Rabøl (1994)
24	Pied Flycatcher	Christiansø	DK	Skallingen	DK	12	Rabøl (1994)
25	Pied Flycatcher	Christiansø	DK	Skallingen	DK	13*	Rabøl (1994)
26	Redstart/Garden Warbler	Blåvand	DK	Christiansø	DK	10**	Rabøl (1994)
27	Whitethroat	Germany	DE	Namibia	NA	1	Sauer and Sauer (1959)
Real displacement: tested under a natural or simulated overcast sky							
28	Northern Wheatear	Tiksi (Siberia)	RU	Petchora (site 4)	RU	20	Åkesson et al. (1995)
29	White-crowned Sparrow	Canada (site 1)	CA	Canada (site 4)	CA	13*	Åkesson et al. (2001)
30	Pied Flycatcher	Christiansø	DK	Klelund	DK	12	Mouritsen and Larsen (1998)
31	Garden Warbler	Blåvand	DK	Ottenby	SE	8*	Rabøl (1969)
32	Robin	Christiansø	DK	Blåvand	DK	13**	Rabøl (1975)
33	Pied Flycatcher/Garden Warbler	Christiansø	DK	Kenya	KE	16	Rabøl (1993)
34	Pied Flycatcher	Christiansø	DK	Skallingen	DK	13**	Rabøl (1994)
35	Whitethroat	Germany	DE	Namibia	NA	1	Sauer and Sauer (1959)
36	American Golden Plover	Alaska	US	San Francisco	US	2	Sauer (1963)
Real displacement: tested under planetarium starry sky							
37	Indigo Bunting	43°N, -84°E	US	43°N, 6°E		1	Emlen (1967b)
38	Blackcap	56, 10	DK	56, 85		6	Mouritsen and Larsen (2001)
39	Pied Flycatcher	56, 10	DK	56, 85		6*	Mouritsen and Larsen (2001)
40	Pied Flycatcher/Redstart	60, 15	DK	60, -15		8	Rabøl (1992, 1998)
41	Pied Flycatcher/Redstart	60, 15	DK	60, 60		9	Rabøl (1992, 1998)
42	Pied Flycatcher/Redstart	60, 15	DK	60, -45		6	Rabøl (1992, 1998)
43	Pied Flycatcher/Redstart	55, 15	DK	30, 20		11	Rabøl (1997, 1998)
44	Pied Flycatcher/Redstart	55, 15	DK	30, -25		11	Rabøl (1997, 1998)
45	Pied Flycatcher/Redstart	55, 15	DK	58, 30		8	Rabøl (1997, 1998)
46	Pied Flycatcher/Redstart	55, 15	DK	15, 15		11	Rabøl (1997, 1998)
47	Pied Flycatcher/Redstart	55, 15	DK	40, 15		8	Rabøl (1997, 1998)
48	Pied Flycatcher/Redstart	55, 15	DK	40, -5		8	Rabøl (1997, 1998)
49	Pied Flycatcher/Redstart	55, 15	DK	10, 35		6	Rabøl (1997, 1998)
50	Pied Flycatcher/Redstart	55, 15	DK	55, 35		10	Rabøl (1997, 1998)

Table 7 (continued)

ID	Species	Trapped at		Displaced to	# birds	Reference
51	Blackcap (#632)	55°N, 10°E	DE	50°N, 48°E	1	Sauer and Sauer (1960)
52	Blackcap (#632)	50, 10	DE	50, -52	1	Sauer and Sauer (1960)
53	Garden Warbler (#637)	50, 10	DE	30, 10	1	Sauer and Sauer (1960)
54	Lesser Whitethroat (Müllerchen)	50, 10	DE	25, 10	1	Sauer (1957) in Wallraff (1960a,b)
55	Lesser Whitethroat (Müllerchen)	50, 10	DE	50, 38	1	Sauer (1957) in Wallraff (1960a,b)
56	Lesser Whitethroat (Müllerchen)	50, 10	DE	50, -27	1	Sauer (1957) in Wallraff (1960a,b)

Table 8 Spring experiments.

ID	Species	Trapped at		Displaced to	# birds	Reference	
Real displacement: tested under a natural starry sky							
57	Bobolink	Florida	US	San Francisco	US	3	Hamilton (1962b)
58	Redstart	Christiansø	DK	Hanstholm	DK	13**	Rabøl (1975)
59	Redstart/Garden Warbler	Christiansø	DK	Blåvand	DK	9**	Rabøl (1975)
60	Robin	Christiansø	DK	Blåvand	DK	17**	Rabøl (1975)
61	American Golden Plover	Alaska	US	San Francisco	US	1	Sauer (1963)
Real displacement: tested under a natural or simulated overcast sky							
62	Redstart	Christiansø	DK	Tisvilde	DK	12**	Rabøl (1972)
63	Redstart	Christiansø	DK	Tisvilde	DK	11**	Rabøl (1975)
64	Robin	Christiansø	DK	Blåvand	DK	8**	Rabøl (1975)
65	Garden Warbler/Redstart	Christiansø	DK	Blåvand	DK	9**	Rabøl (1975)
66	American Golden Plover	Alaska	US	San Francisco	US	1	Sauer (1963)
Simulated displacement in a planetarium: tested under a planetarium starry sky							
67	Indigo Bunting	28°N, -84°E	US	28°N, -129°E		7**	Emlen (1967b)
68	Indigo Bunting	28, -84	US	28, -174		6**	Emlen (1975)
69	Redstart/Garden Warbler 1978	56, 15	DK	49, 15		15	Rabøl (1981)
70	Redstart/Garden Warbler 1978	56, 15	DK	63, 15		13	Rabøl (1981)
71	Redstart/Garden Warbler 1978	56, 15	DK	56, 35		6	Rabøl (1981)
72	Redstart/Garden Warbler 1978	56, 15	DK	56, -5		3*	Rabøl (1981)
73	Pied Flycatcher/Redstart	55, 10	DK	70, 10		10**	Rabøl (1997)
74	Pied Flycatcher/Redstart	55, 10	DK	70, 60		9**	Rabøl (1997)
75	Pied Flycatcher/Redstart	55, 10	DK	55, 60		10**	Rabøl (1997)
76	American Golden Plover	70, -150	US	20, -89		1	Sauer (1963)

Table 9 Experiments with insufficient information for inclusion or bimodal orientation.

ID	Species	Trapped at		Displaced to	# birds	Reference	
Insufficient information (all autumn)							
77	Barred Warbler	Rossiten	RU	Dushanbey	RU	?	Dolnik and Shumakov (1967) in Emlen (1975)
78	Barred Warbler	Rossiten	RU	Chabarowsk	RU	?	Dolnik and Shumakov (1967) in Emlen (1975)
79	Barred Warbler	Rossiten	RU	Dushanbey	RU	?	Potapov (1966) in Emlen (1975)
80	Barred Warbler	Rossiten	RU	Chabarowsk	RU	?	Potapov (1966) in Emlen (1975)
Bimodal distribution							
81	Indigo Bunting (spring, natural)	Alabama	US	Michigan	US	7	Emlen (1967a)
82	Pied Flycatcher (autumn, planetarium)	56°N, 15°E	DK	30°N, 20°E	LI	4	Rabøl (1990)

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