The orientation following geographical displacements. Unpublished experiments.

Jørgen Rabøl 2006.

The first ten samples of displacement experiments were never published before and therefore – after discussions with the editor/referees - omitted for inclusion in the ***Appendix*** *of Thorup and Rabøl 2007: Compensatory behaviour after displacement in migratory birds. A meta-analysis of cage experiments. – Behav Ecol Sociobiol 61: 825-841.*

Three more samples (ID 93, 94, 95) - mostly comprised of adult birds - are added.

Adopting the system (Fig.2) of Rabøl & Thorup (2001) the orientations after displacement could be depicted to the compensatory (+) or counter-compensatory (-) side.

ID 83. 16 Garden Warblers *(Sylvia borin)* were trapped as migrants on Christiansø (55º 19´N, 15º 12É) on May 19 1989 and the very same day transported about 370 km NW to Northern Jutland (Sæby, 57º 17´N, 10º 31´E) where funnel experiments where carried out around midnight between May 19 and 20 under a starry sky. 5 birds failed to show any significant activity, and the sample mean vector was 356° – 0.77∗∗ (n = 11). As the birds arrived to Christiansø in westerly winds we expect an orientation somewhere between NW and NNE (the standard direction is probably about N to NNE, and the mean direction of a greater sample of W–winds arrived Garden Warblers and Redstarts 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 a little to the **counter-compensatory side (-4º)**.

ID 84, 85. 12 Robins *(Erithacus rubecula)* were trapped on Akeroya, SE–Norway (about 59ºN, 11ºE) in end Sep.1980 (most on Sep.26) and transported about 500 km SE-SSE to Christiansø on Sep.29 and 30.

On Oct.1 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 210°. Doubling the angles leads to 346°/(166)° – 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 Oct.3 and 5, and the sample mean vector was 108° – 0.51∗ (n = 16). Some birds were oriented on both nights, but the original notes are 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 4 Redstarts *(Phoenicurus phoenicurus)* were trapped as migrants at Blåvand (55º 33´N, 8º 06É) between 17 and 31 Aug. 1971. 16 of these (2 Redstarts) were transported to Stensoffa in Scania, Sweden (55.7ºN, 13.5ºE, i.e. about 350 km ENE–E) on Sep.2. 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 (both H.G. Wallraff and W. Wiltschko (in litt.) had suspected a navigatory 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, Rabøl 1994)). **Perhaps such a navigatory 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 Sep.4 and 5 under a starry sky. Half of the birds were then tested on Sep.10, and the other half were exposed under the starry sky. These latter birds were then tested under a starry sky on Sep.11.

Sep.12 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 Aug.25, four birds Aug.30, and five birds Aug.31). The mean vector was 168° – 0.26 (n = 10). If we include the 6 other birds trapped and tested at Blåvand Aug.21 to 24 the sample mean vector attains significance (132° – 0.44∗ (n = 16)).

At Stensoffa most birds were oriented on Sep.10 and 11, and the sample mean vector was significant (282° – 0.56∗∗, n = 14). Testing the correspondence between this sample mean vector and the one from Blåvand based on the 16 birds a highly significant difference is achieved ($P < 0.001$, W W test).

The orientation following the displacement is thus to the **compensatory side (+150º)**. However, if we consider the orientation of those birds tested on Stensoffa 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 (158° – 0.65∗, n = 9). Testing this against the sample mean vector at Stensoffa yields highly significance ($P < 0.001$, W-W test). As evident the orientation following the re-displacement is to the **counter-compensatory side (-124º)**. However, testing the orientations at Blåvand as function of the orientations at Stensoffa the sample mean vector (-126° – 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 hybrid between a southerly standard direction and easterly compensatory orientation for previous winddrift.

The W-WNW-orientation at Stensoffa is surprisingly northerly taken the more than one week delayed tests on Sep.10 and 11 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 Sep.12 and 13.

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

ID 88. 40 juvenile Pied Flycatchers *(Ficedula hypoleuca)* were trapped on Christiansø Aug.19 and 20 2001. The birds arrived in easterly winds and presumably were of Finnish or eastern Baltic origin. The birds were transported to Copenhagen on Aug.29, and then to Endelave Sep.3 where caged outdoors from Sep.6 until Sep.28. On Sep.8 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 Sep.

11, 13 and 14. From Sep.6 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 cu8s), 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 were 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 148° – 0.29 (n = 34) 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 (214°) 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 on the 12 outdoor controls were tested under the starry sky on Sep.23. The sample mean vector was 206°– 0.86*** (n = 12). Also the indoor controls were tested (Sep.19) under simulated overcast (i.e. the funnels were covered with a translucent but not transparent plastic sheet). The sample mean vector was 219° – 0.74*** (n = 12). Clearly for both samples it looks like orientation in the standard direction.

ID 89. 14 juvenile Pied Flycatchers and 9 juvenile Redstarts were trapped as migrants on Christiansø between Aug.30 and Sep.5 2002. The arrival winds on Christiansø were from varying directions. The birds were not exposed for the stars when caged on the island. On Sep.6 the birds were transported to Endelave and caged outdoors. On Sep.6 and 7 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 Sep.8 and 9 after experiencing a clear sunset/early night sky in their cages. Here we consider only the orientation of the 7 **control** birds (the experimental group consisted of 16 birds experiencing magnetic N deflected towards E or W).

Two birds were disoriented on Sep.9, and a single bird was bimodally oriented on Sep.8. Two sample mean vectors could be considered: 1) based on Sep.8 except a single bird from Sep.9 (the one which was bimodally oriented on Sep.8), and 2) based on simple means if unimodally oriented on both occasions (4 birds), otherwise based on the single orientations from Sep.8 (two birds) or Sep.9 (one bird). The sample mean vector of 1) is 180° – 0.69* (n = 7), and of 2) 184° – 0.72* (n = 7). Neither directions 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 Sep.6 (8 birds), 8 (15 birds) and 9 (4 birds) 2002. The morning arrival winds on Christiansø was SW, S and E on Sep.6, 8 and 9, respectively. On Christiansø all birds experienced a clear sunset/early night starry sky on Sep.10. On Sep.11 the birds were transported to Jutland, and next day to Endelave.

On Sep.12 and 13 the birds experienced a clear sunset/early starry night in their cages and were later on tested in the funnels during starry night. 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 Sep.13. Two sample mean vectors could be considered: 1) based on the directions of the 8 birds from Sep.12 and the directions from the remaining 3 birds on 13 Sep., and 2) based on the means from Sep.12 and 13 (8) and the directions from the 3 birds tested only on Sep.13: 1) 139° – 0.67** (n = 11) and 2) 144° – 0.76** (n = 11). Both deviate 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 Sep.3 (23) and Sep.4 (7) 2004. The arrivals were in weak NW winds suggesting origin from the north (Sweden).

On 6 sep. the birds were transported to Copenhagen and on 7 Sep. to Endelave. On Sep.8 the birds experienced a clear starry sky in their cages on Endelave (the birds were not exposed for the stars Sep.3 to 7). On Endelave the birds were divided in three groups: 8 and 8 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 Sep.9 and 10 the sample mean vector (all birds only tested once) was 162° – 0.68*** (n = 14). 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 Sep.19 and 21. The sample mean vector (two birds were oriented on both nights and their means were considered, and a single bird was disoriented) was now 202° – 0.72*** (n = 13).

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 35° – 0.64** (n = 13). If the two sample mean vectors are tested against each other applying the W–W 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 compensate in the first period following the displacement. The deviation of 162° from SSW–SW (214°) is very significant (P < 0.01, confidence interval test). Later on the sample mean vector approaches the standard direction.

ID 92. 32 juvenile Robins were trapped on Christiansø Oct.1 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 Oct.4 the birds were transported to Copenhagen, and on Oct.5 to Endelave. On Oct.6 the birds were placed outdoors but no experiments were carried out before Oct.8 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 Sep.30 and Oct.1 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 Oct.8 the birds were not exposed for the stars. Before the experiments on Oct.8, 9, 10 and 11 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 Oct.8 and 9 was 170° – 0.62** (n = 12, the individual birds were tested only once). During Oct.10 and 11 the birds were tested again, and two birds displayed disorientation. The sample mean vector was 197° – 0.59* (n = 10). The clockwise shift (towards 8° – 0.66*) if the individuals are tested as their own controls is not significant (confidence interval test). As the standard direction is supposed to be about SSW–SW (214º) the sample mean vector during Oct.8 and 9 deviates significantly (P < 0.05, confidence interval test) to the **compensatory side (+44º)**.

ID 93, 94, 95. 5 adult Redstarts, 4 adult Garden Warblers, 4 juvenile and 10 adult Pied Flycatchers, and 7 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 Aug. was trapped an adult Pied Flycatcher carrying a Finnish ring).

On Chr.ø the birds were caged outdoors two by two and covered on top during the nights thus unable to watch the starry sky. On August 27 the birds were transported to Endelave where exposed the first time for a clear sunset and a starry sky on August 30. Expositions and experiments were carried out on the clear and starry nights 30 and 31 Aug., 3, 4, 6, 8, 10 and 12 Sep., 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 1 Redstart, 3 Garden Warblers, 4 juvenile and 1 adult Pied Flycatchers, and 3 Spotted Flycatchers. These birds were each tested between 4 and 6 nights and because of no obvious change of orientation in course of the time (see, however, Spotted Flycatcher) all night orientations were pooled, and 3 sub-groups 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), 134º - 0.707*** (n = 23), and 3) 224º - 0.533** (n = 16). In 3) there was (an insignificant) directional change from SW and NW on 30 - 31 Aug., to SE over S to NW on 3 – 4 Sep., into SSE and SW on 6 – 8 Sep.

The standard directions of the Redstarts and Pied Flycatchers are supposed to be SSW-SW (214º), and S (180º) of the Garden Warblers and Spotted Flycatchers. Thus the weighed standard direction of the mixed sample 2) is about 198º (11 contributions from the Garden Warblers).

Considering 1) the orientation following the displacement is to the **compensatory side (+5º)**, but certainly not statistically significant.

Considering 2) the orientation very clearly is to the **compensatory side (+63º)** and highly significant (confidence interval test, P < 0.01).

Considering 3) the orientation is to the **counter-compensatory side (-44º)** and statistically significant (P < 0.05).

Pooling all 13 deviations the sample mean vector is 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 is significantly to the compensatory side (+42º - 0.794, Rayleigh** and confidence interval* tests).

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

Discussion

In the doc. **Displ,** Supplement 1 we presented an example of an about maximal solution for finding compensatory orientation following displacements: The birds should be 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 35É) 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 5ºlongitude (the difference between Christiansø and Endelave) seems to be sufficient.

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