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The orientation following geographical displacements; unpublished experiments and a single correction to Thorup & Rabøl 2007

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(*Med et dansk resumé: Upublicerede forflytningsforsøg; tillæg til Thorup & Rabøl 2007*)

Abstract Thorup & Rabøl (2007) presented the results of all published displacement experiments – real or simulated – using the funnel method (Emlen & Emlen 1966). In short, juvenile birds tested during nights with stars available for orientation on the average compensated the displacement significantly in a way compatible with the hypothesis of goal area navigation as the inherited orientation system of passerine birds. Since 2007 more displacement experiments have been made available and the results and trend – as presented here – developed to even higher significance.

Introduction

Displacement experiments represent a standard way to demonstrate whether the migratory route of birds is programmed as vector orientation/clock-and-compass or (goal area) navigation. To a start, recoveries of banded birds (e.g. Perdeck 1958) was the slow and not very efficient way to gather information. In the US, radio-tracking by means of car and aeroplane developed (a recent contribution is Thorup *et al.* 2007), but the method is not easy and requires a lot of manpower. Then everything changed when Emlen & Emlen (1966) introduced the funnel-method, which made the use of many birds and restricted man-power possible. I soon entered the scene (Rabøl 1969, 1970), but the natural and expected boom of other people never took place. The reasons for that were several: Emlen (e.g. 1975) never found clear indications of navigation in Indigo Buntings *Passerina cyanea*, and Wiltschko & Wiltschko (e.g. Wiltschko 1973) never believed in the possibility of navigation in juvenile birds. Furthermore, before the Germans turned to using funnels, the clumsy Frankfurt-cage with eight radial perches was probably not the ideal gear for demonstrating compensatory orientation. So, over the years, I was rather lonely on the displacement scene as obvious from the few contributions of other people referred to in Thorup & Rabøl (2007). This may be considered a weakness, but if you are sceptic about the generality of the outcome of my experiments, you are welcomed to scrutinize my information for possible errors. In recent years, geolocators and GPS-tracking has once more changed the scene, and in particular Kasper Thorup and his group displacing Common Cuckoos *Cuculus canorus* (e.g. Thorup *et al.* 2020) produced remarkable results, which will not be commented here. However, neither geolocators nor GPS has made the funnels obsolete, because they cannot be used in connection with simulated displacements investigating which cue is used for the compensatory behaviour.

Material

The present contribution is a follow up with further displacements not included in Thorup & Rabøl (2007):

1. Ten samples of displacements (ID 83 until 92) were omitted by the editor for inclusion in the appendix of Thorup & Rabøl (2007); the reason was that they were not previously published; only the results were presented. Now, more information is given.
2. Three samples (ID 93, 94, 95) mostly comprising adult birds are added.
3. The orientation of three different species after displacement from Denmark to the Faroes (ID 96, 97, 98) are included.
4. ID 11 is corrected.
5. Summing up, all my displacements are now available – also those – such as some of (1) – which were not optimally planned and carried out showing bewildering results.

Results

Adopting the system of Rabøl & Thorup (2001 Fig. 2) and this appendix, the orientations after displacement were depicted to the compensatory (+) or counter-compensatory (–) side.

Omitted experiments

ID 83: Sixteen Garden Warblers *Sylvia borin* were trapped as migrants on Christiansø (55º 19'N, 15º 12'E) on 19 May 1989 and the very same day transported about 370 km NW to Northern Jutland (Sæby, 57º 17'N, 10º 31'E) where funnel experiments were carried out around midnight between 19 and 20 May under a starry sky. Five birds failed to show any significant activity, and the sample mean vector was 356º – 0.77 ($N = 11$, $P < 0.01$). As the birds arrived to Christiansø in westerly winds, an orientation somewhere between NW and NNE was expected (the standard direction is probably about N to NNE, and the mean direction of a greater sample of Garden Warblers and Common Redstarts *Phoenicurus phoenicurus* that arrived in westerly winds and tested on Christiansø in spring was N). Clearly, there seems to be no compensation for the displacement, and if the expected orientation on Christiansø is N, the orientation is slightly to the counter-compensatory side (-4º).

ID 84 & 85: Twelve European Robins *Erithacus rubecula* were trapped on Akerøya, SE Norway (about 59ºN, 11ºE) in the end of September 1980 (most on 26 September) and transported about 500 km SE-SSE to Christiansø on 29 and 30 September.

On 1 October the birds were tested under an overcast sky and the directional distribution was bimodal with the major peak between NW and NE (6 birds) and the remaining two birds in 150° and 210º. Doubling the angles leads to 346º/(166)º – 0.47 (N = 8). The main orientation could be perceived as reverse standard or compensatory back towards Norway. If the standard direction is considered as 200º, the main peak orientation is to the compensatory side (+146º).

The birds were also tested on the two starry nights of 3 and 5 October, and the sample mean vector was 108º – 0.51 (N = 16, P < 0.05). Some birds were oriented on both nights, but the original notes were lost, and therefore means are not considered. This counter-compensatory (-92º) orientation is not easily interpreted.

ID 86 & 87: A total of 22 Garden Warblers and four Redstarts were trapped as migrants at Blåvand (55º 33'N, 8º 06'E) between 17 and 31 August 1971. 16 of these (including two Redstarts) were transported to Stensoffa in Scania, Sweden (55.7ºN, 13.5ºE, i.e. about 350 km ENE–E) on 2 September. All experiments (both Blåvand and Stensoffa) were carried out under a starry sky.

The purpose of the experiment was to investigate whether it was possible to imprint the birds on the 'position' of Stensoffa, and then after a re-displacement to Blåvand find out whether there was a compensatory (component of) orientation back towards Stensoffa. W. Wiltschko (in litt. in Rabøl 1972) had suspected a navigational component back towards the place of trapping, which in composition with a standard direction vector – as an alternative to goal area navigation – could be responsible for the compensatory orientation normally following the displacements in the experiments of mine (model B in Fig. 1 in Rabøl 1994). Perhaps such a navigational component could also be directed towards another place (here Stensoffa) than the place of trapping (here Blåvand). As obvious from the results below this hypothesis could not be confirmed.

At Stensoffa the birds were caged outdoors during nights 4 and 5 September under a starry sky. Half of the birds were then tested on 10 September, and the other half were exposed under the starry sky. These latter birds were then tested under a starry sky on 11 September.

On 12 September the birds were displaced back to Blåvand, where tested both the same and the following night under a starry sky.

Of the 16 birds displaced to Stensoffa, 10 were oriented at Blåvand before the displacement (a single bird was tested on 25 August, four birds on 30 August, and five birds on 31 August). The mean vector was 168º – 0.26 (N = 10). If six other birds trapped and tested at Blåvand 21-24 August are included, the sample mean vector attains significance (132º – 0.44, N = 16, P < 0.05).

At Stensoffa most birds were tested on 10 and 11 September, and the sample mean vector was significant (282º – 0.56, N = 14, P < 0.05). Testing the correspondence between this sample mean vector and the one from Blåvand based on the 16 birds a highly significant difference is achieved (P < 0.001, Watson-Williams' test).

The orientation following the displacement is thus to the compensatory side (+150º). However, if the orientation of those birds tested on Stensoffa considered as function of the orientation of the same birds at Blåvand, there is no tendency of a compensatory orientation, and in fact the insignificant sample mean vector (-7º – 0.32, N = 8) is even to the wrong side.

After re-displacement to Blåvand – and using means of the five birds tested on both nights – the sample mean vector at Blåvand was significant (158º – 0.65, N = 9, P < 0.05). Testing this against the sample mean vector at Stensoffa yields highly significance (P < 0.001, Watson-Williams test). As evident, the orientation following the re-displacement is to the counter-compensatory side (-124º). However, testing the orientations at Blåvand as a function of the orientations at Stensoffa, the sample mean vector (-126º – 0.19, N = 9) is far from attaining significance (though the shift is to the expected side).

Clearly, these results are not easily interpreted.

The initial SE-SSE orientation at Blåvand is typical for the site, and probably as a general rule arises as a mixture between a southerly standard direction and easterly compensatory orientation for previous wind drift.

The W-WNW orientation at Stensoffa is surprisingly northerly taken the more than one week delayed tests on 10 and 11 September into consideration. Perhaps there was some city light attraction from the towns Malmø and Lund (the horizontal glow was fairly prominent). Therefore, 282º is probably also a bad reference direction for comparison with the subsequent SSE-orientation at Blåvand on 12 and 13 September.

Perhaps for the sake of clarity these experiments (as also ID 84, 85 to a smaller extent) should never have been included in the present context, but I feel it important that all data available should be presented.

Christiansø-Endelave displacements

ID 88: 40 juvenile European Pied Flycatchers *Ficedula hypoleuca* were trapped on Christiansø 19 and 20 August 2001. The birds arrived in easterly winds and presumably were of Finnish or eastern Baltic origin. The birds were transported to Copenhagen on 29 August, and then to Endelave 3 September, where caged outdoors from 6 until 28 September. On 8 September, the birds experienced a clear starry night (for the first time after the trapping), and the first experiments were carried out on the starry nights of 11, 13 and 14 September. From 6 September, the birds were divided in three groups: 1) 12 outdoor controls (experiencing the natural magnetic field and the sun, sunset and stars most of time), 2) 12 indoor controls (never exposed for celestial cues), and 3) 16 outdoor experimentals (caged and tested in magnetic fields where magnetic N was deflected towards E or W). Here we consider only the controls.

The orientation of the outdoor controls was extremely varying also within the individuals during the first three starry nights following the displacement. In the sample distribution, two peaks were prominent, one in the standard direction sector of SSW-SW and a slightly larger second one in E-ESE. The sample mean vector of the 34 individual bird nights was 148º – 0.29 (N = 34, 0.05 < P < 0.10) and in fact not significantly different from random if relying on the Rayleigh test. However, the deviation from the expected standard direction of SW-SSW (214º) was significant on the 0.05 level (confidence interval test). Certainly, it looks like some of the birds were compensating the displacement from Christiansø to Endelave. However, the compensatory orientation (+66º) could also be a response to displacements towards W by the easterly winds preceding the arrival to Christiansø.

Later, the 12 outdoor controls were tested under the starry sky on 23 September. The sample mean vector was 206º – 0.86 (N = 12, P < 0.001). Also, the indoor controls were tested (19 September) under simulated overcast (i.e. the funnels were covered with a translucent but not transparent plastic sheet). The sample mean vector was 219º – 0.74 (N = 12, P < 0.001). Clearly for both samples it looks like orientation in the standard direction.

ID 89: 14 juvenile Pied Flycatchers and nine juvenile Redstarts were trapped as migrants on Christiansø between 30 August and 5 September 2002. The arrival winds on Christiansø were from varying directions. The birds were not exposed for the stars when caged on the island. On 6 September the birds were transported to Endelave and caged outdoors. On 6 and 7 September, the sunset was covered by clouds whereas during the two nights, the birds sometimes experienced the stars. The birds were tested under a clear starry night sky on 8 and 9 September after experiencing a clear sunset/early night sky in their cages. Here we consider only the orientation of the seven control birds (the experimental group consisted of 16 birds experiencing magnetic N deflected towards E or W).

Two birds were disoriented on 9 September, and a single bird was bimodally oriented on 8 September. Two sample mean vectors could be considered: 1) based on 8 September except a single bird from 9 September (the one which was bimodally oriented on 8 September), and 2) based on simple means if unimodally oriented on both occasions (4 birds), otherwise based on the single orientations from 8 September (two birds) or 9 September (one bird). The sample mean vector of 1) is 180º – 0.69 (N = 7, P < 0.05), and of 2) 184º – 0.72 (N = 7, P < 0.05). Neither direction deviated significantly from the standard direction of SSW-SW (confidence interval test). Anyway, both are to the compensatory side (the first +34º).

ID 90: 15 juvenile Pied Flycatchers and 12 juvenile Redstarts were trapped as migrants on Christiansø 6 September (8 birds), 8 September (15 birds) and 9 September (4 birds) 2002. The morning arrival winds on Christiansø was SW, S and E on 6, 8 and 9 September, respectively. On Christiansø, all birds experienced a clear sunset/early night starry sky on 10 September. On 11 September, the birds were transported to Jutland, and the next day to Endelave.

On 12 and 13 September, the birds experienced a clear sunset/early starry night in their cages and were later tested in the funnels during starry nights. As in the previous cases only control birds were used (16 experimentals were caged and tested within magnetic fields where magnetic N was deflected towards E or W). On the first night, 8 of 11 control birds were tested, whereas all 11 controls were tested on 13 September. Two sample mean vectors could be considered: 1) based on the directions of the eight birds from 12 September, and the directions of the remaining three birds on 13 September, and 2) based on the means from 12 and 13 September (8), and the directions from the three birds tested only on 13 September, the means were: 1) 139º – 0.67 ($N = 11$, $P < 0.01$) and 2) 144º – 0.76 ($N = 11$, $P < 0.01$). Both deviated significantly from the expected standard direction of SW-SSW ($P < 0.01$, confidence interval test). Both orientations are to the compensatory side (the latter +90º).

ID 91: 16 juvenile Redstarts and 14 juvenile Pied Flycatchers were trapped as migrants on Christiansø 3 September (23) and 4 September (7) 2004. The arrivals were in weak NW winds suggesting origin from the north (Sweden).

On 6 September, the birds were transported to Copenhagen and on 7 September to Endelave. On 8 September, the birds experienced a clear starry sky in their cages on Endelave (the birds were not exposed for the stars 3 to 7 September). On Endelave, the birds were divided in three groups: two times eight birds were caged and tested within changed magnetic fields simulating geographical displacements to N and S, respectively, whereas 14 birds were controls caged and tested in the natural magnetic field. Only the controls are considered here.

On the starry nights of 9 and 10 September, the sample mean vector (all birds only tested once) was 162º – 0.68 ($N = 14$, $P < 0.001$). Clearly, this orientation is to the compensatory side (+52º). In the next period the weather was mostly rainy and windy and no starry sky experiments were carried out before 19 and 21 September. The sample mean vector (two birds were oriented on both nights and their means were used, and a single bird was disoriented) was now 202º – 0.72 ($N = 13$, $P < 0.001$).

The clockwise shift is significant ($P = 0.05$) if the individuals are used as their own controls (confidence interval test). The sample mean vector is 35º – 0.64 ($N = 13$, $P < 0.01$). If the two sample mean vectors are tested against each other applying the Watson-Williams test (based on the assumption of two independent samples) the difference is not significant as $t = 2.03$ ($P = 0.05$ corresponds to $t = 2.06$).

As the standard direction of Swedish Redstarts and Pied Flycatchers is supposed to be about SSW-SW it looks like the birds compensated in the first period following the displacement. The deviation of 162º from SSW-SW (214º) is very significant ($P < 0.01$, confidence interval test). Later, the sample mean vector approaches the standard direction.

ID 92: 32 juvenile Robins were trapped on Christiansø 1 October 2004. The wind was from NE. Probably the birds originated in the eastern part of Sweden on a rather southerly heading. A more remote possibility is an about 800 km non-stop flight from Finland.

On 4 October, the birds were transported to Copenhagen, and on 5 October to Endelave. On 6 October, the birds were placed outdoors, but no experiments were carried out before 8 October because of windy and cloudy weather. The purpose of the experiment was to simulate geographical displacements towards N and S, respectively, by caging and testing the experimental birds within magnetic fields with changed inclinations and intensities. As in the Redstart/Pied Flycatcher experiments mentioned above, only the controls (13 birds) are considered here. During the night between 30 September and 1 October the birds experienced an at least partly starry sky (the sky was half covered with clouds on the arrival to Christiansø). However, in the next period until the first experiments were carried out on 8 October the birds were not exposed for the stars. Before the experiments on 8, 9, 10 and 11 October the birds were exposed for a clear sunset/early night sky and tested under a starry night sky.

The sample mean vector of the Robins tested during 8 and 9 October was 170º – 0.62 ($N = 12$, $P < 0.01$; the individual birds were tested only once). During 10 and 11 October the birds were tested again, and two birds displayed disorientation. The sample mean vector was 197º – 0.59 ($N = 10$, $P < 0.05$). If the individuals are tested as their own controls, the clockwise shift (towards 8º – 0.86, $P < 0.05$) is not significant (confidence interval test). As the standard direction is supposed to be about SSW-SW (214º) the sample mean vector during 8 and 9 October deviates significantly ($P < 0.05$, confidence interval test) to the compensatory side (+44º).

ID 93, 94 & 95: five adult Redstarts, four adult Garden Warblers, four juvenile and 10 adult Pied Flycatchers, together with seven adult Spotted Flycatchers were trapped on Christiansø between 17 and 25 August 2005. The weather in this period was homogeneous with high temperatures and weak, mostly easterly winds suggesting arrivals from N or NE (on 23 August an adult Pied Flycatcher carrying a Finnish ring was caught).

On Christiansø, the birds were caged outdoors two by two and covered on top during the nights thus unable to watch the starry sky. On 27 August, the birds were transported to Endelave where exposed the first time for a clear sunset and a starry sky on 30 August. Expositions and experiments were carried out on the clear and starry nights 30 and 31 August and 3, 4, 6, 8, 10 and 12 September, and on all these nights the birds also experienced a clear and uncovered sunset.

The purpose with the experiment was the same as in the previous year, and in the present context only the controls are considered. The number of control birds were one Redstart, three Garden Warblers, four juvenile and one adult Pied Flycatchers, together with three Spotted Flycatchers. These birds were each tested between four and six nights, and because of no obvious change of orientation in course of the time (see, however, Spotted Flycatcher) all night orientations were pooled, and three subgroups were considered: (1) juvenile Pied Flycatchers, (2) adult Redstarts, Garden Warblers and Pied Flycatchers, and 3) adult Spotted Flycatchers.

The sample mean vectors were: 1) 209º – 0.597 (N = 14, P < 0.01), (2) 134º – 0.707 (N = 23, P < 0.001), and (3) 224º – 0.533 (N = 16, P < 0.01). In (3) there was (an insignificant) directional change from SW and NW on 30-31 August, to SE over S to NW on 3-4 September, into SSE and SW on 6-8 September.

Following recoveries of ringed birds from Christiansø (Lausten & Lyngs 2004), the standard directions of the Redstarts, Pied Flycatchers, Garden Warblers and Spotted Flycatchers are supposed to be SSW-SW (21º), SW (227º), SSW (205º) and SSE (160º), respectively. Thus, the weighed standard direction of the mixed sample (2) is about 213º (11 contributions from the Garden Warblers).

Considering subgroup (1) the orientation following the displacement was to the compensatory side (+16º), but not statistically significant.

Considering subgroup (2) the orientation very clearly was to the compensatory side (+79º) and highly significant (confidence interval test, P < 0.01).

Considering subgroup (3) the orientation was to the counter-compensatory side (-64º) and statistically significant (P < 0.05).

Pooling all 13 deviations in ID 83 to 95 incl., the sample mean vector was to the compensatory side (+45º – 0.373, z = 1.80), but far from being statistically significant. However, if the last 8 autumn displacements from Christiansø to Endelave are considered in isolation, the sample mean vector was significantly to the compensatory side (+42º – 0.794, Rayleigh (P < 0.01) and confidence interval (P < 0.05) tests).

Anyway, the results are in the same direction as found by Thorup & Rabøl (2007).

Blåvand-Endelave-Suðuroy displacements

ID 96, 97 & 98: In autumn 2009 we trapped migrant passerines at Blåvand (55ºN, 8ºE) and displaced them for funnel-testing to Akraberg on Suðuroy, southernmost Faroes (62ºN, 7ºW), i.e. about 1170 km towards NW (312º). The displacement was part of a compound experiment where migrant passerines were also trapped in Sumba (nearby Akraberg) and released and followed with radio-transmitters. The results of the funnel experiments were published in Thorup *et al.* (2011), however in a form/compilation not suited for the present investigation.

The birds trapped at Blåvand, westernmost Denmark were grounded migrants in the period 1 through 10 September. The arrival winds were southerly or westerly indicating an active heading in the standard direction (SSW-SW). A total of 34 birds (all juveniles) were kept pairwise in 17 baskets (for a description see Rabøl 2010). The species and numbers were 16 Blackcaps *Sylvia atricapilla*, 12 Garden Warblers, and six Willow Warblers *Phylloscopus trochilus*.

It was not possible to funnel-test the birds in the Blåvand-area because of hunting, so the birds on 10 September were transported by car and ferry to the island of Endelave (56ºN, 10ºE). Here the birds were outside in their baskets during sunset/early night on 10 September. The cloud cover was 3/8, and in the end all the bright stars were on the sky. There was a lot of migratory restlessness in the baskets.

On 11 September everything was ready for funnel experiments. Remember, we had 32 birds, but we only intended to make experiments with 16 birds per night. Eight Garden Warblers and eight Blackcaps were selected for funnel-experiments. However, because of increasing cloudiness and an early Moon rise we had to start early – and it became too early with clear sunset taxes in six birds and probably also photo-taxes towards city-illuminated clouds. So, we had to abandon these experiments on 11 September.

The 16 last birds were ready for experiments on 12 September, but in the sunset-phase the sky turned overcast. It also rained a little, so no birds came into the funnels.

Finally, everything went all right during sunset and night on 13 September, so the 16 birds from yesterday were tested in funnels during night under a clear starry sky and no disturbing lights from the sunset, cities nor Moon. Funnel experiments were carried out for 60 or 75 minutes more than two hours after sunset. All three species were tested, and the sample mean vector was 222º – 0.718 (N = 16, P < 0.001). Considered separated in species: Blackcap 239º – 0.708 (N = 8, P < 0.05), Garden Warbler 200º – 0.967 (N = 4, P < 0.05), and Willow Warbler 216º – 0.624 (N = 4).

On 14 September, the birds in their baskets were transported by car to Copenhagen, and 16 September by aircraft to the Faroes, and then by car, ferry and car again to Akraberg. The next day I was ready for experiments, but the weather was terrible; strong winds, overcast and sometimes rain. On 22 September, the weather improved, and the cloud cover was 0-2/8 during the experiments with a clear starry sky. However, it was not possible to expose the birds in the baskets during sunset/early night, so the birds were put directly into the funnels. Four Garden Warblers and eight Blackcaps were tested. The Garden Warblers showed 193º – 0.988 (N = 3, P < 0.05), and the Blackcaps 152º – 0.511 (N = 7). On 23 September, another 10 birds from Blåvand were tested in the funnels, again under cloud cover 0-2/8 and a clear starry sky. The birds were: two Blackcaps showing 135º and bimodal 195º/(110º) orientation, four Garden Warblers 160º, 220º, 165º and 195º orientation, and three Willow Warblers 70º, 210º, 190º orientation besides one dis-orientated.

If the samples from 22 and 23 September are combined, the following arise: Blackcap 158º – 0.580 (N = 9, P < 0.05), Garden Warbler 183º – 0.941 (N = 7, P < 0.01), and Willow Warbler 170º – 0.511 (N = 3). These mean vectors could be compared with the mean vectors from Endelave 13 September. All mean directions were to the compensatory side: Blackcap (+81º), Garden Warbler (+17º) and Willow Warbler (+46º). The difference in the Blackcap is significant (0.001 < P < 0.01, Mardia-Wheeler-Watson two-sample test). Because of the high sample concentrations in the Garden Warbler, the parametric Watson-Williams test was applied, but the difference of 17º was too small to attain significance (P > 0.05).

An old experiment revisited

ID 11: This displacement of Garden Warblers from Hanstholm to Dueodde was presented in Appendix Tab.7 in Thorup & Rabøl (2007), and as Tab. 6 in Appendix 1 in Rabøl & Thorup (2001). Unfortunately, the Garden Warbler ID 11 was used as the example on how the calculations were made and should be understood. Garden Warblers trapped at Hanstholm on 16, 17, 18 and 21 August showed 96º – 0.537 (N = 12), and birds displaced to Dueodde on 24 August 236º – 0.681 (N = 7, P < 0.05). This is counter-compensatory orientation. The problem is that only Garden Warblers from Hanstholm on 21 August should have been used as the reference group to the test at Dueodde. On 21 August the birds at Hanstholm showed 124º – 0.585 (N = 7), and since the direction from Hanstholm to Dueodde is 117º, the 236º orientation at Dueodde was in fact significantly compensatory (+112º).

Magnetic displacements

Rabøl (2014) simulating magnetic displacements towards N and S found no compensations neither during stellar nor overcast conditions. Rabøl (2014) also presented and discussed the few other magnetic displacement experiments published until 2014 but found no clear evidence of magnetic gradient navigation.

Summing up

In the autumn displacements (juvenile birds) carried out under the natural starry sky compensation was carried out significantly in six cases, whereas in two significant counter-compensation appeared. Adding 6/2 to the 12/2 distribution in Tab. 2 in Thorup & Rabøl (2007), a 18/4 distribution emerges. Applying a Chi-square test and testing against 11/11 ends up with Chi-square = 8.92 and 0.01 < P), i.e. the tendency to compensate is clearly significant.

Discussion

The close to optimal solution for documenting compensatory orientation following displacements should be birds displaced symmetrically at right angles to the standard direction, or even better somewhat forward to the ‘left’ and ‘right’ in reference to the standard direction. An ideal example within the borders of Denmark could be trapping on Hesselø (56º 12’N, 11º 42’E) or Anholt (56º 45’N, 11º 35’E) and then after testing the orientation here, displacements to Blåvand (55º 33’N, 15º 12’E) and Christiansø (55º 19’E, 8º 06’E).

The question is whether the about 3½º longitudinal displacements are large enough to be detected by a gradient/coordinate navigation (or what-so-ever-compensatory) system. This may be revealed only by experience, but at least 5º longitude (the difference between Christiansø and Endelave) seems to be sufficient for compensations to occur.

Furthermore, the experiments should be carried out as soon as possible after the displacement (and preferably some of them also later on to find out whether a compensatory reaction changes with time). To maximize the reaction birds should be tested under starry skies.

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Resumé

Upublicerede forflytningsforsøg; tillæg til Thorup & Rabøl 2007

Rabøl & Thorup (2001) – der senere blev til Thorup & Rabøl (2007) – var en milepæl i forflytnings-litteraturen. Der var tale om en metaanalyse af (på den tid) samtlige tragt-/burforsøg foretaget i forbindelse med reelle eller simulerede geografiske forflytninger med nattrækkende småfugle. Ligesom mine planetarieforsøg (Rabøl 1998) er Thorup & Rabøl (2007) imidlertid en meget lidt omtalt og citeret artikel måske fordi mange forskere ikke ganske forstår, hvad der er gjort og derfor vælger at ignorere artiklen.

I en metaanalyse kan man generalisere på objektiv grund og fx (som her) konkludere, at der i tragtforsøg med ungfugle på stjerneklare nætter om efteråret er en gennemgående tendens til at fuglene kompenserer for forflytninger. Hvis vi ser på antallet af forsøg på stjerneklare nætter om efteråret, så er der ifølge Thorup & Rabøl (2007) – med en enkel korrektion givet i dette appendiks – en signifikant kompensatorisk reaktion i 12 ud af 14 forsøg. I de to sidste forsøg var reaktionen signifikant modsat kompensatorisk. Hvis vi tilføjer de otte signifikante forsøg fra de her tilføjede, kommer vi op på en samlet 18/4-fordeling med hensyn til kompensatorisk/modsat kompensatorisk. Sandsynligheden for at det er en tilfældig variation ud af en basalt set ligelig fordeling (11/11) kan findes på objektiv vis ved hjælp af fx et Chi-square test. Sandsynligheden for en tilfældighed er mindre end 1 %, hvorfor man ifølge vedtagen tradition vil sige, at der er en statistisk signifikant tendens til at kompensere for en geografisk forflytning. En sådan konklusion kan ikke med rimelighed ignoreres med modvægt i udvalgte enkeltforsøg, der viser eller tyder på ikke-kompensering.

Kasper Thorup lavede et kæmpearbejde for at få Thorup & Rabøl (2007) publiceret i et stort, anerkendt tidsskrift. Samtlige referenter på artiklen anbefalede artiklen til forkastelse, men redaktøren Wolfgang Wiltschko publicerede den alligevel, ikke fordi han kunne lide den, for det kunne han ikke, og han citerer den aldrig, men vi var gamle bekendte, så han var storladen, dog ikke mere end at han fik strøget flere afsnit, oplysninger om kompensationsgraden og resultaterne af 10 forsøg, som han fastslog ikke var dokumenterede i tilstrækkelig grad. Det sidste havde han ikke uret i, men hans redaktion bidrog klart nok negativt til artiklens citations-index. Never mind. Artiklen blev publiceret, og her kommer så de 10 forsøg, der ikke slap igennem nåleøjet (samt nogle nyere forsøg), og de bekræfter blot – med undtagelser – den generelle tendens og konklusion: At unge trækfugle navigerer mod et vandrende målområde. Der er medtaget yderligere forflytningsforsøg, der er kommet til siden – og en korrektion af ID11. Jeg skulle måske også have inkluderet nogle enkelte magnetismeforsøg, såsom Henshaw *et al.* (2010), men det er et forårsforsøg på kanten af det relevante i disse efterårsforsøg. Sidstnævnte er kommenteret i Rabøl (2014).

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