Appendix 2 for J. Rabøl 2023: Displacement experiments in night migrating passerines. – Dansk Orn. Foren. Tidsskr. 117: 37-46.

Orientation experiments with night-migrating passerines using prisms for simulating latitudinal displacements on the starry sky

Jørgen Rabøl

(*Med et dansk resumé: Orienteringsforsøg med nattrækkende småfugle, hvor breddegradsforflytning er simuleret ved hjælp af prismer*)

Abstract Compensatory orientation following simulated geographical displacements is the most powerful way to demonstrate the presence and importance of one or another potential navigational parameter. Rabøl (1998) simulated displacements on a planetary 'stellar sky' and found significant compensatory orientation. This was a strong indication that the real starry sky was used for gradient navigation. Here, I report on compensations during autumn following a latitudinal 'displacement' of the stellar sky 4º towards S mediated through prisms mounted on top of 'Emlen funnels'.

Introduction

It is a controversial question whether birds can use the stellar sky for goal navigation and in particular whether juvenile birds can. Wiltschko & Wiltschko (1978) argue that "navigation to an unknown goal based on site-specific coordinates seems to be excluded by Perdeck's (1958, 1967) results". Apart from the invalid argumentation based in two selected examples, Wiltschko & Wiltschko as well as H.G. Wallraff (in Rabøl 1972) use a wrong word, "unknown". Of course, birds – and humans – cannot navigate towards an unknown goal, but the objection "unknown" is not necessarily synonymous with 'a position never visited before'. Furthermore, some years ago in the debate forum on RIN (Royal Institute of Navigation), R. Wiltschko claimed that S. Emlen "proved" that stars were only used for compass orientation. However, again this wording is invalid. Perdeck and Emlen proved nothing, but their results were instrumental for the common view and paradigm settled that the stellar sky was not used for navigation, and juvenile birds were not able to navigate.

Nowadays, there is too much talk and group-pressure and all too few investigations on whether juvenile birds may navigate, and whether the stars are used for navigation. Since the days of F. Sauer in the late fifties and early sixties I was more or less the only person to oppose the paradigms of vector orientation and non-stellar navigation, and people focusing on their career kept their occupations far away from star navigation. The whole area is strongly avoided and undeveloped. Together with my planetary investigations (Rabøl 1998) – and the survey by Thorup & Rabøl (2007) – the present prism experiments are an attempt to keep the discussion alive. Hence, the purpose was to find out whether migrant birds use the altitude of the rotational point of the stellar sky, Polaris as the N/S-coordinate in a goal-area navigation process.

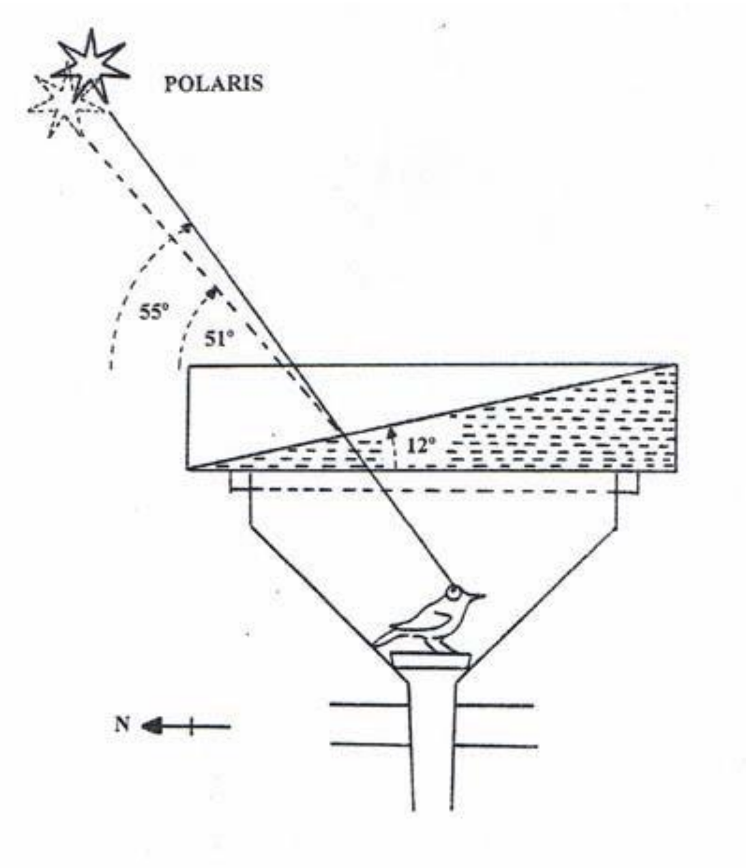

Fig. 1. The waterfilled prism situated on top of the funnel. If the thin side of the prism is turned geographical N, the bird inside the funnel experiences the sight of a starry sky displaced 4º to the S. *Det vandfyldte prisme på toppen af tragten med fuglen i. Hvis den tynde prismeside er vendt mod geografisk N, ser fuglen en stjernehimmel, der er tippet 4º mod S. Hvis fuglen bruger stjernehimlen til N/S-navigation, og målområdet befinder sig mindre end 4º mod S, reagerer fuglen med en N-rettet respons. Men orienteringen i tragten behøver ikke komme ud som en strikt N-orientering. Måske synes fuglen – på grundlag af stjernernes omdrejningsfase eller andet – at den også er V for sit målområde. I så fald bliver orienteringen før prismet kommer på måske SV. Efter prismets påsætning ændrer denne kurs sig til omkring NV.*

Material and methods

Four prisms were in use. The prisms were constructed by means of sheets of transparent plexiglass glued together as a hollow prism and then filled with water (Fig. 1). The dimensions of the ground plane were 40 × 40 cm and the opening angle 12º. The high side of the prism thus measured 8.5 cm. Each prism was placed horizontally above the funnel on top of a woody square box without bottom and top encompassing the funnel. The top of the box was about 1 cm above the upper edge of the funnel. When the thin side of the prism was turned N, the bird in the funnel throughout the prism observes a starry sky corresponding to a position 4º to the S (same longitude). Fig. 2 shows the expected scenario when the birds experience a simulated displacement from A at 55º N to B at 51º N.

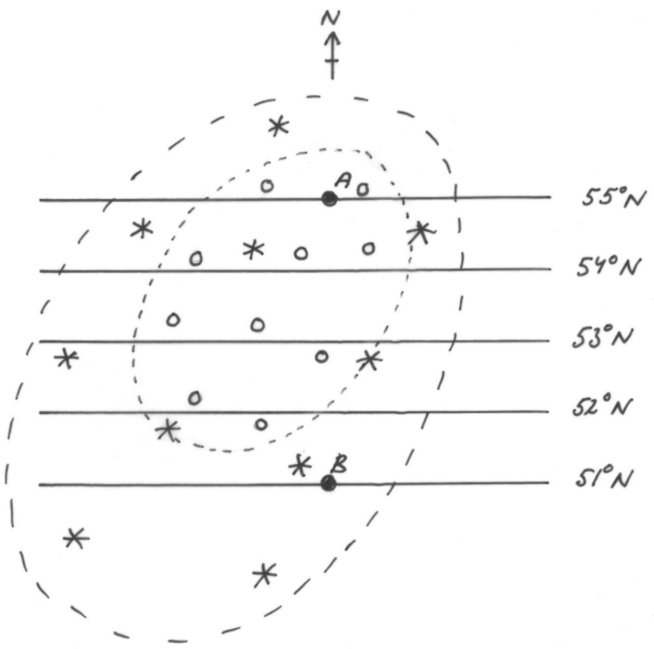

Fig. 2. Goal area navigation when the thin side of the prisms is turned N (autumn). Birds are trapped and funnel experiments are carried out at A. The controls tested under the natural starry sky observe Polaris 55º above the horizon. The experimental birds are situated in A but observe through a prism a starry sky where Polaris appears to be 51º above the horizon. Therefore – if star navigating – the birds believe they are at B at latitude 51º. Birds trapped at A are on their way towards goal areas situated within the hatched ellipsoid the large axis of which is directed in the standard direction. Ten such goal areas (the crosses) are denoted. The sample mean vector of the ten goal areas as seen from A is 214º – 0.637 ($P < 0.05$), and from B 317º – 0.641 ($P < 0.05$). If the goal areas were closer to A (the 10 white dots within the dotted ellipsoid) the sample mean vector of the ten directions as seen from A is 204º – 0.668 ($P < 0.05$), and from B, 339º – 0.926 ($P < 0.001$). If the ellipsoid had been a far distance towards SSW-SW, the sample mean vectors from A and B approach each other. The lesson learned from the examples is that in a bi-coordinate navigation system where latitude is one of the coordinates and the standard direction has a significant component towards W, we expect the orientations in A and B to converge towards each other in the western half-circle. If the standard direction has an eastern component, the converging orientations will be in the eastern half-circle. Only in the special case with a standard direction towards S, the two orientations would be opposite or the same.
Målområdenavigation når den tynde prismeside er vendt mod N (efterår). 10 fugle befinder sig og tragttestes i A, og de 10 krydser viser deres her og nu-positioner indenfor den stiplede ellipse med den lange akse pegende i normaltrækretningen mod SSW-SW. Gennemsnitsvektoren af retningsfordelingen fra A mod de 10 positioner er 214º – 0.637 ($P < 0.05$). Hvis de samme 10 fugle i tragtene ser stjernehimlen gennem et prisme, opfører de sig som de var i B. Gennemsnitsvektoren mod de 10 positioner bliver nu 317º – 0.641 ($P < 0.05$). Hvis de 10 positioner (nu de hvide cirkler) er tættere på A, bliver koncentrationen i gennemsnitsvektoren fra B større (339º – 0.926, $P < 0.001$). Er de 10 positioner langt mod SSW-SW i forhold til A, og SSW for B, nærmer de to gennemsnitsvektorer fra A og B sig hinanden.

The birds were trapped as grounded migrants on the same day or the day before the experiments were carried out. Each bird was used only once. In the 1975-experiments the birds were transferred directly from depot inside a house into the funnels placed on The Bastion of Bielke, easternmost Christiansø in the Baltic Sea (55º 19'N / 15º 11'E). In 2007 and onwards the birds were transferred to the cages about one hour before sunset on the experimental site in the southeast corner of Christiansø on the Bastion of the Queen from the depot site in a garden in the middle of the island. From the cages the birds had an unobstructed view of the sky and the surroundings down or almost down to the horizontal level. Afterwards, the birds were transferred into the funnels about two hours after sunset and spent the next about 1½ hour within the funnels. Therefore, the prism-birds did not experience the changed starry sky until they were placed in the funnels. The orientation and amount of activity of the individual birds within the funnels were estimated as previously described in e.g. Rabøl (1981, 2010, 2014).

To a start, all experiments were carried out under a starry sky, and the thin side of the prism (autumn) was turned N in all four prisms (Fig. 3). In order to investigate for a spurious effect of the thin side we also a few times tested birds at sunset or in overcast without stars on the sky. Furthermore – in order to reveal a possible thin-side attraction – on some starry nights the thin side of the four prisms was turned towards N, E, S, and W, or concomitantly turned towards E (two funnels) or W (another two funnels), respectively. If turned S, the birds will observe a stellar sky 4º to the N. It is not known how the birds appreciate and interpret the slightly skewed stellar sky as seen through prisms with the thin side turned E or W. There will be no latitudinal shift nor change in the rota-

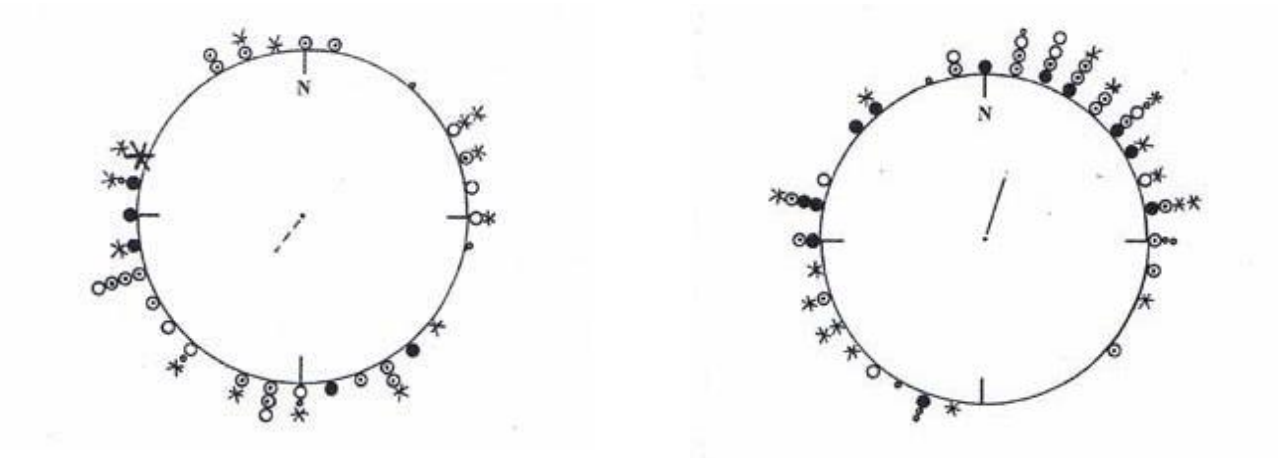

Fig. 3. Redstarts, Pied Flycatchers and Garden Warblers, September 1975. The sample orientation of the controls (left figure) and prism-birds (right figure) during starry nights. The thin side of the prisms is turned N (cf. Fig. 1). The sample mean vectors are 218º – 0.277 (N = 35) and 18º – 0.387 (N = 44, P < 0.01), respectively. The lower distribution looks bimodal with peaks in 40º – 0.814 (N = 30) and 256º – 0.765 (N = 14).
Tragtforsøg med Afrika-trækkere i september 1975. Orienteringen af fuglene under prismet ses til højre: de er NNØ-orienterede. Måske skal det opfattes sådan, at de fleste i snit orienterer sig mod NØ, medens en mindre del er er VSV-orienterede. Til venstre ses kontrollerne – uden prismer. De fleste er spredt SV-orienterede og viser således en ikke-signifikant orientering i normaltrækretningen. Måske inducerer prismerne i de fleste fugle omvendt kompasorientering, medens et mindretal forsøger at stjernenavigere.

tional phase of the stellar sky, whereas the direction towards geographical N will only be changed by a few degrees. However, there may be some visual distortions which disturbs or confuse the bird – or skew the orientation in one way or another.

Results and short interpretations

Autumn 1975

In autumn 1975, the most homogenous series of prism-experiments involved Common Redstarts *Phoenicurus phoenicurus*, Garden Warblers *Sylvia borin* and European Pied Flycatchers *Ficedula hypoleuca* (numbers 23, 15 and 4, and 32, 17 and 3, respectively, as controls and prism-birds) from most nights (all starry) in the period 1 through 9 September. Almost all birds were juveniles. All prism-birds were tested with the thin-side towards N.

As depicted on Fig. 3 the sample mean vector of the controls was 222º – 0.297 (N = 30), or – including the smaller dots – 218º – 0.277 (N = 35). According to the Rayleigh test the distribution is random (0.05 < P < 0.10). If the supposed standard direction is SSW-SW (214º) and applying a V-test the test-statistic U yields 0.01 < P < 0.05, i.e. the orientation is significantly in the standard direction. The sample mean vector of the prism-birds was 13º – 0.467 (N = 36, P < 0.001), or including the smaller dots 18º – 0.387 (N = 44, P < 0.01). However, the distribution does not appear unimodal. There seems to be a major peak in about 40º, and minor peak in about 265º.

The difference between the controls and experimentals was tested, and according to the Mardia-Wheeler-Watson test the difference was statistically significant (P < 0.01).

In conclusion, the 'displacement' as seen through the prism apparently induces 'something' but more reverse than compensatory orientation. I.e. the prism-orientation is not supporting a hypothesis of goal-area gradient navigation in a strict bi-coordinate sense (predicting a NW-NNW-response in the prism birds, Fig. 2), but looks more like a prevailing 180º reverse directional response. Anyway, the orientation does not appear as a thin-side response.

2007, Africa-migrants, autumn, sunset

Sunset experiments on Christiansø were carried out 23, 24, 29, 30, 31 August 2007 testing Africa-migrants. The thin side of the four prisms was turned W, N, E and S, respectively. In these sunset experiments the sky was sometimes overcast and sometimes clear. i.e. the birds were able to observe the setting sun and the sunset polarization pattern, but no stars were available even on clear evenings. These experiments were carried out to investigate a possible thin-side effect.

In reference to geographical N the sample mean vector of the prism-birds (Fig. 4, left) was 210º – 0.211 (N = 14), and in reference to thin side the prism (Fig. 4, right, double arrow) 246º – 0.273 (N = 14).

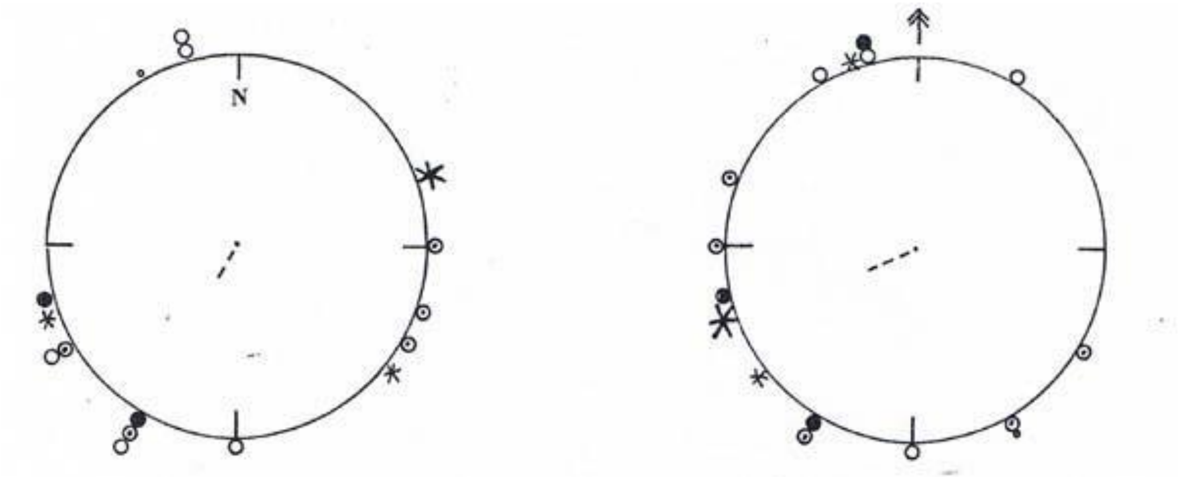

Fig. 4. Prism-birds, Africa-migrants tested at five sunsets in the period 23 through 31 August 2007. The thin side of the prisms was turned N, E, S, and W, respectively. The left figure shows the orientation in reference to N. The sample mean vector is 210º – 0.211 (N = 14). The right figure shows the orientation of the same birds in reference to the thin side of the prism (double arrow). The sample mean vector is 246º (114º to the left) – 0.273 (N = 14). The controls to these experimentals are shown in Fig. 5.
Afrika-trækkere testet ved solnedgangstide under prismer med den tynde side vendt mod henholdsvis N, Ø, S og V. Der er tale om forsøg, der primært skal vise, om der er en taxisk reaktion mod den tynde prisme-side. Men det viser fuglene ikke (til højre), ligesom de heller ikke er signifikant orienterede i normaltrækretningen (til venstre). Kontrollerne til disse fugle er vist på Fig. 5 og viser tendens til orientering i normaltrækretningen.

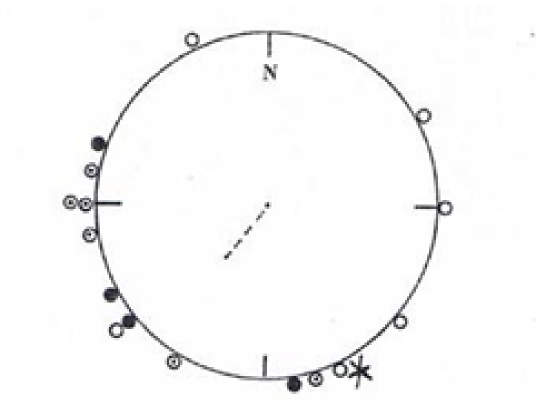

Fig. 5. The orientation of the control birds to the prism-birds (Fig. 4) at sunset 23 through 31 August 2007. The sample mean vector is 219º – 0.398 (N = 17). According to the Rayleigh-test the sample mean vector is statistically insignificant (0.05 < P < 0.10). However, according to the V-test and a standard direction in SSW-SW, the orientation is significant (P < 0.01).
Kontrolfuglene til prismefuglene vist i Fig. 4. Afhængig af testproceduren (Rayleigh-test eller V-test) viser de desorientering eller signifikant orientering i normaltrækretningen mod SW.

The orientation of the contemporary controls (Fig. 5) was 219º – 0.398 (N = 17). Clearly, there was no directional difference between prism and control birds and if added together the sample orientation in reference to geographical N was significant, 216º – 0.313 (N = 31, P < 0.05). The mean orientation is very close to the suspected standard direction (SSW-SW).

In conclusion there seems to be a fairly weak tendency to orient in the standard direction (could be navigation or compass orientation), but no thin-side effect was observed.

2007, Africa-migrants, autumn nights

On four starry nights 4 through 16 September 2007, Pied Flycatchers and Redstarts were tested mimicking the 1975-experiments (Fig. 3), i.e. the thin side of the prism was turned geographical N in all four prisms producing a starry sky as observed by birds in the funnels simulating a latitudinal displacement 4º towards S.

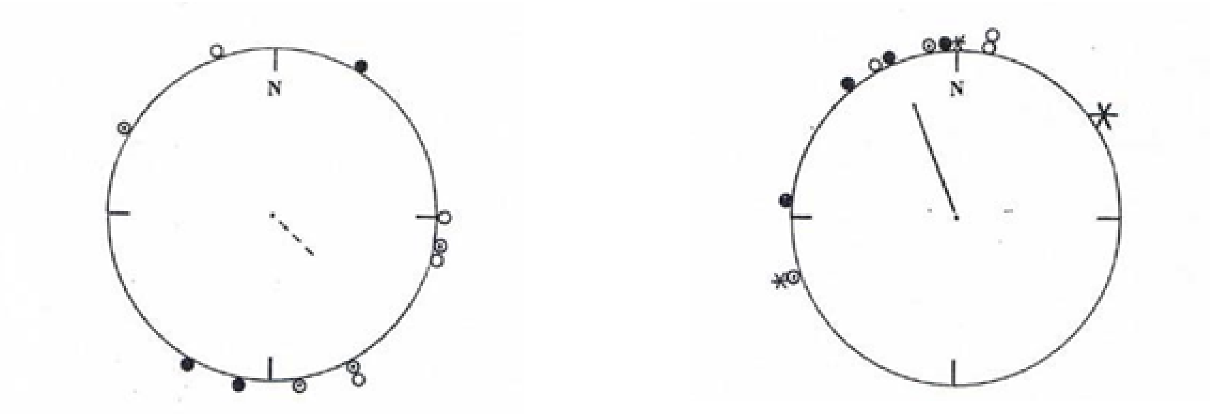

Fig. 6. Pied Flycatchers and Redstarts, 4 through 16 September 2007. Starry nights and the thin side of the prisms turned N. The sample orientation of the controls (left figure) and prism-birds (right figure) during starry nights. The sample mean vectors are 134º – 0.350 (N = 11) and 339º – 0.729** (N = 10, P < 0.01), respectively.
Afrika-trækkere i forsøg på stjerneklare nætter mellem 4 og 16 september 2007. Til venstre ses kontrolfuglene testet uden prisme påsat. De er ikke signifikant SØ-orienterede. Til højre prismefuglene (alle tynde sider vendt mod N). De er meget signifikant NNV-orienterede, hvad der kan tydes som navigation mod et målområde i denne retning, men SV for Christiansø.

The sample orientation (Fig. 6) of the prism-birds was 339º – 0.729 (N = 10, P < 0.001), and of the controls 134º – 0.350 (N = 11). The difference between the two distributions was significant (Mardia-Wheeler-Watson test, 0.01 < P < 0.02). Clearly, the controls were not displaying standard orientation, but this does not necessarily invalidate the presumption of navigation in the prism birds. Perhaps the goal areas in the controls are close to Christiansø and mostly SE of the island. If so, goal area navigating birds under the prisms should orient NNE. However, the NNW-orientation found resembles (though mirroring) the reverse NE-orientation of Fig. 3 and Fig. 7. Anyway, the simplest explanation of the NNW orientation of the prism birds is a thin-side attraction.

2007, Robins, autumns nights

On seven starry nights between 6 and 18 September 2007 Robins were tested as both prism-birds and controls. Otherwise, same procedure as above.

The sample mean vector (Fig. 7) of the prism-birds was quite insignificant: 78º – 0.076 (N = 16), but certainly the distribution appeared bimodal with the slightly larger mode in 'NE'. Doubling the angles improved the description: 32º/(212º) – 0.398 (N = 20, P < 0.05). The sample mean vector of the controls was 201° – 0.583*** (N = 37, P < 0.001). The difference was tested applying a Mardia-Wheeler-Watson test (0.05 < P < 0.10), i.e. the difference was not quite statistically significant, but clearly the test in consideration is not very powerful when one of the distributions is bimodal. Again, there is a mismatch – considering the hypothesis of stellar navigation – between the easterly and westerly components in the two groups.

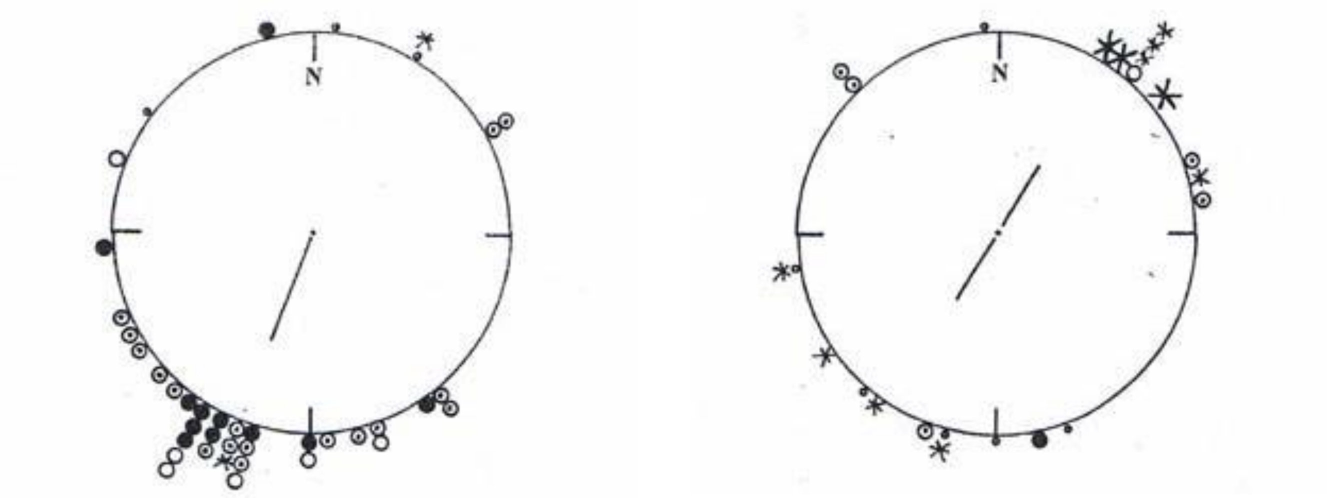

Fig. 7. Robins, 4 through 18 September 2007. The sample orientation of the controls (left figure) and prism-birds (right figure) during starry nights. In all prisms the thin side was turned N. The sample mean vectors are 201° – 0.583 (N = 37, P < 0.001) and 78º – 0.076 (N =16), respectively. Doubling the angles improved the latter description: 32º/(212º) – 0.398 (N = 20, P < 0.05). The prisms seem to reverse the orientation rather than producing a navigational reaction under condition of an unchanged E/W-coordinate.
Rødhalse i september 2007. Den tynde side af prismerne var vendt mod N og himlen stjerneklar. Til venstre ses den meget klare SSV-lige orientering af kontrollerne. Til højre den to-toppede orientering af prismefuglene, der også som individer viser meget to-toppethed (de mange 'stjerner'). Det ligner mere omvendt kompasorientering end en navigatorisk kompensation.

2008, autumn, starry nights

Four prisms were in use on nine starry nights, and the thin side of the four prisms was directed towards geographical N, E, S, and W, respectively. On most nights, controls were also tested. The expectation was that the controls should be significantly oriented in reference to the standard direction (i.e. about SSW-SW). The orientation of the experimentals is more difficult to predict. If the migratory readiness is high, standard orientation is expected with a smaller sample-concentration than in the controls. If the migratory readiness is low, then perhaps thin-end attraction will dominate.

Africa-migrants were tested during four sunset-early nights/nights 24 August through 9 September. The two first sunset-early nights follow below.

The experiments on the first sunset/early night started half an hour after sunset, and were finished a little more than one hour later, i.e. with the major stars on the sky after about 50 minutes. Very probably, a sunset phototaxis was acting. Also, the next night (29 August) started a little early, 1 hour and 40 minutes after sunset leaving a weak sunset sky in WNW for the first about 15 minutes. For that reason, 24 and 29 August were considered isolated. The sample mean vector in the prism-birds in reference to N was 105º – 0.161 (N = 5), and in reference to thin-side of the prism 359º – 0.896 (N = 5, P < 0.05). The controls oriented 313º – 0.654 (N = 9, P < 0.05). Clearly, it looks like a thin-end attraction.

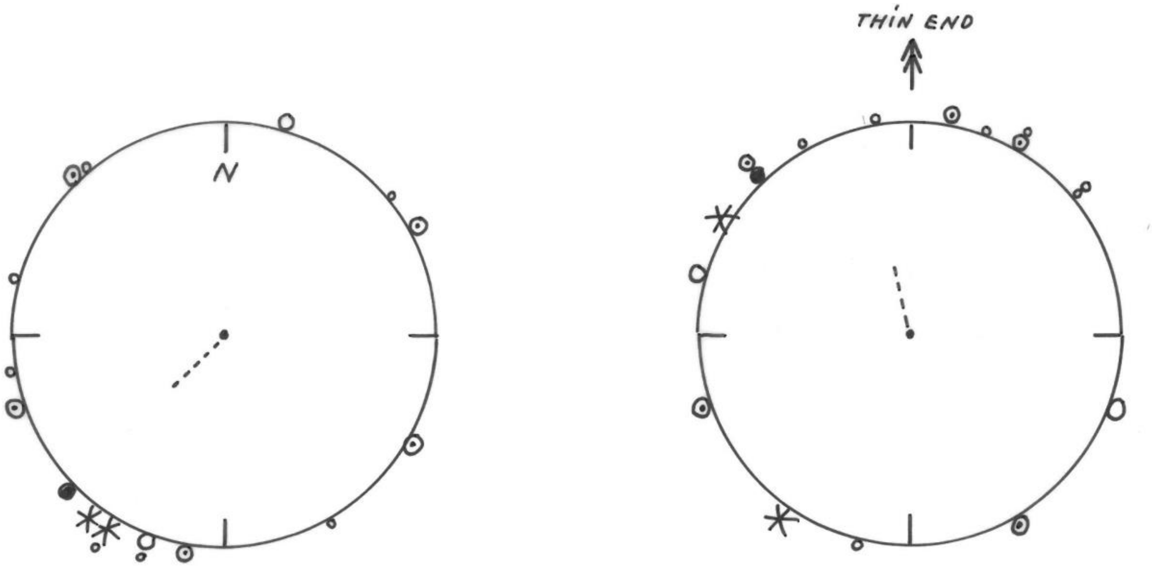

Fig. 8. Robins, 24 through 28 September 2008. Thin sides of the prisms turned N, E, S, and W, respectively. The sample orientation of the prism-birds in reference to N (left figure) and thin-end of the prism (right figure) during starry nights. The sample mean vectors are 225º – 0.335 (N = 17) and 348º – 0.339 (N =17), respectively. The sample mean vector of contemporary controls (not shown) tested under the natural starry sky was 199º – 0.583 (N = 10, P < 0.05).
Rødhalse i september 2008. Den tynde prismeside var vendt henholdsvis mod N, Ø, S og V på de fire prismer. Fuglene viser svag tendens til både normalorientering og orientering mod den tynde prismeside.

On the two last starry nights (8, 9 September) the orientation of the prism birds in reference to N was 234º – 0.698 (N = 8, P < 0.05), and in reference to thin-side bimodal 81º/261º – 0.732 (N = 8, P < 0.05). The controls oriented very differently on the two nights: On 8 September the sample mean vector was 160º – 0.662 (N = 8, P < 0.05), and on 9 September 305º – 0.702 (N = 7, P < 0.05)! Clearly, there is no thin-side orientation here.

Robins tested during five nights 24 through 28 September oriented 225° – 0.345 (N = 17) in reference to N, and 348° – 0.339 (N = 17) in reference to the thin side of the prism (Fig. 8). Both are significant (P < 0.05) according to the V-test and the theoretical directions 214º (SSW-SW) and 0º. Controls from the three nights 25 through 28 September oriented 199º – 0.583 (N = 10, P < 0.05). It looks like both standard orientation (compass or navigation) and some thin-side attraction.

When combined, the orientation of Africa-migrants and Robins in reference to N (226° – 0.361, N = 30, P < 0.05) is statistically significant as also the orientation in reference to the thin side of the prism (3° – 0.370, N = 30, P < 0.05).

However, this thin-side 'attraction' may be spurious and caused by inclusion of some very minor activities: The 10 directions derived from these minor activities considered as a sample were disoriented in reference to N (213° – 0.357, N = 10), but significantly oriented in reference to the thin side of the prism (27° – 0.702, N = 10, P < 0.01). The 20 orientations derived from at least 'small' activity or larger (i.e. 'medium', 'large' or 'very large') considered as a sample were not significantly oriented in reference to N (233° – 0.371, N = 20), and also disoriented in reference to the thin side of the prism (331° – 0.277, N = 20). However, both are significant according to the V-test (P < 0.05) – tested against 0º (thin side) and 225º (standard direction).

The conclusion should be that sometimes a thin-side tendency of the prism is observed, but mostly displayed of birds showing 'very small' activities.

2011-12, autumn, starry nights

On eight starry nights in the autumns 2011 and 2012 prism-experiments were carried out. Each night four freshly trapped birds (mostly Robins) were tested; two of these observed the starry sky through a prism where the thin side was turned W. In the two other birds the thin side was turned E.

Such a procedure will not change the latitude/Polaris altitude, but the starry sky apparently tilts 4° towards E or W, respectively. Whether or not this has an effect on the direction chosen is not known, but in principle could be deduced from the results obtained. Unfortunately, no control experiments – i.e. tests without prisms on top of the funnels – were carried out.

The orientation of the W- and E-birds is shown at Fig. 9: The sample mean vector of the W-birds (upper figure) in reference to N is 283°- 0.167 (N = 13). However, the distribution looks axial and doubling the angles improves to 14°/194° – 0.324 (N = 13). There seems to be no effect of the thin side towards 270°. The sample mean vector of the E-birds (lower figure) in reference to N is 97° – 0.462 (N = 10, z = 2.13, i.e. P little more than 0.10). Applying a V-test leads to 0.01 < P < 0.05, i.e. the orientation towards the thin side towards 90° is significant.

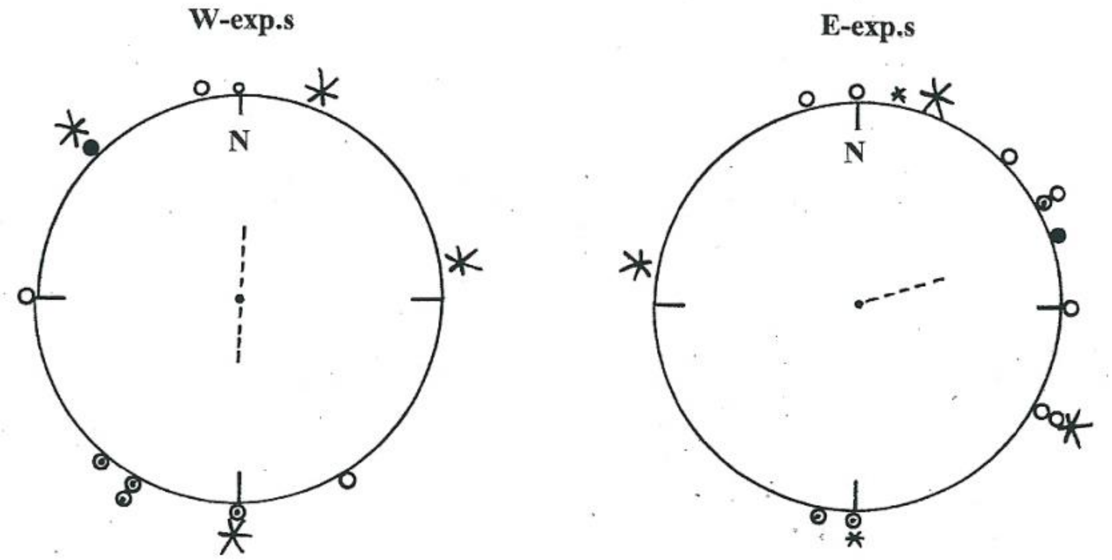

Fig. 9. Experiments 2011-12. Birds (mostly Robins) were tested on starry nights. In two prisms, the thin side was turned W (left), and in another two E (right). No control tests were carried out. The sample mean vector of the W-birds is 250º – 0.196 (N = 13), or after doubling the angles 3º/183º – 0.344 (N = 13). The sample mean vector of the E-birds is 72º – 0.438 (N= 14).
Forsøg 2011-12. Den tynde prismeside var vendt mod V i figuren til venstre, og mod Ø i figuren til højre. Sidstnævnte viser måske en reaktion med orientering mod den tynde side af prismet.

If the two distributions are expressed as function of the direction towards the thin side of the prism, this could be done by deflection of the W-birds 180° and then add the new distribution to the E-birds (thin side 90°). Combining these two distributions leads to 69° – 0.191 (N = 23). Applying the V-test the thin side tendency (towards 90°) is insignificant (P > 0.05).

One may wonder about the lack of standard orientation – in fact reverse orientation is more prominent. The set-ups should be ideal for demonstrating a thin side effect – but there seems to be no such effect in the W-birds, but perhaps in the E-birds (the interpretation of the V-test is not straightforward).

In conclusion, this investigation adds to previous studies on a superstition of an occasional and rather slight thin side effect.

Discussion

The first night experiments consisted of a control-group tested under the natural starry sky, and a group of four birds tested under prisms where the starry sky as seen by the birds in the funnels was tilted/displaced to a position 4º S of Christiansø. If the control birds showed orientation in a southerly standard direction, whereas the prism-birds displayed northerly orientation, the interpretation would be that a) the birds showed stellar navigation towards a goal area situated somewhere between Christiansø and the border between Poland and the Czech Republic 4º south of Christiansø.

Perhaps 4º seems too short a distance for a displacement eliciting compensation, but it corresponds to 444 km, and – at least in my universe – a normal migratory step of a nocturnal passerine migrant should be perhaps about 240 km (8 hours with an airspeed of 30 km/hour). Anyway, even if goal-area navigation is a fact, no one knows what the mean distance (and its variation) between actual position and goal area position is before the bird normally initiates a migratory leg.

To a start I did not realize that there could be other explanations for a northerly orientation, such as e.g. b) the prism-birds show a response related to the bilateral shape of the prism itself, or perhaps c) the birds were not navigating in reference to the stellar sky but showed reverse orientation in a star-compass system (or in reference to magnetic N). Clearly, we have to scrutinize the possibilities of b) and c) in order to be more precise about the mechanism. b) could have something to do with more light coming in through the thin side of the prism, or perhaps the prism tilts the outlook towards the thin side, or perhaps there is something looking like a 'wall' of some kind (the thick side of the prism) towards S? c) could be about a change in motivation because of something 'wrong' in the view through the prism.

Summing up, if the birds are tested under a starry sky beneath a prism where the thin side was turned N, then you cannot deduce the mechanism behind the compensatory orientation, because there may be several different explanations, and it is not possible to argue which one is the simplest and therefore the one following Occam's Razor should be considered the most probable. At least this holds true if the standard direction is close to due S.

However, if the orientation of the controls is significantly different from due S, you have some different expectations of the outcome of the three systems above: If the orientation of the controls is SW, you would expect 'NW' orientation in a), 'N' orientation in b), and 'NE' orientation in c). Clearly, the patterns in Figs 3, 6 and 7 are in best correspondence with model c). However, perhaps the reaction to E/W-position of B (Fig. 2) is delayed compared with a navigational N-response, and therefore different E/W components in the sample orientation of controls and prism-birds does not necessarily invalidates the goal area navigation hypothesis.

In order to distinguish between a) and c) on the one side and b) on the other the conditions for the prism-birds should be changed. If tested under a starry sky we could turn the thin side of the four prisms towards (1) N, E, S, and W, or (2) towards E (two prisms) and towards W (another two prisms). We could also test the birds (3) without the sight of a starry sky, i.e. outside night time (e.g. during sunset), or when overcast or 'overcast' (Rabøl 2018). The latter refers to a state where the funnels are covered with a sheet of translucent but not transparent plastic.

Applying Occam's Razor, orientation with a not understood mechanism for reverse orientation under some conditions, stellar compass would be the most complicated hypothesis; it appears constructed in order to fit a certain hypothesis. However, it was not so, because to a start I focused on goal area navigation. Perhaps the E/W-coordinate also reverses under the conditions employed. Perhaps the N/S- and E/W-coordinates are not acting independently of each other?

Unfortunately, these prism-experiments were mostly accessory in the years 2007 through 2012 and carried out during the same nights where compass conflicts or experiments considering magnetic navigation was the main theme. Therefore, considering the procedure never had my full attention. I assumed I could figure it out later, but the optimal conditions for doing this were missed.

Looking at the experiments shown at Figs 4, 5, 8, and 9 there are few and small indications of a thin side taxis in itself. However, it looks like stellar compass orientation (including reverse orientations) plays a greater role than stellar navigation (Figs 3, 6, and 7). Possibly, the pattern on Fig. 3 is bimodal with a large reverse modus in NE and a smaller navigational modus in WSW-W. However, there are more assumptions in the compass/reverse model making it ‘dubious’ in reference to Occam’s Razor. Perhaps, initially the bird feels goal area navigation with a southerly component is just the same as reverse orientation, i.e. NE. Expressed differently, reverse orientation in a compass system is close the be a kind of navigation. So, the overall conclusion should be that at least some (kind of) stellar navigation is involved in these prism-experiments. Anyway, the experiments call for repetitions from other people who dare to challenge the prevailing paradigm.

Acknowledgements

Two anonymous referees provided constructive suggestions for improvements of the paper, and the editors did a great job in helping to improve the paper and all the appendixes. Thanks a lot!

Resumé

Orienteringsforsøg med nattrækkende småfugle, hvor breddegradsforflytning er simuleret ved hjælp af prismer

Hvis man vil finde ud af, om trækfugle navigerer efter stjernehimlen, kan man tage dem ind i et planetarium, putte dem i tragte og præsentere dem for roterende ’stjernehimle’ svarende til forskellige her og nu positioner på Jorden. En Rødstjert fanget på træk på Christiansø befinder sig således på positionen 15ºØ, 55ºN, og det kan Rødstjerten i princippet finde ud af ved at se på den stedlige stjernehimmel. Hvis den nu ifølge sin medbragte indre flyveplan har Frankfurt som øjeblikkeligt mål, kan den for sit indre blik fremkalde sig stjernehimlen over Frankfurt (på 8ºØ, 50ºN). Omsat til menneskesprog og tankegang fortæller det fuglen, at den skal trække 5º mod S og 7º mod V, dvs. ca. SV. Det viser Rødstjerten så ved at flagre op af siden på tragten og dermed kradse i tragtens kridtbelægning i retningen mod SV, som jeg så kan ’aflæse’.

Madrid og Beograd befinder sig tilsvarende på positionerne 5ºV, 40ºN og 20ºØ, 45ºN. Nordstjernens højde over horisonten afspejler breddegraden, så sammenlignet med Christiansø står Nordstjernen noget lavere på himlen i Beograd og endnu lavere i Madrid. Set fra Jorden drejer stjernerne på nordhimlen modurs rundt om Nordstjernen med en fuld omdrejning (minus 4 minutter) i døgnet. Jo østligere man befinder sig, desto længere fremme er stjernerne i deres rotationsfase. Karlsvognen drejer rundt om Nordstjernen, og de to bagerste stjerner i ’bagsmækken af vognen’ peger næsten direkte på Nordstjernen, så forbindelseslinjen mellem Nordstjernen og

’bagsmækken’ kan derfor sammenlignes med en urviser. Hvis klokken på ’himmeluret’ i dette øjeblik er 135º i Beograd, er den derfor 140º på Christiansø og 160º i Madrid.

Hvis man nu havde flyttet Rødstjerter fra Christiansø til henholdsvis Madrid og Beograd ville deres trækkurser mod Frankfurt være henholdsvis ca. NØ og ca. VNV, og disse to trækkurser kan de i princippet finde ud af ved at se op på stjernehimlen det sted, hvor den er og sammenligne den med stjernehimlen over Frankfurt, som den udfolder sig for dens indre flyveplan (Nordstjerne-højde 50º, og klokken på ’himmeluret’ = 147º). Prøv selv at regne efter, og se om du har forstået det.

Stjernehimmelnavigation lyder meget indviklet og derfor usandsynligt. Kan en Rødstjert virkelig være så klog/vel-programmeret? Men forsøger man at forestille sig andre navigationssystemer baseret på Solen eller jordmagnetismen, bliver det mindst lige så kompliceret.

Der er ikke lavet mange forsøg i stjerne-planetarier for at se, om fuglene navigerer efter et mål på trækruten. Frankfurt kunne være et sådant midlertidigt mål på efterårstrækruten for svenske Rødstjerte fra det østlige Småland. Fuglene viser det ved en SV-orientering på Christiansø og ved henholdsvis NØ- og VNV-orientering efter de simulerede forflytninger til Madrid og Beograd. Som man kan se, kompenserer fuglene for ’forflytningerne’ i forhold til målet i Frankfurt, og denne kompensation, hvis man får den frem som den gennemgående tendens i en serie planetarie-forsøg, er ’beviset’ på, at fuglene stjernenavigerer. Dette var, hvad Thorup & Rabøl (2007) i princippet gjorde og fandt.

Nu er det ikke alle, der råder over et stjerneplanetarium, som jeg gjorde i sin tid. Først Tycho Brahe Planetariet i København, og senere Steno i Århus. Rabøl (1998) omtaler, hvad der kom ud af det; der var en gennemgående tendens til kompensation for de simulerede forflytninger, så konklusionen var, at fuglene (Broget Fluesnapper og Rødstjert) brugte stjernehimlen til at navigere efter.

Men man kan også i princippet bruge den naturlige stjernehimmel til at finde ud af, om trækfuglene breddegrads-navigerer. Som det vil være de fleste bekendt, så ’knækker’ billedet, hvis man ser på noget gennem et prisme. På Fig. 1 har jeg vist den opstilling, som jeg brugte til at teste, om fuglene breddegrads-navigerede. Hvis den tynde side af et stort prisme anbragt oven på en tragt vendes N-på om efteråret, ser fuglen gennem prismet en Nordstjerne, der står 4º lavere end på forsøgsstedet. Det simulerer en forflytning 4º mod S, og hvis forsøgsstedet er Christiansø (55ºN) svarer det til breddegraden på grænsen mellem Polen og Tjekkiet (51ºN). De anvendte prismer var lavet af plexiglas og vandfyldte, og de var noget uhåndterlige. Generelt bryder et prisme 1/3 af topvinklen, så en simuleret forflytning noget længere mod S end 4º – fx 8º – ville derfor kræve en topvinkel på 24º og et prisme godt dobbelt så tungt og formentlig med en øget forvrængningsgrad. Så det prøvede jeg ikke på, men en forflytning på 4º (444,44 km) mod S er godt nok ikke meget, og umiddelbart ville jeg nok forvente målområder for de på Christiansø rastende fugle på mellem -2º og +8º mod S, med en median i +2º, dvs. omkring 75 % af de fugle, der ser stjernehimlen gennem prismet vil bedømme, at de er flyttet S for deres mål. Og denne procent vil ret hastigt falde for hver dag, der går på Christiansø med et målområde, der vandrer længere og længere frem i trækruten. Længdemålet 1 m blev i sin tid defineret som en 10-milliontedel af afstanden fra Nordpolen til Ækvator. Da man havde indlagt 90º mellem Nordpolen og Ækvator kom det til at svare til, at breddegraderne blev adskildt med 10 mio. m divideret med 90 = 111,111 km. Til sammenligning er afstanden mellem længdegraderne afhængig af breddegraden.

Da jeg startede med at lave disse prismeforsøg i 1975, var det med den tynde side af prismet vendt mod N for alle mine fire prismer. Hvis fuglene (efterår under stjernehimlen) viste nordlig orientering under prismerne, ville det for mig være en indikation på en kompensation for en forflytning sydpå, og agenten her måtte være stjerne-navigation. Jeg så ikke andre muligheder. Da resultaterne kom ind (Fig. 3) kunne jeg godt fornemme, at der var noget 'galt'; prisme-orienteringen var for NØ-lig, hvor den med en normaltrækretning omkring SV burde have været NV-lig (Fig. 2), hvis der var tale om stjernenavigation (der var jo ikke rørt ved den ukendte Ø/V-lige koordinat i navigationssystemet). Det lignede mere omvendt kompasorientering. Spørgsmålet var også, om den nordlige orientering var et artefakt rettet mod den tynde prismeside, der jo vendte N-på. Den store NØ-top tyder dog ikke umiddelbart på dette.

Mange år efter genoptog jeg prismeforsøgene, dels forsøg i samme opstilling, men også forsøg a) ved solnedgangstide uden stjerner på himlen, og forsøg med den tynde prismeside vendt b) N, Ø, S, V, eller c) to med den tynde side vendt mod Ø, og to andre med den tynde side vendt mod V. Dette for at se, om der var en tyndside-effekt.

På figurerne kan ses, hvad der kom ud af det, og konklusionen er, at tyndside-effekten i sig selv synes at betyde lidt. Fortolkningen er sværere, når der stilles spørgsmålet: Er det stjernenavigation eller stjerne-kompasorientering med et betydeligt islæt af omvendt kompasorientering i de to tilfælde med 135º forskel mellem tyndside-retningen og kompasretningen i normaltrækretningen (SV). Inklusionen af omvendt orientering er svær at placere entydigt som kun kompas-relateret; det kan også opfattes som et navigatorisk svar.

Så den endelige konklusion på disse prismeforsøg må være, at tyndside-effekten er svag, medens reaktionen på en simuleret forflytning fra 55ºN til 51ºN befinder sig i det diffuse grænseland mellem stjernenavigation og omvendt stjernebaseret kompasorientering.

References

Perdeck, A.C. 1958: Two types of orientation in migrating Starlings *Sturnus vulgaris* L., and Chaffinches *Fringilla coelebs* L., as revealed by displacement experiments. – Ardea 46: 1-37.

Perdeck, A.C. 1967: Orientation of Starlings after displacement to Spain. – Ardea 55: 194-202.

Rabøl, J. 1972: Displacement experiments with night-migrating passerines. – Z. Tierpsychol. 30: 14-25.

Rabøl, J. 1981: The orientation of Robins *Erithacus rubecula* after displacement from Denmark to Canary Islands, autumn 1978. – Ornis Scand. 12: 89-98.

Rabøl, J. 1998: Star navigation in Pied Flycatchers *Ficedula hypoleuca* and Redstarts *Phoenicurus phoenicurus*. – Dansk Orn. Foren. Tidsskr. 92: 283-289.

Rabøl, J. 2010: Orientation by passerine birds under conflicting magnetic and stellar conditions: no calibration in relation to the magnetic field. – Dansk Orn. Foren. Tidsskr. 104: 85-102.

Rabøl, J. 2014: Do european chats and warblers use magnetic gradient navigation. – Dansk Orn.Foren. Tidsskr. 108: 232-250.
Rabøl, J. 2018: Dominance and calibration of magnetic, sunset and stellar compasses in cue conflict experiments with night-migrating passerines. – Dansk Orn. Foren. Tidsskr. 113: 23-35.
Thorup, K. & J. Rabøl 2007: Compensatory behaviour after displacement in migratory birds. A meta-analysis of cage experiments. – Behav. Ecol. Sociobiol. 61: 825-841.
Wiltschko, W. & R. Wiltschko 1978: A theoretical model for migratory orientation and homing in birds. – Oikos 30: 177-178.

Author's address

Jørgen Rabøl (jrabol@hotmail.com), Department of Biology, University of Copenhagen, p.t. Søndermølle 16, DK-8789 Endelave, Denmark