

Supplementary notes to Thorup and Rabøl 2007: Compensatory behaviour after displacement in migratory birds. A meta-analysis of cage experiments. – Behav. Ecol Sociobiol 61: 825-841.

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

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

In Fig.1.1 birds trapped on migration in site I on the average orient towards N (0°). 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 sample of birds were displaced to each of the four sites, and the mean orientations of each of these samples are denoted by the arrows; as an example the mean orientations of the five samples 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. (on the average) N-directed (see below).

First step: In the example (Fig.1.1) the (mean) orientation (in I) before displacement is due N. Following a displacement to A a NE-directed orientation is perceived a compensatory reaction and we choose to depict such compensatory orientation as 45° to the **right** in reference to the N-orientation in I (of course, our choice instead could had been 45° to the left). NE-orientation in D is depicted in the same way, i.e. 45° to the right. The N-orientations in A and D are neither compensatory nor counter-compensatory and are depicted as 0° , whereas NW-orientation in D is counter-compensatory and – as such - depicted as 45° to the left. On the contrary the two NW-orientations in B and C are compensatory and depicted 45° to the right. Following this procedure the directional distribution of the 20 orientations in A, B, C and D (Fig.1.1) come out as depicted in Fig.1.2 fourth row, right column. The mean vector is $67.5^\circ - 0.446$, and according to the **confidence interval test** the deviation from 0° is significant ($P < 0.05$) as the 95% confidence interval for $n = 20$ and $r = 0.446$ is $\pm 43^\circ$. 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 through 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 symphony with the outcome of the Rayleigh-test ($P < 0.05$) and the deflection (67.5°) towards right.

Second step: On the 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 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, 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.1.2 second row, left column). If instead the 20 orientations are depicted in relation to the directions from A, B, C and D towards sites I and III considered as "goals" the mean vectors are still "goal"-directed but the concentrations are lowered to 0.341 and 0.402, respectively (Fig.1.2 first row, left column, and Fig.1.2 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 are 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 is still "goal"-directed (Fig.1.3 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 are 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 the orientations in reference to a distant site in the direction of N converge towards the same mean vector ($67.5^\circ - 0.446$) as calculated in reference to standard/unaltered in the first step.

Consider a "goal" "IV" 14 unities to the N of site I (the distance between sites I and II is one unity). Now draw the lines from A, B, C and D towards "IV". These lines point towards 4.4° , -4.4° , -4.1° and 4.1° , 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 -4.4° (i.e. 4.4° to the left) of the "goal" direction, the NE-orientation 40.6° (to the right), and so on. From A the five orientations come out as -4.4° , 40.6° , 85.6° , 130.6° , and 175.6° , and from D -49.1° , -4.1° , 40.9° , 85.9° , and 130.9° . Now the ten orientations in the relation to the "goal" direction from B and C come out as 4.4° , -40.6° and so on; just the same as the ten 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 are $63.3^\circ - 0.447$ 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 63.3° deviates significantly from 0° at the 0.05 level as the 95% confidence limits are $\pm 43^\circ$. 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 -45° , 0° , 45° , 90° and 135° , and as 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 (45° , 0° , -45° , -90° and -135°).

The mean vector towards the sites I, II and III comes out as $-45^\circ - 0.483$, $0^\circ - 0.483$, and $31^\circ - 0.471$ respectively (cf. Fig.1.2 first row, right column, Fig.1.2 second row, right column, and Fig.1.2 third row, right column, respectively). Only the first of these deviates significantly from 0° ($P < 0.05$, the 95% confidence limits for $n = 20$ and $r = 0.483$ is $\pm 38^\circ$), 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 are converging.

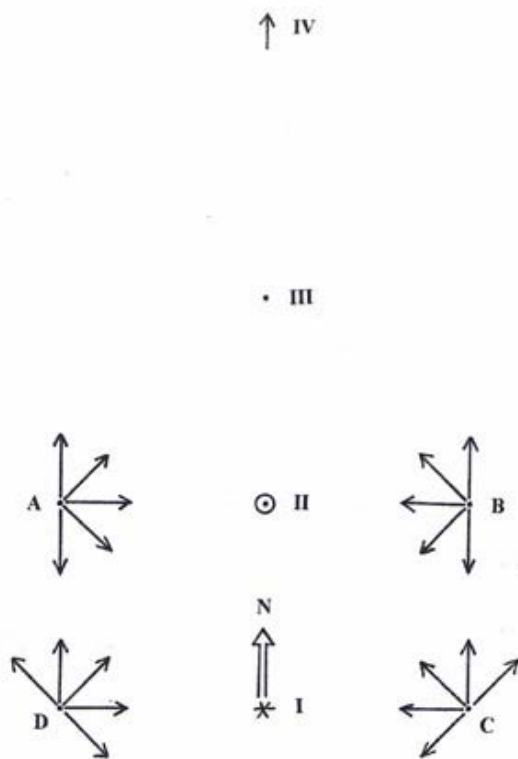


Fig.1.1. Constructed example (Suppl.1). Migrants trapped in I orient towards N (0°). Now five samples are displaced to each of the four positions A, B, C and D. Here the mean directions of the twenty samples are as depicted. II, III and IV constitute positions ahead in the direction of the orientation in I.

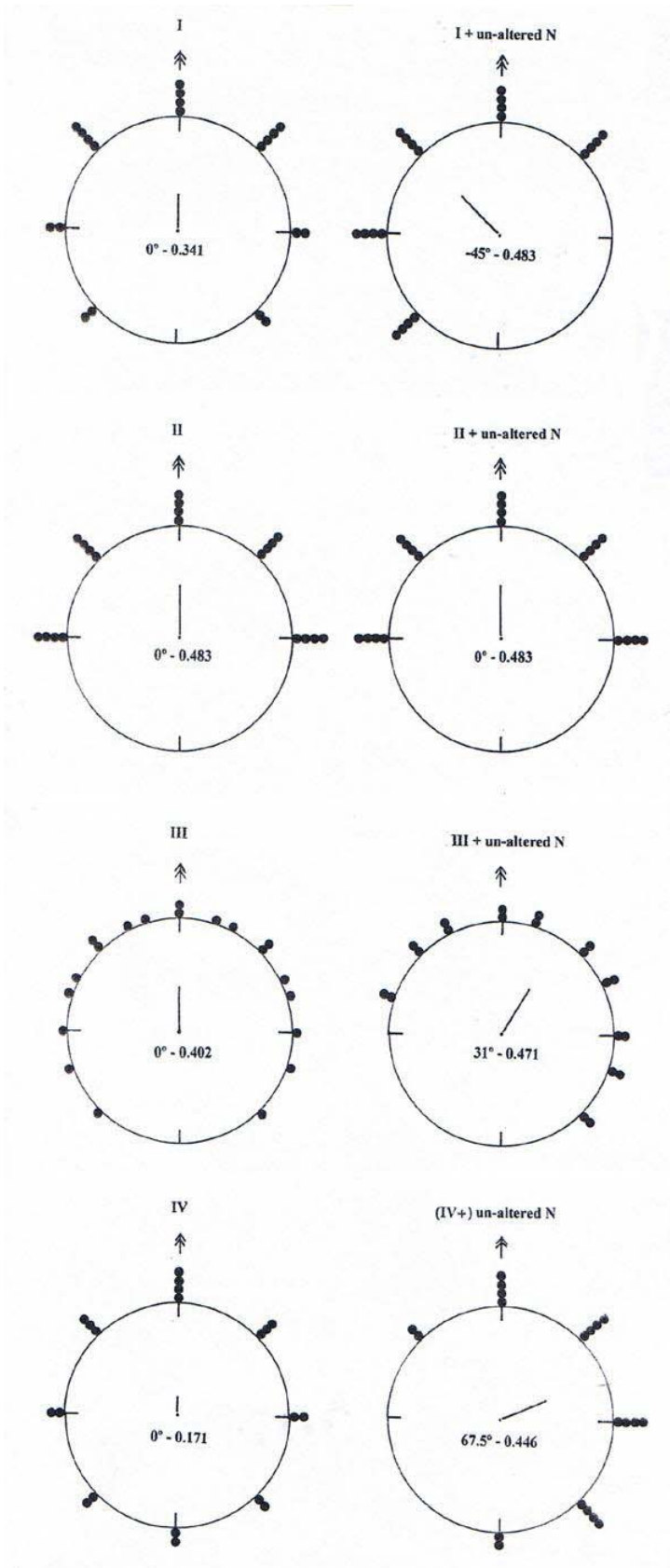


Fig.1.2. The orientation of the twenty samples of the displaced birds in Fig.1.1 in relation to the direction (second step method) towards the positions of I, II, III and IV (left column) or in relation to the corrected direction (third step method) towards I, II, III and IV.

Supplement 2. Pseudo-navigation and aliens

A star(pattern) in the southern sky (in its arc and about the same in azimuth) “moves” clockwise 15° per hour in course of the night. In order to keep a constant course the bird has to make time-compensated corrections for this “movement” and/or very 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 considered is not displaced by man – or wind – such reactions as mentioned above will result in an about constant/unchanged migratory course throughout the night. However, if the bird is geographically displaced – say - 10° E **in course of 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 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 (1997, 1998) 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 testings (as in most displacement experiments of mine before 1978) they perhaps only time-compensated but not re-calibrated 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 sceptical 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° .

Until now focus has been on a possible un-calibrated, time compensated **stellar S** compass during **autumn**. Consider such a compass during **spring** with a more or less northerly course; now it leads to **counter-compensatory** orientation. Anyway, we should not expect a **eye-based** compass where the bird has to look 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 obvious 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** (Rabøl 1997, 1998). 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 $\pm 30^\circ$. 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 $\pm 45^\circ$. 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.

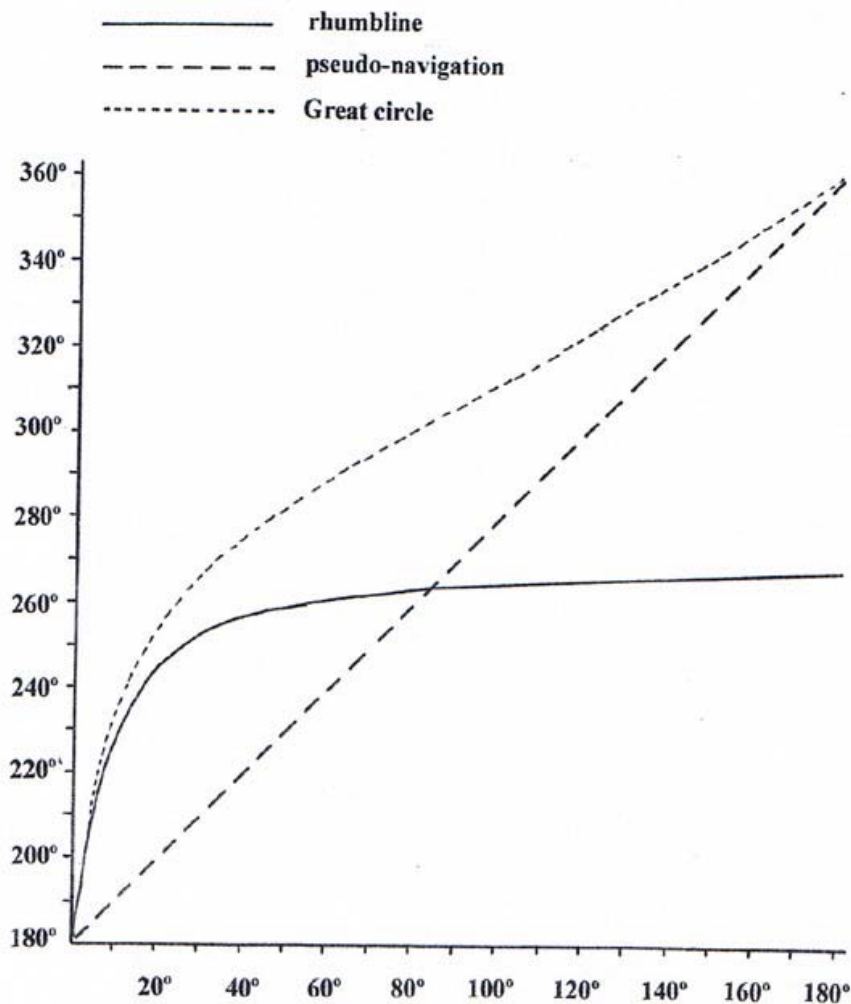


Fig.2.1. True navigation (great circle and rhumbline) and pseudo-navigation in relation to a goal in 55°N/0°. The Capture site is in 60°N/0°, the standard direction S (180°) and the birds are displaced in successive steps of 10° towards E until 60°N/180°. As will be obvious when carrying out simulations 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 being identical to the trapping place. In general, it is not possible to distinguish (in terms of loxodrome courses) when the goal is situated X° to the S and the displacement is X° to the E or W.

Supplement 3. 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 Pied Flycatchers and Blackcaps in autumn under a stationary planetarium “stellar sky”, where the longitudinal/rotational phase was set to 02:35 h local time (local sunrise 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 5 or 6 hours (i.e. 75° or 90°) 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. Mouritsen & Larsen (2001) proposed and tested five different orientation/navigation hypotheses most of which were transformed from Fig.16 in Rabøl (1997). 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 1997, 1998). Furthermore, that there was no signs of “a time-dependent compass” (i.e. an uncalibrated time-compensated stellar S compass in the terminology of Rabøl 1997, 1998) nor stellar navigation. This conclusion was reasonable on 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 Flycatcher 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 is 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, 1997, 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 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 for finding out the natural orientation/navigation system in charge. First, the “stellar sky” should be rotating (with normal speed), and second – as stressed by Rabøl (1997, Fig.16) – “shifts between 5° and 30° (20 minutes through 2 hours) are the most appropriate to distinguish between navigation and clock- and compass orientation” (see also Fig.2.1).

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 Emlens experiments – including the famous Betelgeuse experiment – the “sky” was not rotating in the test phase. Anyway if rotated, the “stellar sky” was never rotated during the first 15 minutes but then was turned abruptly 3.75° counter-clockwise (**Emlen said 4° but presumably meant 3.75°**. **Anyway, the difference does not matter in the present context**). Then again the “sky” was stationary for 15 minutes before again turned abruptly 3.75°, and so on. In this way the “sky” rotated with the normal speed of a stellar sky, i.e.15° per hour. Anyway, the procedure of Emlen was not optimal but at least more appropriate than the procedure by Mouritsen & Larsen (2001).

Katz et al.

Katz et al. (1988) tested Great Reed Warblers 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 15° per hour counter-clockwise, 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 20-22h, 22-24h and 00-02h the mean orientation shifted from 160° over 124° to 76°. 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 48°-shift between the last two periods - can also be considered as a navigatory 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 the Ables. 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 “navigatory” responses or perhaps because of the influence of something like an un-calibrated stellar S compass. At least the orientation of the **control** Garden Warblers 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 on 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) are not commenting on this pronounced discrepancy between the expectation and the results, but certainly 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 90° clockwise in course of the period considered). Rabøl (1997) gives more details.

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 4° 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).

Supplement 4. Clockshifts.

Rabøl (1970a, b) simulated a ‘displacements’ 8 hours clockwise (from Denmark to about Chabarowsk, easternmost Russia) in an autumn sample and 8 hours counter-clockwise (from Denmark to about Manitoba, Canada) in a spring sample. In the autumn experiments there was no difference in the orientation between controls and clockshifted birds; both oriented about SSE, i.e. there was no indications of compensatory stellar navigation nor presence of pseudo-navigation, i.e. influence of an un-calibrated time-compensated stellar S compass. The clockshift “displacement” to Manitoba in spring is more difficult to interpret. Both controls and clockshifted birds oriented N-NNE. Such an orientation could be great-circle navigation towards the Scandinavian breeding ground (about NNE-NE in the clockshifted “displacements”), but not refer to use of an un-calibrated stellar S compass (WSW), nor an un-calibrated lower stellar N compass (about NW-NNW), nor rhumbline navigation (a little N of E). However, the experimental treatment in clockshift experiments might cause the birds to recalibrate their stellar S or stellar N compasses using rotational or magnetic north. Anyway, true navigatory compensation should still manifest itself – and as mentioned does not so at least in the autumn clockshifts. However, this finding

cannot be used as an argument against stellar navigation. Perhaps clockshifts and true displacements are not treatments which can replace each other.

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