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

Introduction

The question is whether night migrants use the stellar sky for gradient-navigation. If so the sight of a stellar sky to the south of the contemporary goal in autumn should result in a shift in orientation from southerly to northerly.

Material and methods

We simulated geographical latitudinal displacements 4º to the south by means of prisms.
Four prisms were in use. The prisms were constructed by means of sheets of transparent plastic glued together and filled with water. The dimensions were 40 times 40 cm with an opening angle of 12º. Each prism was placed horizontally on top of a funnel*. If the thin end of the prism was turned N the bird in the funnel through the prism sees a starry sky corresponding to a position 4º to the south (Fig.1).
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. The birds were transferred to the cages on the experimental site (Dronningens Bastion, Rabøl 2006) about one hour before sunset. From the cages the birds had an unobstructed view of the sky and the surroundings down or almost down to the horizontal level. The birds were transferred to the funnels about 1½ to 2 hours after sunset, and spent the next about 1½ hour within the funnels. Therefore, the prism-birds first experienced the changed starry sky 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 (1979, 1993, 2006).
* In 2007 the prism was placed on top of an open square box (made by tree) surrounding the funnel. The top of the box was about 1 cm above the upper edge of the funnel. In 1975 (see below) the prism was placed directly on the (inverted) net-frame on top of funnel (leaving an open air-space on about 1 cm between the upper edge of the funnel and the prism).

Results

Sunset experiments on Christiansø were carried out 23-24-29-30-31 Aug. 2007 testing for influence of the prism in itself; **thin end of the four prisms** was turned W, N, E and S, respectively.
In reference to geographical N the sample mean vector of the **prism-birds** (Fig.2) was 210º - 0.211 (n = 14), and in reference to **thin end the prism in N** (Fig.3, double arrow) 246º - 0.273 (n = 14).
The orientation of the contemporary **controls** (Fig.4) was 219º - 0.398 (n = 17). Clearly, there seems to be no directional difference between prism and control birds and if added

together the sample orientation in reference to geographical N was 216º - 0.313* (n = 31). The mean orientation is close to the suspected standard direction (SSW-SW).
Prism-birds without controls were also tested on 21 Aug. (afternoon) and 27 Aug. (sunset). The sample orientation on the 7 dates 21 through 31 Aug. was 230º - 0.139 (n = 20) in reference to geographical N, and 265º - 0.238 (n = 20) in reference to the thin of the prism in N.
In these sunset experiments sometimes the sky was overcast and sometimes clear. i.e. the birds were able to observe the setting sun and the sunset polarization pattern of the sky, but as no stars were visible the **interpretation** of the results of these experiments is, that the **thin end/bilateral symmetry of the prism does not in itself influences the orientation.**

On **four starry nights** 4 through 16 Sep. 2007 we tested Pied Flycatchers *Ficedula hypoleuca* and/or Redstarts *Phoenicurus phoenicurus* as both prism-birds and controls. In these experiments the thin and of the prism was turned geographical N in all 4 prisms producing a starry sky as observed by the birds in the funnels simulating a latitudinal displacement 4º towards S.
The sample orientation (Fig.5) of the prism-birds was 339º - 0.729** (n = 10), and of the controls 134º - 0.350 (n = 11). The distribution of the controls looked a little bimodal but doubling the angles did not improve the description (**150º**/330º - 0.246, n = 11). We tested the difference between the two distributions by means of the M-W-W test, and the Chi-square value was 8.40, which with two degrees of freedom means $0.01 < P < 0.02$.
On **seven starry nights** between 6 and 18 Sep. 2007 (not including 11 Sep., see below) we tested Robins *Erithacus rubecula* as both prism-birds and controls. Otherwise same procedure as above.
The sample mean vector (Fig.6) 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). The sample mean vector of the controls was 201º - 0.583*** (n = 37). We tested the difference applying a M-W-W test, and for a Chi-square = 5.61 this corresponds to $0.05 < P < 0.10$ (probably P about 0.06, 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).
In the **night**-experiment 11 Sep. (Robins, no Moon on the sky) the cloudiness changed from 7/8 (first 5 minutes) into total overcast. Under such a condition we should not expect reverse orientation of the prism-birds but standard orientation in both exp.s and controls Nevertheless, a single bird oriented towards 30º, whereas two other birds oriented 155º and 205º (both displayed very small activity). 4 out of 7 controls were oriented (160º, 215º, 40º, and **250º**/120º). The bird orienting towards 40º displayed very small to small activity. Anyway, the singles cases of reverse orientation are not surprising, and there is no difference between the patterns in controls and exp.s.

In **conclusion**, the autumn 2007 prism-experiments on Christiansø lend **additional support** to the hypothesis, that even small-scale latitudinal “displacements” on the starry sky leads to compensatory/navigatory orientation (Thorup & Rabøl 2007).

“Additional support” also because already 32 years ago similar experiments on Christiansø in principle yielded the same results. However, a final appreciation of these older results were never attained, because the necessary controlling for ruling out the possibility that the response was not induced by the changed starry sky but spuriously directed towards the thin end of the prism was never carried out.

In **autumn 1975** the most homogenous series of prism-experiments involved Redstarts, Garden Warblers *Sylvia borin* and Pied Flycatchers (23, 15 and 4, and 32, 17 and 3, respectively as controls and prism-birds, respectively) from most nights in the period 1 through 9 Sep.

As depicted on Fig.7 the sample mean vector of the controls was 222º - 0.297 (n = 30), or – including the smaller dots - 218º - 0.277 (n = 35). The distribution looks perhaps a little bimodal. However, doubling the angles leads to a smaller sample concentration (**228º**/48º - 0.098, n = 42). The sample mean vector of the prism-birds was 13º - 0.467*** (n = 36), or including the smaller dots 18º - 0.387** (n = 44). The latter distribution looks more bimodal, but doubling the angles leads to no improvement: **49º**/229º - 0.316** (n = 52).

The difference between the two distributions was tested and according to the M-W-W test the difference is statistically significant (P < 0.01).

In conclusion, the “displacement” as seen through the prism apparently induces some compensatory orientation, but as evident in the Robins, autumn 2007 the prism-orientation is not supporting a hypothesis of goal-area gradient navigation in a strict sense (predicting a NNW-response in the prism birds), but looks more like an about 180º reverse response.

Addition

During the preceding nights, 30 and 31 Aug.1975, the combined orientation of the three species were rather different: The controls were oriented 340º - 0.600 (n = 10), whereas the prism-birds oriented bimodally 162º/342º - 0.450 (n = 11). Thus, the controls were more northerly oriented than the prism-birds, and in fact this tendency was most pronounced on 31 Aug., where the two mean vectors were 343º - 0.613* (n = 8), and 185º - 0.513 (n = 6) for the controls and prism-birds, respectively. Applying the M-W-W-test the difference was not significant (0.05 < P < 0.10), whereas P < 0.01 using the W-W test (which perhaps should not applied because of two rather small concentrations). Anyway, the “opposite” orientations to the expectation of southerly controls and northerly prism birds are remarkable (see spring 1975 below).*

During 30 and 31 Aug. 1975 we also investigated the orientation of Willows Warblers Phylloscopus trochilus *and Lesser Whitethroats* Sylvia curruca *in the prisms “displacing” the birds 4º to the S. The control birds oriented 352º - 0.404 (n = 10), whereas the prism-birds were absolutely disoriented as a sample (147º - 0.192, n = 9).*

*However, in the period 1 through 8 Sep. the controls of these two species were well oriented (166º - 0.717***, n = 20), whereas the prism-birds were not so well oriented*

(202º - 0.453, n = 6). Four of these six prism-birds were tested in 20 cm. funnels and under smaller prisms "displacing" the stars only 3º towards S.

Summing up, the prism-birds were not always northerly oriented, and though not tested directly (as done in 2007, Figs.2-3) this observation speaks against the thin edge of the prism enforcing a spurious influence on the orientation.

*During **spring 1975** many prism-experiments were carried out using a smaller prism **"displacing" the prism-birds 3º towards N**.* This smaller prism was painted black on the upper surface except for at circle of a diameter of 30 cm directly above the funnel..

*During the four nights 28 April through 3 May the control sample of 17 **Robins** was 322º - 0.774*** (n =19).*
The contemporary prism-birds showed a sample mean vector of 276º - 0.328 (n = 24), but otherwise the distribution looked bimodal with a main peak in NW (as the controls) and a slightly smaller peak in about SSW-SW.

*During five nights between 8 through 14 May the control **Redstarts** displayed a very clear standard orientation; 344º - 0.667*** (n = 34), whereas the prism-Redstarts showed a bimodal pattern with the larger peak in about SSE (doubling the angles leads to **166º**/346º - 0.411** (n = 35), whereas the straight calculation leads to 153º - 0.393** (n = 35).*

*On the three starry nights, 30-31 May and 5 June two mixed samples of **Garden** and **Willow Warblers** were tested. The orientation of the controls was 35º - 0.868*** (n = 23), and of the prism-birds "displaced" 3º towards N 96º - 0.563*** (n = 22). Applying the M-W-W test the difference is statistically significant ($P < 0.05$).*

*On the two nights of 2 and 3 June the sky was overcast in the start of the experiment but later on changed into starry. The two control groups of Garden Warblers oriented very differently on the two nights: 2 June 144º - 0.486 (n = 7), and 3 June 337º - 0.855** (n = 7), whereas there was no difference between the two groups of prism-birds ("displaced" 3º towards N), and the combined mean vector was 141º - 0.624** (n = 14).*

*Finally, we should consider the orientation on 4 June (Garden Warblers tested under an overcast night-sky) and 6 June (Garden Warblers tested during sunset). On both occasions we should expect no "S"-orientation in the prism-birds, because no stars were available, and if "S"-orientation it should be a signal that the thin end of the prism in it self directed the activity. On 4 June the control birds were oriented towards 115º- 0.503 (n = 6), whereas the prism-birds were oriented towards 154º - 0.955*** (n = 8). Applying a M-W-W test no significant difference was found between the two distributions ($0.10 < P < 0.20$). On 6 June the orientation of the controls was 310º - 0.561 (n = 6), and the prism-birds 198º - 0.903** (n = 7). The difference is significant (M-W-W test, $0.01 < P < 0.02$), i.e. in this latter case it looks like there is some spurious influence of the thin edge of the prism leading to southerly orientation, where southerly orientation is not* *expected/predicted. If so the spuriousity is perhaps induced not by the thin edge as by the partly black painted prism (see above) looking asymmetric/skewed from below).*

Discussion

In conclusion, the "displacement" as seen on the natural starry sky through the prism apparently induces compensatory orientation, but as evident in both the Robins, autumn 2007 (Fig.6) and in the long-distance migrants in autumn 1975 (Fig.7) the prism-orientation is not indicative of goal-area navigation in a strict sense, but looks more like an about 180^o reverse response: In a strict bi-coordinate navigatory system and a standard orientation in – say – SSW a "displacement" along the N/W-gradient towards S (and no manipulation of the second gradient/coordinate) should result in a compensatory orientation somewhere between SSW and N. Clearly, this is not observed.

On the whole the prism-experiments in spring and autumn 1975 is supporting the hypothesis of some sort of stellar navigation. However, the southerly orientation of the prism-birds on 6 June under an overcast sky is difficult to explain without thinking in terms of a spurious influence of (something connected to) the thin edge of the prism.

The results of these prism-experiments in many ways resemble and parallel the results of simulated magnetic displacements in newts Fischer et al. 2001, Phillips et al. 2002), juvenile turtles (Lohmann et al. 2004), spiny lobsters (Boles & Lohmann 2003) and Tasmanian Silver-eyes (Fischer et al. 2003, Freake et al. 2006). However, we still do not know exactly what is going on, but hopefully the future will bring us a deeper insight.

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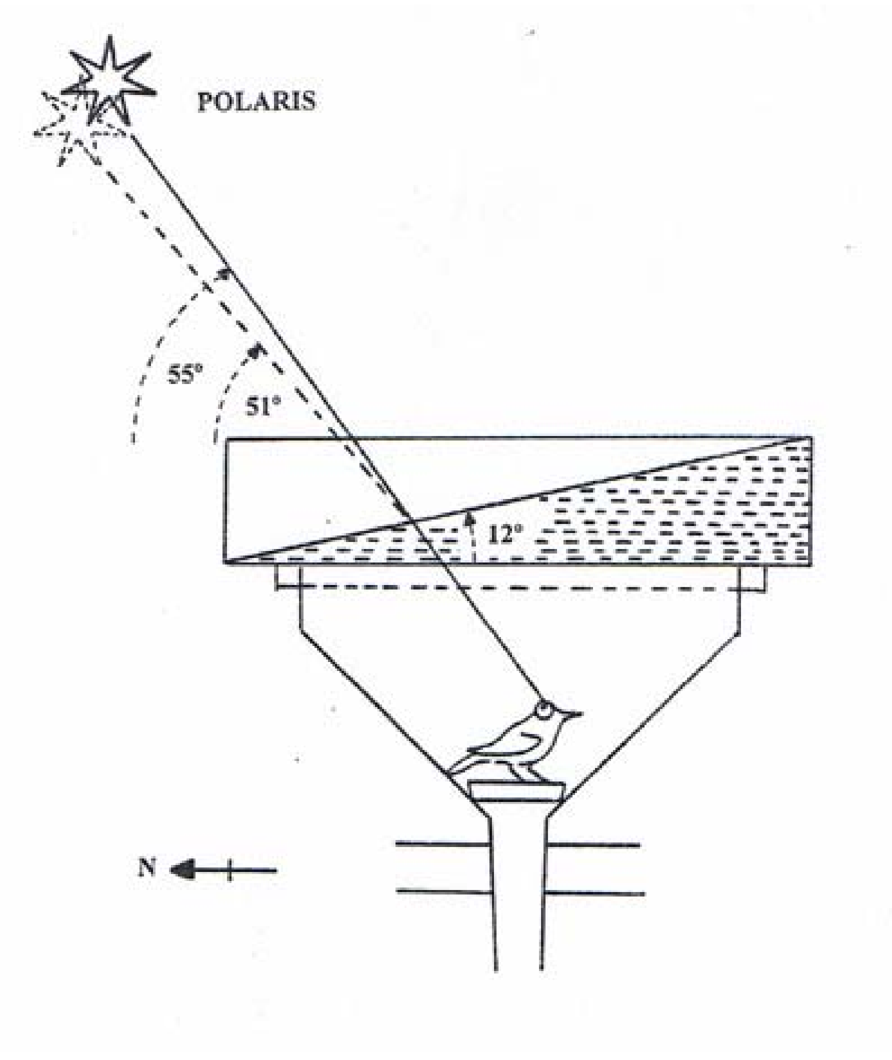
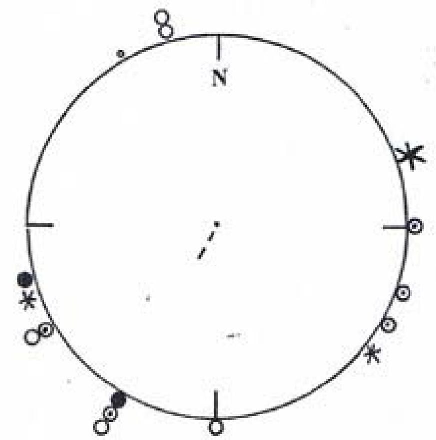


Fig.1: The waterfilled prism situated on top of the funnel. If the thin edge of the prism is turned geographical N the bird inside the funnel experiences a starry sky displaced 4º to the S.



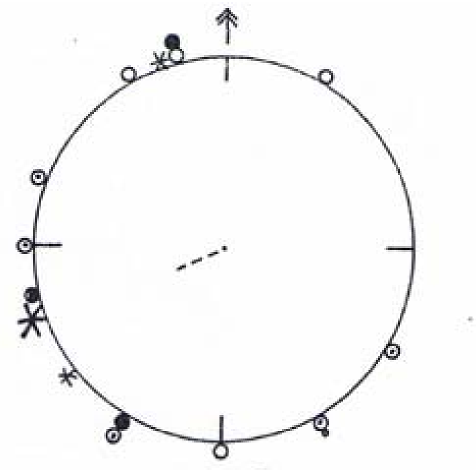


Fig.2: Left figure. Prism-birds tested at sunset. The sample mean vector in reference to geographical N is 210º - 0.211 (n = 14),

Fig.3: Right figure. Same as Fig.2 but now the orientation is depicted in reference to the thin end the prism in N (double arrow)**.** The sample mean vector is 246º - 0.273 (n = 14).

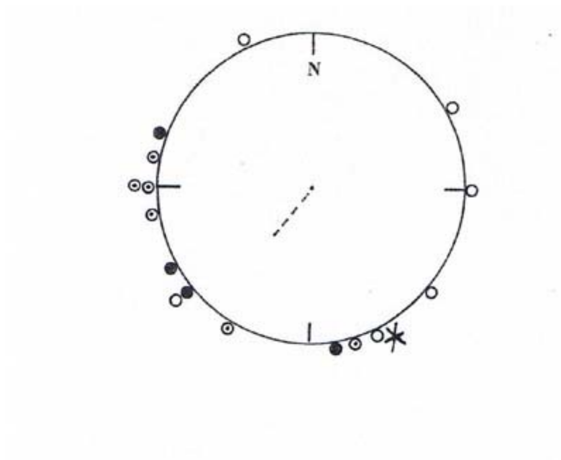


Fig.4: The orientation of the contemporary controls at sunset. The sample mean vector is 219º - 0.398 (n = 17).

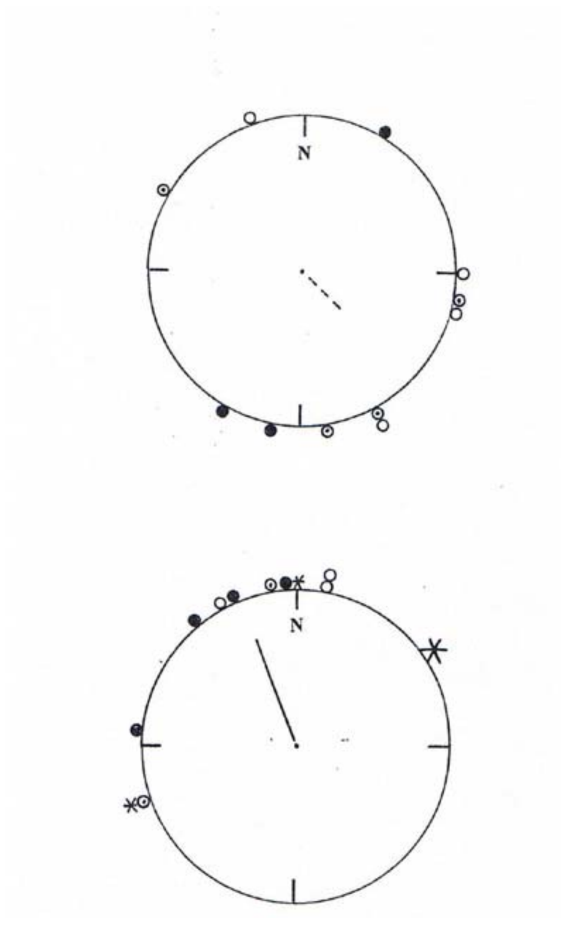


Fig.5: Pied Flycatchers and Redstarts. The sample orientation of the controls (upper figure) and prism-birds (lower figure) during starry nights. The sample mean vectors are 134º - 0.350 (n = 11) and 339º - 0.729** (n = 10), respectively.

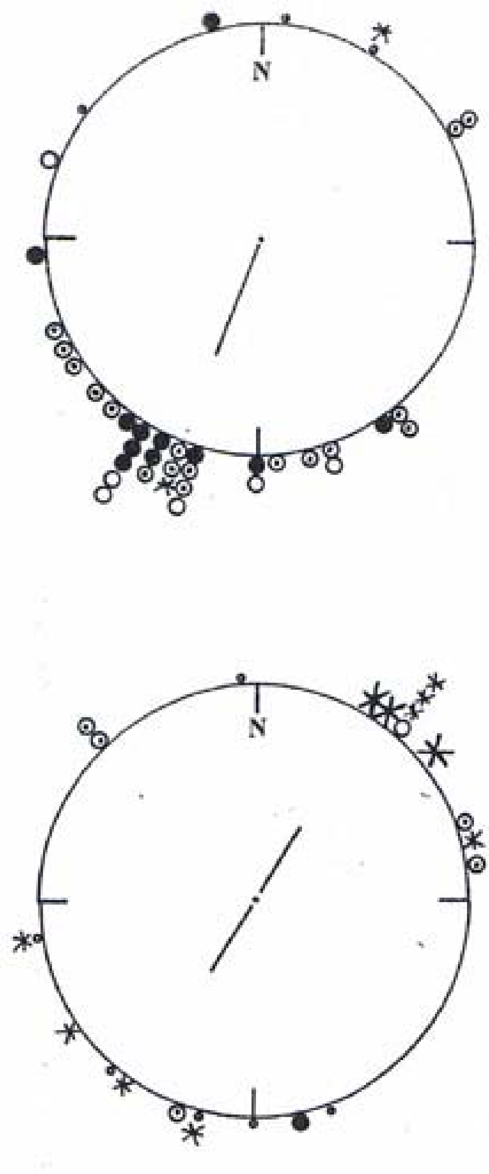


Fig.6: Robins. The sample orientation of the controls (upper figure) and prism-birds (lower figure) during starry nights. The sample mean vectors are 201º - 0.583*** (n = 37) and 78º - 0.076 (n =16), respectively.

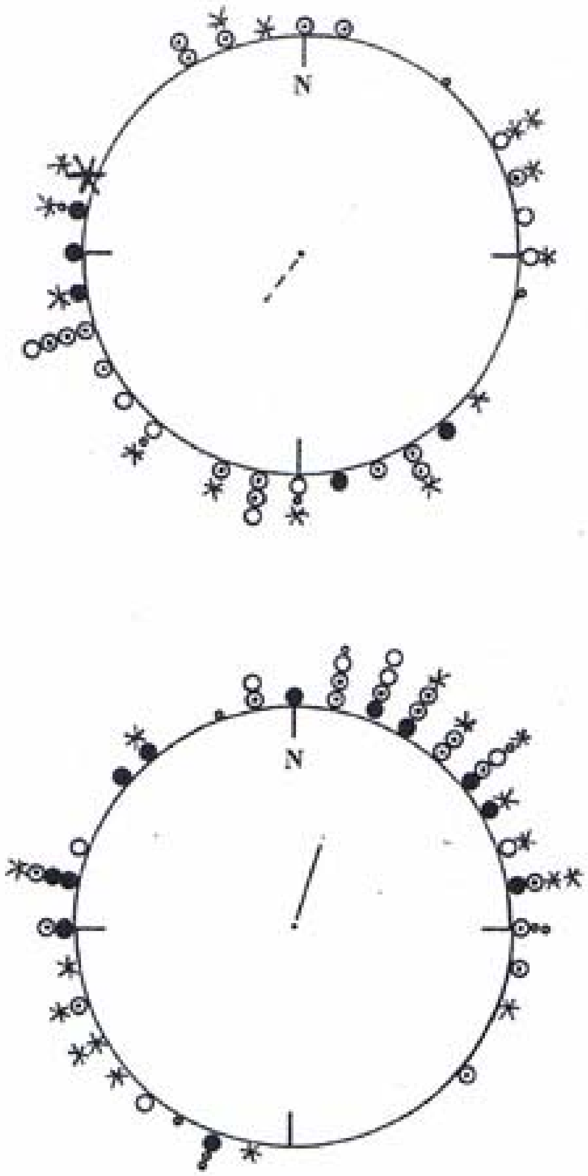


Fig.7: Redstarts, Pied Flycatchers and Garden Warblers, autumn 1975. The sample orientation of the controls (upper figure) and prism-birds (lower figure) during starry nights. The sample mean vectors are 18º - 0.387** (n = 44) and 218º - 0.277 (n = 35), respectively.