Supplementary notes to Thorup & Rabøl (2007): Compensatory behaviour after displacement in migratory birds. A meta-analysis of cage experiments

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(*Med et dansk resumé: Supplerende noter til Thorup & Rabøl 2007*)

Preface

The following comments (with later modifications) appeared on my homepage www.jorgenrabol.dk soon after the publication of Thorup & Rabøl (2007) to help people understand what is necessary to know about 1) compensatory orientation after a displacement, 2) pseudo-navigation, 3) stationary 'stellar skies' and 4) clock-shifts and orientation. These points also refer much to the planetarium experiments of mine (Rabøl 1998).

1. Demonstration of 1) compensatory orientation and 2) goal orientation following geographical displacements

By means of a construction it is exemplified how (a pattern of) orientation following displacement will reveal itself as compensatory and can be tested for statistical significance. A first step was presented by Rabøl & Thorup (2001). A second and third step further investigates whether such orientations converge towards a common goal.

In Fig. 1, birds trapped on migration at site I on the average orient towards N (0º). Now, birds trapped in I were displaced to A, B, C and D situated to the NW, NE, E and W of I, respectively. Five birds (or samples) were displaced to each of the four sites, and the orientations (or mean direction) of each of these birds (or samples) are denoted by the arrows; as an example, the orientations of the five birds in A point towards N, NE, E, SE and S, respectively. If the birds are not compensating the displacements, the orientations in A, B, C and D should be unaltered/standard i.e. N-directed (see below).

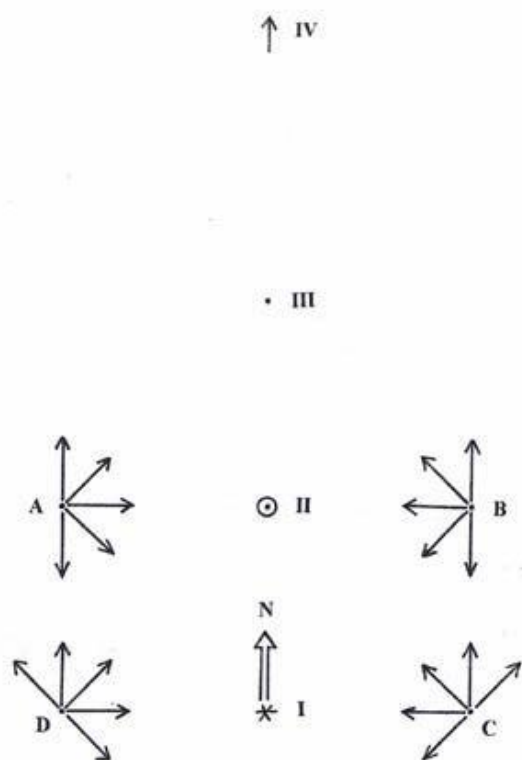*First step [er der ikke noget galt med denne figur?]*

Fig. 1. Constructed example. Migrants trapped at I orient towards N (0º). Now five samples are displaced to each of the four positions A, B, C and D. Here the mean directions of the twenty samples are as depicted. II, III and IV constitute positions ahead in the direction of the orientation at I.
Konstrueret eksempel. Trækfugle fanget i I orienterer sig mod N (0º). Fem sampler (grupper) flyttes fra I til hver af de fire positioner A, B, C og D. Pilene viser gennemsnitsretningerne af de 20 prøver. II, III og IV er positioner, der ligger N for og i forskellig afstand fra I.

In the example (Fig. 1) the orientation (in I) before displacement is due N. Following a displacement to A, a NE-directed orientation is perceived as a compensatory reaction and I choose to depict such compensatory orientation as 45º to the right in reference to the N-orientation at I (of course, our choice instead could have been 45º to the left). NE-orientation in D is depicted in the same way, i.e. 45º to the right. The N-orientations in A and D are neither compensatory nor counter-compensatory and are depicted as 0º, whereas NW-orientation in D is counter-compensatory and – as such – depicted as 45º to the left. On the contrary the two NW-orientations in B and C are compensatory and depicted 45º to the right. Following this procedure, the directional distribution of the 20 orientations in A, B, C and D (Fig. 1) come out as depicted in Fig. 2 fourth row, right column. The mean vector is 67.5º – 0.446, and according to the confidence interval test, the deviation from 0º is significant ($P < 0.05$) as the 95% confidence interval for N = 20 and r = 0.446 is +/-43º.

In conclusion, the orientation is significantly compensatory following the displacements. One may also apply the V test: According to this test the 'homeward' component, i.e. the (cos) projection (0.171) of the mean vector on the line running N trough I is not significant ($P > 0.05$). This is just another way to express that the orientation following displacement is not standard/unaltered. Now, this outcome of the V test does not bring direct support that (instead) the orientation is compensatory. However, this is a reasonable conclusion in harmony with the outcome of the Rayleigh-test ($P < 0.05$) and the deflection (67.5º) towards right.
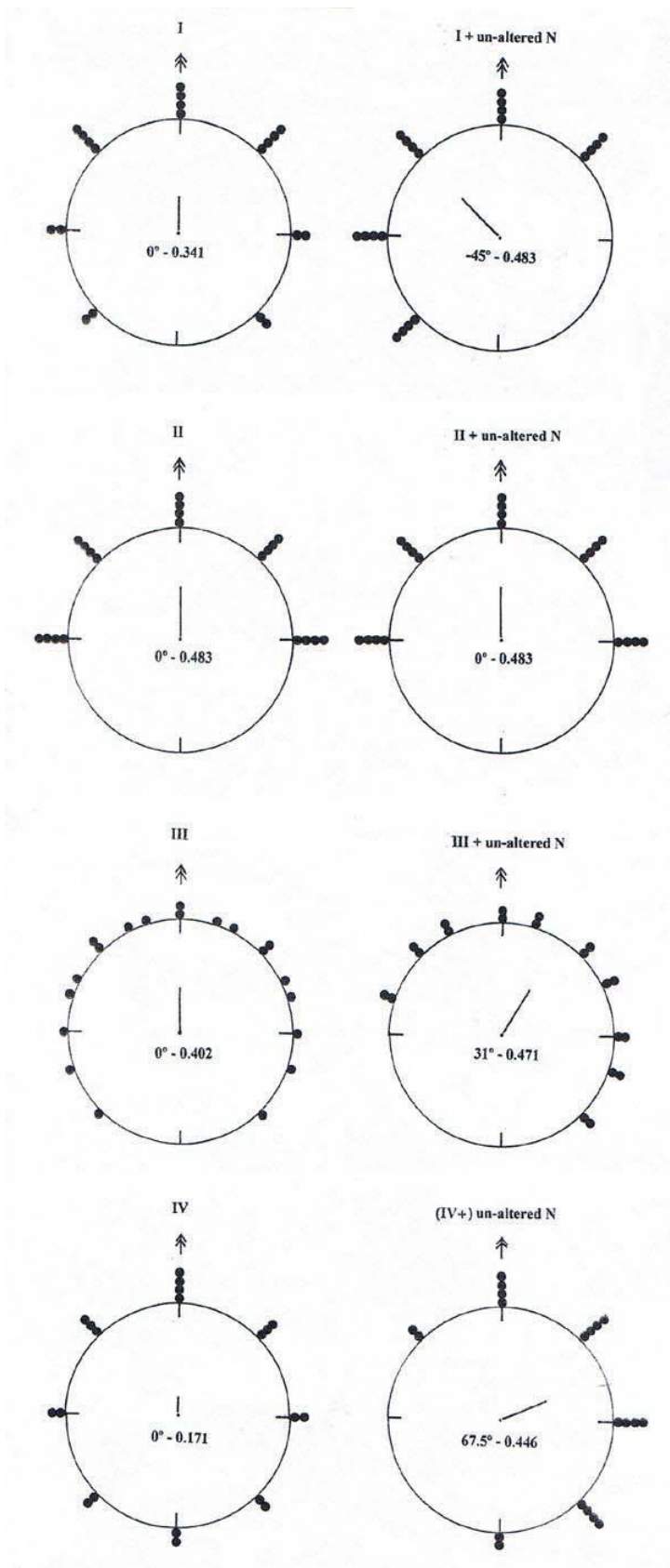
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Fig. 2. The orientation of the twenty displaced samples in Fig. 1 in relation to the direction (second step method) towards the positions of I, II, III and IV (left column) or in relation to the corrected direction (third step method, right column) towards I, II, III and IV.
Orienteringen af de tyve forflyttede sampler på Fig. 1 i relation til retningerne mod positionerne I, II, III og IV (den venstre søjle, anden step metoden) og i relation til den korrigerede retning mod I, II, III og IV (den højre søjle, tredje step metoden).

Second step

On average the orientation of the displaced birds is directed towards site II situated to the N of the trapping site I, i.e. II could be considered as a (temporary) goal for the birds. III is another site N of sites I and II, and IV could be considered as a site to the N very far from sites I, II and III.

We have not – as in the release procedure of homing pigeons introduced and used by H.G. Wallraff – displaced the birds in a radial symmetrical way around the home/goal in II (except in the present constructed example we do not know the position of II). What is depicted is a scenario of the ideal (first step) procedure for displacements of migrant birds according to Fig. 1 in Rabøl & Thorup (2001), i.e. the displacements are mostly in about right angles to or obliquely forwards compared with the standard (or registered) migratory direction in I.

As site II is the (average) goal for the 20 samples displaced to A, B, C and D the mean vector of the 20 directions is goal-directed (i.e. directed towards '0°') and the concentration is calculated as 0.483 (Fig. 2 second row, left column). If instead the 20 orientations were depicted in relation to the directions from A, B, C and D towards sites I and III considered as 'goals', the mean vectors would still be 'goal'-directed but the concentrations would be reduced to 0.341 and 0.402, respectively (Fig. 2 first row, left column, and Fig. 2 third row, left column, respectively). As neither site I nor site III are the true goals, we used the designation 'goal'. Finally, if the 20 orientations were depicted in relation to the direction of a site IV far to the N of site III, the mean vector concentration converges towards 0.171, but the mean direction would still be 'goal'-directed (Fig. 2 fourth row, left column). Clearly, the highest concentration at site II is a signal that II should be considered as the best estimate of a goal towards which the orientations of the displaced birds converge. The concentration peaks when the orientations of bi-lateral symmetrical displaced samples are depicted in relation to the true goal direction. In the real world this goal is not known but an approximate position of the average (temporary) goal could be found by means of iteration, i.e. we may guess that the goal is – say – 500 km, 1000 km or 2000 km away in the direction of the observed or standard direction as seen from the capture site of I. Of course, other directions than standard/unaltered may also be investigated; the point is that somewhere there must be a site with a maximum concentration of the sample mean vector, and this site may be considered the goal.

However, this method depicting the orientation to the left or right of the goal/'goal' direction is sub-optimal – leading to skewed distributions (in relation to '0°') for that reason alone (besides stochastic variation) if the number of displacements to the left and right in relation to standard/unaltered were not the same. Now the procedure developed in Rabøl & Thorup (2001), i.e. step 1 is useful also in cases where the number of displacements to the left and right are not the same, i.e. appropriate corrections are built in. We therefore developed a third step as a 'mixture' of the first and the second step. One may describe this step as an extension of the first step into the second step.

Third step

First, we want to demonstrate that when using this third method i.e. the orientations in reference to a distant site in the direction of N converge towards the same mean vector (67.5º – 0.446) as calculated in reference to standard/unaltered in the first step.

Consider a 'goal' 'IV' 14 units to the N of site I (the distance between sites I and II is one unit). Now draw the lines from A, B. C and D towards 'IV'. These lines point towards 4.4º, -4.4º. –4.1º and 4.1º, respectively. Now the 20 orientations in A, B, C and D are depicted in relation to their respective 'goal' directions. The N-orientation in A is directed -4.4º (i.e. 4.4º to the left) of the 'goal' direction, the NE-orientation 40.6º (to the right), and so on. From A the five orientations come out as -4.4º, 40.6º, 85.6º, 130.6º, and 175.6º, and from D -49.1º, -4.1º, 40.9º, 85.9º, and 130.9º. Now the 10 orientations in the relation to the 'goal' direction from B and C come out as 4.4º, -40.6º and so on; just the same as the 10 orientations from A and D but with the opposite signs. In order to change the ten orientations from B and C to the compensatory side we have to change their signs and therefore we end up with the same ten directions as in A and D. The grand mean vector of the 20 corrected directions is 63.3º – 0.447 which is very close the mean vector found in relation to N-orientation as described above in the first step (corrected in relation to both the 'goal' direction (as seen from the experimental position) and to the position of the experimental site to the left or right of the line of orientation running through the capture site, I (the orientations from the right sites are sign shifted)). Applying a confidence interval test 63.3º deviates significantly from 0º at the 0.05 level as the 95% confidence limits are +/-43º. In conclusion, 'IV' should not be considered as a reliable goal for the orientation in A, B, C and D (nor I).

The next point should be to consider the corrected orientation in relation to the sites I, II and III following the procedure outlined above. As an example, the orientations from C in relation to I as a 'goal' are -45º, 0º, 45º, 90º and 135º, and since C is to the right of the line running N through I we have to change the signs in order to obtain the corrected orientations (45º, 0º, -45º, -90º and -135º).

The mean vector towards the sites I, II and III comes out as -45º – 0.483, 0º – 0.483, and 31º – 0.471 respectively (cf. Fig. 2 first row, right column, Fig. 2 second row, right column, and Fig. 2 third row, right column, respectively). Only the first of these deviates significantly from 0º (P < 0.05, the 95% confidence limits for N = 20 and r = 0.483 is +/-38º), and obviously the one in the middle offers the best description. The conclusion should be that birds after displacement orient towards site II – and no one should wonder about that as the data were constructed with that purpose in mind.

The important lesson to be learned is that by way of the third step exemplified above and reasonable iteration one may find the approximate position of the actual/temporary goal area towards which the orientation of the displaced birds converges.

2. Pseudo-navigation, loxodromes, orthodromes & different stellar compasses

A star (pattern) in the southern sky (in its arc and about the same in azimuth projection) 'moves' clockwise 15° per hour in course of the night (just like the Sun on the northern hemisphere during daytime). Using such a star as compass-reference, the bird – in order to keep a constant course – has to make time compensated corrections for the 'movement' of the star and frequently check back with magnetic N and/or rotational stellar N and transfer a new course in reference to the star (pattern) in the southern sky (or to another – now more convenient – star (pattern) in the southern sky).

If the bird considers itself not displaced by man – nor wind – such reactions as mentioned above will result in an about constant/unchanged migratory course throughout the night. However, if the bird is displaced/'displaced' – say – 10° E in course of the night after the start of migratory activity, the star (pattern) in the southern sky functioning as the compass reference in the new geographical position appears displaced 10° clockwise, and if not calibrated for (by magnetic N or rotational stellar N) the migratory direction of a bird released or tested in a funnel immediately after the displacement the very same night will change its direction 10° clockwise e.g. from 160° to 170°. This shift is compensatory, and it looks like the outcome of a process based in gradient/coordinate navigation. However, only compass orientation is involved. Therefore, Rabøl (1998)[1] termed it pseudo-navigation.

To my knowledge, no birds have been displaced and tested in this way except in the planetarium 'displacements' by Sauer (1957) and Sauer & Sauer (1960). Normally, displaced or 'displaced' birds are not tested before the next night, and if so – and if not presented for the sunset/early night stars prior to the following starry sky tests (as in most displacement experiments of mine before 1978) – they perhaps only time-compensate but not re-calibrate their (previously used) stellar S compass. However, in most displacements the birds were exposed for the sunset/early night stars prior to the testing, or these were carried out several nights and days after the trapping/displacement. Therefore, in all probability we should expect such birds to (re)calibrate their stellar S compass, i.e. pseudo-navigation should mostly be considered a possible (theoretical) experimental artefact or as a useful pseudo-phenomenon for people who for some reason or another are sceptic about star-navigation.

Finally, in the department for details it should be noted that for every 24 hours passing between capture and testing following displacement, a star on the southern sky 'moves' 1° clockwise, i.e. after 10 days and nights a displacement 10° towards W will give no pseudo-navigation, whereas a displacement 10° towards E will give a pseudo-navigation of 20°.

Fig. 3 shows the outcome of pseudo-navigation in an autumn scenario compared with the outcomes of loxodromic and orthodromic navigation. The goal area is 5° to the south of the position where the

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[1] Rabøl (1998) rests on an extensive report "Star-navigation in Pied Flycatchers *Ficedula hypoleuca* and Redstarts *Phoenicurus phoenicurus*" (Rabøl 1997) which unfortunately was never published in a proper way. In the report is treated many of the challenges (including parallaxic ones) met when carrying out funnel experiments in a star-planetary. The report is available on request to the author.

birds were trapped and tested, and the testing site is displaced in steps of 10º towards E (same latitude) until half the way around the earth.
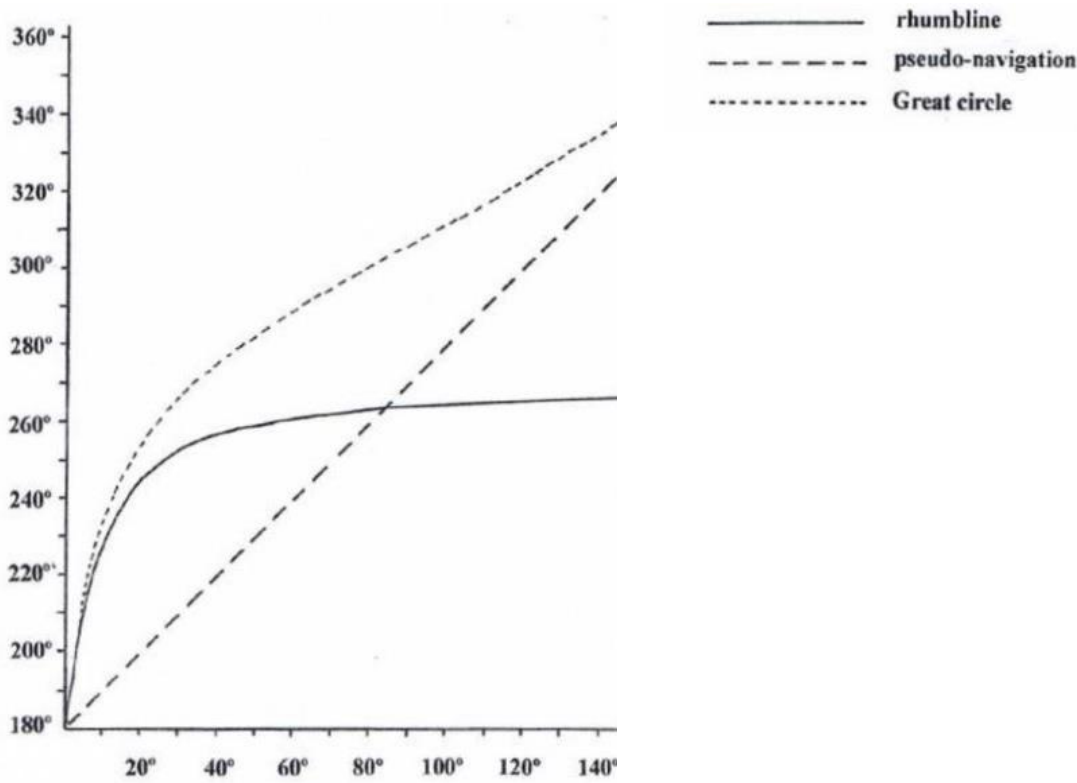

Fig. 3. The orientation following successive displacements from 0º E towards180º E (latitude all the time 60º N). True navigation (great circle/orthodrome or rhumbline/loxodrome) and pseudo-navigation in relation to a goal in 55º N / 0º. The capture and test-site is 60º N / 0º, the standard direction S (180º) and the birds are displaced in successive steps of 10º towards E until 60º N / 180º E. The ordinate shows the course taken depending on which orientation/navigation system is used. If vector orientation and rotational N of the starry sky is used as the compass reference, there will be no change in the course towards 180º. The same holds true for use of a time-compensated stellar-compass. As will be obvious when carrying out simulations it will be increasingly difficult to distinguish between pseudo-navigation and true goal navigation, if the goal is situated several 1000 km to the S of the trapping place; the angular difference will peak for the goal on a latitude being identical to one of the trapping/testing places. In general, it is not possible to distinguish (in terms of loxodrome courses) when the goal is situated Xº to the S and the displacement is Xº to the E or W. *Konstrueret eksempel. Fuglene er fanget og først testet i 60º N / 0º Ø. Hvis der er tale om navigation, er der et mål i 55º N / 0º Ø; hvis der er tale om vektororientering og pseudonavigation er normal-trækretningen S (180º). Den fuldt optrukne og den prikkede kurve viser henholdsvis loxodrom- og orthodrom-navigation mod målet i 55º N / 0º Ø, hvor test-stedet bevæger sig i 10º spring mod Ø til 60º N / 180º Ø. Som det fremgår af ordinat-forskellene på de to navigationskurver og pseudo-navigationskurven er en skelnen mellem de to systemer maximal i området 20º-30º Ø. Så længere forflytninger – også mod S – skal man holde sig fra, hvis intentionen er (og det er den primært) at kunne skelne mellem navigation og vektororientering. Maksimal skelnen mellem de to navigation-former er ved en 180º Ø/V-forflytning, men spørgsmålet er, om en så lang forflytning giver mening for en trækfugl.*

Until now, focus has been on a possible un-calibrated, time compensated stellar S compass during autumn. Considering such a compass during spring with a more or less northerly course; now counter-compensatory orientation appears. Anyway, we should not expect an eye-based compass where the bird has to look more or less backwards while migrating. During spring, rotational N/Polaris is the obvious candidate for a stellar compass. However, perhaps the circumpolar star patterns such as Cassiopeia or the Big Dipper are more eye-catching candidates and if so their counter-clockwise rotation around Polaris has to be time-compensated and calibrated too. As the azimuth movement is more complicated than in case of a star (pattern) moving on the southern sky, time-compensation (and calibration) is less easily carried out. Anyway, Emlen (1967) considered the possibility of such a stellar N compass in spring. Rabøl (1997, 1998) designated this compass a stellar N compass above Polaris.

On low latitudes, stars above Polaris (in direction of about due N) 'moves' to the left and if not calibrated will lead to pseudo-navigation though in general much less than 15° for each 15° of longitudinal displacement (and the maximum – own calculations – will be about 8°-9°/hour in the direction about due N). We made calculations for 20°N and a circumpolar star(pattern) in the distance of 30° from Polaris. Such a star(pattern) 'moves' around within the azimuth limits of about +/-30°. On the contrary, use of an un-calibrated stellar N compass below Polaris on high latitudes in general will lead to counter-compensatory orientation though again normally much less than 15° for each 15° of longitudinal displacement (and again the maximum will be about 8°-9°/hour in the direction about due N). We here made calculations for latitude 60°N, where a star (pattern) in a distance of 30° from Polaris 'moves' around within the azimuth limits of about +/-45°. As most displacements/'displacements' in spring have been on about the latitude of Denmark, we should perhaps consider the possibility of the use of a stellar N below Polaris. If so, an un-calibrated compass should not lead to pseudo-navigation but quite contrary mask the possible effect of true navigation. As the displaced/'displaced' birds compensated in spring, the conclusion should be that probably true navigation was responsible for that.

3. Comments on published studies with stationary 'stellar skies'

Mouritsen & Larsen

Sometimes nocturnal migrants are tested under a stationary planetarium 'stellar sky' (e.g. Emlen 1975, Beason 1987, 1989, Katz *et al.* 1988 and Mouritsen & Larsen 2001). The question in the present context is whether a stationary 'stellar sky' out of rotational phase with the local starry sky is perceived by the birds as a longitudinal geographical displacement. Mouritsen & Larsen (2001) asked this question explicitly whereas implicitly the same question is burrowed in some experiments by other authors who asked different questions.

Mouritsen & Larsen (2001) tested two samples of European Pied Flycatchers *Ficedula hypoleuca* and Eurasian Blackcaps *Sylvia atricapilla* in autumn under a stationary planetarium 'stellar sky', where the longitudinal/rotational phase was set to 02:35 h local time (local sunset about 19:00 h).

The orientation was now depicted for the same sample in one-hour intervals for the next 10 to 12 hours throughout the night. The question was whether the birds navigated as a response to the following scenario: during the first hour the birds were supposed to experience a geographically displacement of 5 or 6 hours (i.e. 75º or 90º) towards E; then during the second hour a displacement of 4 or 5 hours towards E and so on, finally ending up feeling displaced about 5 or 6 hours towards W. The other possibility was that the birds made use of a stellar compass only and were not experiencing any longitudinal displacement.

As the orientation seemingly remained constant and in about the standard direction throughout the night, their conclusion was that the birds "use stellar cues for a time-independent compass" (i.e. a rotational N stellar compass in the terminology of Rabøl 1998). Furthermore, that there were no signs of "a time-dependent compass" (i.e. an uncalibrated time-compensated stellar S compass in the terminology of Rabøl 1998) nor stellar navigation. These conclusions were reasonable on the basis of the results and the validity of the assumption that the five hypotheses can be tested against each other under a stationary planetarium 'stellar sky'. Unfortunately, Mouritsen & Larsen (2001) overlooked that the orientation in the Pied Flycatchers in fact shifted significantly counter-clockwise in course of the night (P < 0.02). This shift was much smaller than predicted by the hypothesis of an un-calibrated stellar S compass and in particular the navigation hypotheses. However, the initial Pied Flycatcher orientation during the first two hours was rather westerly and could be considered as compensatory and as such slightly indicative of an (initial) stellar S compass or navigation.

Mouritsen & Larsen (2001) never discussed whether a stationary planetarium 'stellar sky' is appropriate as a substitute for a rotating planetarium 'stellar sky' (as the one used by Rabøl 1992, 1998 and also by Mouritsen & Larsen 2001 in a cue conflict between magnetic N and 'stellar' N). Perhaps, birds are not feeling geographically displaced under a stationary 'stellar sky' or only do so during the first – say – 10 minutes, half an hour or two hours. In Thorup & Rabøl (2007, Table 1, ID 38 and 39) we considered the orientation of the Pied Flycatchers and Blackcaps during the first two hours of 'displacement'.

Clearly, the stationary 'stellar sky' procedure carried out in course of a single night by Mouritsen & Larsen (2001) is not optimal (and very probably unsuited) for elucidating the natural orientation/navigation system in charge.

First, the 'stellar sky' should be rotating (with normal speed), and second shifts between 5º and 30º (20 minutes through 2 hours) are the most appropriate to distinguish between navigation and clock- and compass orientation (Fig. 3).

Emlen

In the 'displacements' by Emlen (1967) it is not clear whether the birds in the about two-hour period when tested, experienced a rotating or a stationary 'stellar sky'. In many of Emlen's experiments – including the famous Betelgeuse experiment – the 'sky' was not rotating in the test phase.

If rotating, the 'stellar sky' never rotated during the first 15 minutes but then was turned abruptly 3.75º counter-clockwise (Emlen said 4º but presumably meant 3.75º; the difference does not matter in the present context). Then again, the 'sky' was stationary for 15 minutes before again turned abruptly 3.75º, and so on. In this jerky way the 'sky' rotated with the normal speed of a stellar sky, i.e. 15º per hour. Anyway, the procedure of Emlen was not optimal but at least more appropriate than the procedure of Mouritsen & Larsen (2001).

Katz et al.

Katz *et al.* (1988) tested Great Reed Warblers *Acrocephalus arundinaceus* in autumn under a stationary planetarium 'stellar sky' following exposure under a rotating 'stellar sky' in the pre-migratory period. The orientation was reported to shift roughly 15º counter-clockwise per hour, and this was taken as an indication of a (un-calibrated) time-compensated stellar S compass (the purpose of the experiments was not to find out whether the birds navigated by the stars but to throw light on whether a stellar rotational N or a stellar S compass was used). However, the conclusions of Katz *et al* (1988) may be questioned as only half of the birds behaved fairly well according to the expectations of a time-compensated stellar S compass: in course of three two-hour-periods 20-22 h, 22-24 h and 00-02 h the mean orientation shifted from 160º over 124º to 76º. The other half of the birds showed orientation until 0400 h in the night, and this difference was the only 'justification' for a distinction between the two groups. The second group showed no change in orientation during the night. Anyway, the counter-clockwise shifts in the first half of the birds – and in particular the large 48º shift between the last two periods – can also be considered as a navigational response: the stationary 'stellar sky' was perceived by the birds as a displacement towards W and compensated for (contrary to the finding/claim of Mouritsen & Larsen 2001). As often in science there is some room for different views and interpretations.

The '16-star-sky'

A special kind of a 'planetarium' is the '16-star-sky' introduced by Wiltschko & Wiltschko (1976) and then very often later on used by the Wiltschkos and co-workers and also by Able & Able (1990) who in a drawing (their Fig. 1) show the experimental set up. The birds were placed in a cross in four cages/funnels in the bottom of a large cylinder (2 m in height and 1.5 m in diameter). The upper disk rotates counter-clockwise with the normal speed of a starry sky and was equipped with 16 lights/'stars' in eight groups intended to substitute the starry sky. From their cages the birds observed the 'stars' rotate around an invisible point on the average about 74.5º above horizontal level supposed to be perceived the direction towards rotational N of the starry sky. Very often the interpretation of '16-star-sky' experiments is not easy (or at least the interpretation of the authors may be questioned) – perhaps because the birds sometimes display aberrant 'navigational' responses or perhaps because of the influence of something like an un-calibrated stellar S compass (or perhaps the light-dots up there just mean nothing). At least the orientation of the control Garden

Warblers *Sylvia borin* in Weindler *et al.* (1996) could be explained in one or both ways. In these experiments juvenile birds were exposed under a rotating '16-star-sky' in the pre-migratory period and later during autumn tested under a stationary 'sky'. According to the clock-and-compass hypothesis the orientation of German Garden Warblers should change from about SW to SSE in course of the autumn (Gwinner & Wiltschko 1978). However, in these experiments the orientation shifts from S in early autumn over SW-WSW in September to W in late autumn. Surprisingly, Weindler *et al.* (1996) did not comment on this pronounced discrepancy between the expectation and the results, but it can be explained as stellar 'navigation' or compass orientation in reference to something like an un-calibrated stellar S compass (a 'star' in the southern sky moves about 90º clockwise in course of the period considered).

In conclusion, stationary planetarium 'stellar sky' experiments are probably – like clock-shift experiments – not suitable for demonstrating the influence and significance of stellar navigation. This links to the many planetarium experiments of Emlen (see also earlier); very often it is not clear whether the birds were tested under a stationary sky (as in case of the Betelgeuse experiments) or whether the sky was rotated a little less than 4º for every 15 minutes (but even in the latter case the sky was not rotating for the first 15 minutes and perhaps this had some effect on whether navigational or only compass reactions were displayed).

4. Clock-shifts

When using the designation clock-shifts, two conditions could be understood: 1) the biological clock of the bird is shifted clock-wise or counter-clock-wise following a shift in the light/dark-rhythm, or 2) the rotation-phase of the celestial sky presented for the birds is shifted for- or backwards (could be the natural starry sky after displacements towards E or W, or E/W phase-shifts on a planetary 'starry sky'). Apparently, for Emlen (1975) 1) and 2) were interchangeable considering the output: it does not matter for the response of the bird. However, in all probability it does, and the effect of clock-shifts of or under a starry/'starry' sky are about the most opaque bird orientation scenarios to consider and figure out. Experiments are much needed, but only a few old experiments are available and nowadays they are out of fashion, and none are carried out anymore.

First, it is well known that clock-shifts change compass orientation in a predictable way on sunny days in both pigeons and migrant birds (Rabøl 1988). If e.g. the light/dark shift is retarded six hours the orientation shift 90º to the right/clockwise from e.g. W to N, whereas an advanced light/dark shift on six hours changes the orientation 90º to the left/counter-clockwise (here from W to S). The sunset-sky apparently acts like the Sun as the compass reference in clock-shift experiments (Able & Cherry 1986), whereas clock-shifts seemingly have no influence on the compass orientation when the starry sky was acting as the compass reference (Matthews 1968, Emlen 1975).

The question is whether clock-shifts influences star-navigation. Emlen (1975) found no influence in released White-throated Sparrows *Zonotrichia albicollis* as also Rabøl (1970a, b) intending to simu-

late a 'displacement' eight hours clockwise (from Denmark to about Khabarovsk, easternmost Russia) in an autumn sample, and an eight-hour counter-clockwise 'displacement' (from Denmark to about Manitoba, Canada) in a spring sample. In the autumn sample the light/dark shift was advanced eight hours from 18:00 – 06:00 to 02:00 – 14:00 supposed to – under the natural starry sky – telling the birds about a displacement eight hours/120° towards the far east meaning a changed compass course from SSE – 120° = NNE-NE, or – if navigating – a course little S of W (loxodrome) or about NW (orthodrome).

However, the orientation remained unchanged like in the controls about SSE. Nevertheless, the expectation and procedure were possibly wrong. Perhaps, the biological clock concerned about E/W-navigation (if existing) is not vulnerable to light/dark shifts. In fact, it should not be so if used for navigation. Perhaps, when exposed under the Danish starry sky this is not perceived by the birds as indicating a position eight hours to the E but eight hours to the W. If so, the sight of the starry sky should had resulted in SSE + 120° = W-WNW (compass orientation), or – if navigation – a little S of E (loxodrome), or about NE (orthodrome). Anyway, the unchanged SSE-orientation signalled that neither pseudo-navigation nor true navigation were involved.

The result of the clock-shift 'displacement' to Manitoba in spring was more difficult to interpret. The light/dark shift was retarded eight hours (dark 13:00-19:00). Both controls and clock-shifted birds oriented NNE. Such an orientation could be great-circle navigation towards the Scandinavian breeding ground (about NNE-NE in the clock-shifted 'displacements') but does not refer to use of an un-calibrated stellar S compass (WSW), nor an un-calibrated lower stellar N compass (about NW-NNW), nor loxodromic navigation (a little N of E).

However, the experimental treatment in clock-shift experiments might cause the birds to recalibrate their stellar S or stellar N compasses using rotational stellar N or magnetic north as the reference. Anyway, true navigational compensation should still manifest itself – and as mentioned does not at least in the autumn clock-shifts. Obviously, this finding cannot be used as an argument against stellar navigation.

Resumé

Supplerende noter til Thorup & Rabøl 2007

Disse supplerende noter behandler nogle vanskeligt forståelige emner, der måske har været medvirkende til, at den meget vigtige og centrale artikel, Thorup & Rabøl (2007) er så lidt citeret, som den er.

Først eksemplificeres hvordan man både i et a) enkelt sample og i en b) metaanalyse af et stort antal sample-gennemsnitsretninger kan teste, om der sker en statistisk signifikant kompensation for en forflytning eller gennemgående for et stort antal forflytninger. Der anvises også en metode til at skønne målområdets beliggenhed (normalt noget fremme) i trækruten.

Den næste afdeling behandler fænomenet pseudo-kompensation, der (især) er relevant i forbindelse med kompasorientering eller navigation om efteråret i forhold til en stjerne på S-himlen. Problemet er (hvis der er et problem), at stjernerne på S-himlen bevæger sig som Solen medurs/til højre med en vinkelhastighed i deres bane på 15 grader i timen, så en stjerne, der på Christiansø på længdegrad 15 grader Ø kl. 23 står i retningen mod 170° på S-himlen, står – samtidig i London på 0° længdegrad i 155° Ø. Hvis fuglen nu kompasorienterer med en fast vinkel i forhold til stjernen, fx 45° til højre for stjernen på Christiansø mod 215°, så vil den med de samme 45° til højre være orienteret mod 200° i London, hvad der fejlagtigt kan opfattes som en navigations-betinget kompensation for en forflytning 15° V til London. Men det er det så ikke – nødvendigvis. Det bliver mindre udtalt – og kan gå den anden vej – hvis fuglen kompasorienterer efter en stjerne på N-himlen, afhængigt af stjernens position i forhold til Nordstjernen.

Tredje afdeling er om relevansen og 'godheden' af test under en stationær, dvs. ikke-roterende planetariestjernehimmel samt den af Frankfurt-gruppen indførte og ofte anvendte '16-stjerne-himmel'. I sidstnævnte tilfælde er fuglene anbragt i tragte/bure excentrisk i bunden af en bred cylinder, hvorfra de kigger op på et mønster af 16 lysprikker, der i en indledende fase roterer, men som regel er stationære i test-fasen. Wiltschko & Wiltschko (1976 og senere) mener, at dette scenario kan substituere den rigtige stjernehimmel (eller en roterede planetariestjernehimmel). Det tror jeg ikke nødvendigvis på, og man skal være meget varsom med at drage for vidtrækkende konklusioner ud fra den orientering, der fremkommer i denne meget unaturlige situation. I al almindelighed: Der har været alt for få tests under en naturlig, roterende stjernehimmel og alt for mange forsøg under stationære, såkaldte 'stjernehimle', og det er en meget afgørende grund til, at man efter min opfattelse har en for forvrænget opfattelse af, om og hvordan fuglene orienterer/navigerer i forhold til stjernehimlen.

Den sidste afdeling handler om muligheden for at simulere geografiske Ø/V-forflytninger ved at faseforskyde lys/mørke-rytmen. Hvis man fx gennem længere tid udsætter fuglene for en otte timers fremadskridende lys/mørke rytme, tror fuglene så, at de er flyttet otte timer (120 længdegrader) mod Ø? Jeg undersøgte sådanne otte timers skift mod Ø (efterår) og mod V (forår) (Rabøl 1970a, 1970b). Efterårsforsøgene er lettest at fortolke; der var ingen forskel mellem

forskudte fugle og kontroller. Så hverken stationære stjernehimle eller faseskiftede lys/mørke-rytmer kan simulere Ø/V-forflytninger. Der skal reelle forflytninger til eller simulerede forflytninger under en roterende planetariestjernehimmel.

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