Comparison of the Overcast and a Starry Sky Orientation in Nightmigrating Passerines

By
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(Med et dansk resumé: Sammenligning af retningsvalgene hos nattrækkere under en overskyet og en stjerneklar himmel.)

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INTRODUCTION

Orientation experiments carried out under condition of overcast and starry skies are presented and compared. Such an investigation should be of great interest in the light of the recent experiments by WILTSCHKO et al. (1971), which demonstrate as good or even better orientation in overcast, whereas other authors (e. g., EMLEN 1967) have claimed disorientation in overcast as the general rule.

MATERIALS AND METHODS

The experiments were carried out in three places: *Blåvand* (the westernmost point in Jutland), *Hesselø* (in the southern part of Kattegat), and at *Ottenby* (the Swedish bird observatory in the Baltic Sea). The experiments are distributed in seven spring and autumn periods in the years of 1968–71 (Figs 1–10). Except for the finches (Fig. 10) all experiments were carried out during the night.

Apart from a single exception, only experiments at or nearby the trapping place are included in the present paper. The experimental birds were not long time caged birds but were mostly trapped within 15 hours (and never more than a few days) before the experiments. All birds were migrants trapped en route.

The »Zugunruhe« was registrated by means of our modification of the Emlen-funnel technique (RABØL 1972).

In the first three of the seven groups (Figs 1–6) the estimated number of jumps in the 16 $22^1/_2$°-sectors follows the transformation: Jumps = $0.4 \cdot 2^{\text{c.d.-1}}$ (RABØL 1972). However, the Garden Warblers *(Sylvia borin)* at Hesselø in the autumn of 1969 (Fig. 7) and the finches at Hesselø in the spring af 1969 (Fig. 10) follow: Jumps = $1.7^{\text{c.d.-1}}$ (RABØL 1970a, 1970b). The Garden Warblers at Ottenby in the autumn of 1968 (Fig. 8) follow: Jumps = $1.4^{\text{c.d.-1}}$ (RABØL 1969), and finally are both directions and activities of the Blackcaps *(Sylvia atricapilla)* at Hesselø in the spring of 1970 (Fig. 9) simple estimations (RABØL 1970b).

As the purpose with the present paper is comparison within the same period these somewhat different procedures should have no influence on the results and conclusions.

Until now the concentration (r) of the

individual mean vector was tested against a uniform distributed activity, and if p was greater than 0.05, no attention was paid to the direction (Rabøl 1970a, 1970b, 1972). Such a procedure might be disadvantageous. Due to small activity too many »true« orientational responses are rejected. Furthermore, other investigators, e. g., Wiltschko et al. (1971) make use of all individual mean vector directions irrespective of the concentration.

At the figures (see Fig. 1) the individual mean vectors are grouped in four categories. The lower of these categories either contains less than or equal to 5 independent jumps (95 % of the cases) or the concentration (r) is lesser than 0.10 (5 % of the cases).

Birds showing no activity at all or a disoriented activity ($r = 0$) are not included in the figures. Such birds constitute a minor part of the experiments.

At the figures a *sample mean vector* is constructed on the basis of the individual mean directions. A hatched sample mean vector includes all directions, whereas a full-drawn vector omits the lower category of individual mean vectors (see above).

Crosses in connection with the indices at the figures mean $p < 0.05$ for the sample mean vector concentration tested against a uniform circular distribution (Raleigh test, Batschelet 1965). Upper and lower crosses are related to the full-drawn and the hatched sample mean vectors respectively. A ratio is set nearby the indices at Figs 2 and 4. This ratio is the presumed amount of the experimental birds which have arrived to Hesselø within 24 hours.

In general, we have focused on the individual mean vectors and activities, and the single night sample mean vectors, and *not* on the all over sample mean vectors. Sometimes great directional shifts are observed from night to night producing a small all over sample mean vector even though the concentration of the single night sample mean vectors might be high.

When comparing the concentration of the individual mean vectors and the activities in the overcast and starry sky groups a Mann-Whitney U-test (one tailed – Siegel 1956) was applied. Experiments showing less than 5 independent jumps were omitted in the concentration tests.

RESULTS

The results are presented in Figs 1–10. We have not informed about the polar coordinates of the sample mean vectors, simply in order to reduce the text, and also because there is no need for such information in the present context.

1) Robin *(Erithacus rubecula)*, Hesselø, spring 1971 (Figs 1–2).

Especially Fig. 1B looks somewhat 180° bimodal distributed (NW-SE), and it seems like the concentration of the individual mean vectors is lesser in the »reverse« SE-sector.

The concentration of the individual mean vectors under condition of an overcast (Fig. 1A) and a starry sky (Fig. 1B) are tested against each other. The concentration is higher in the case of a starry sky. The difference is highly significant ($p = 0.0005$).

The individual activities (number of jumps) is also higher in the starry sky group, but the difference is not statistically significant ($p = 0.064$).

2) Garden Warbler *(Sylvia borin)* and Redstart *(Phoenicurus phoenicurus)*. Hesselø, spring 1969 (Figs 3–4).

The concentration in the individual mean vectors is higher in the starry sky group (Fig. 3) but the difference is just insignificant ($p = 0.055$).

Contrary, the activity in overcast is a

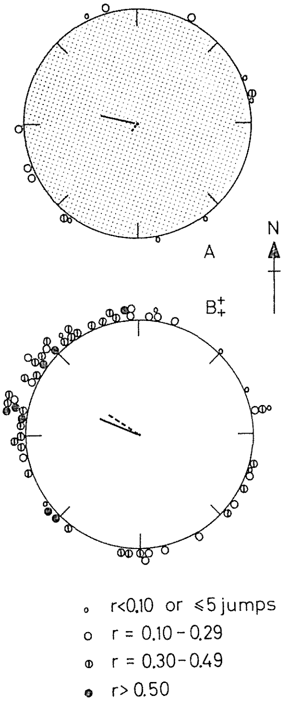

Fig. 1. Robin *(Erithacus rubecula)*, Hesselø, spring 1971. A and B show the orientation under condition of an overcast and a starry sky, respectively. In this and the following figures, the overcast night(s) is indicated. A is the sum of Figs 2A and D, whereas B is the sum of Figs 2B, C, E, F, G and H. Each dot denotes the direction and concentration (r) of an individual mean vector. On the basis of the individual mean directions two sample mean vectors are constructed. The hatched sample mean vector includes all individual directions whereas the full-drawn sample mean vector omits the lower category of individual mean vectors ($r < 0.10$, or $\leqslant 5$ jumps). The crosses in connection with B mean that both the hatched sample mean vector (lower cross) and the full-drawn sample mean vector (upper cross) are statistically significantly different from a uniform circular distribution at the 0.05 level. The experimental time was ³/₄–1 hour.

Fig. 1. Rødhals, Hesselø, forår 1971. A og B viser retningsvalgene, når det er henholdsvis overskyet (den prikkede cirkel) og stjerneklart. A er summen af Fig. 2A og D, B summen af Fig. 2B, C, E, F, G og H. Hver prik viser retningen og koncentrationen af én forsøgsfugls opspring. På basis af disse enkeltretninger er der konstrueret 2 slags gennemsnitsvektorer, hvoraf den stiplede vektor inkluderer alle enkeltretningerne, medens den fuldt optrukne vektor udelader den mere problematiske del af enkeltretningerne (de små pletter).

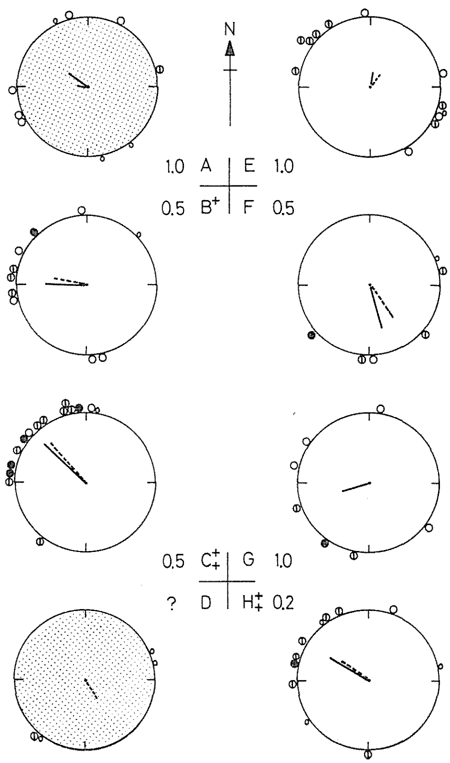

Fig. 2. Robin *(Erithacus rubecula)*, Hesselø, spring 1971.

Index	Date	Number	Cloudiness
A	9.4.	13	8
B	13.4.	11	0
C	15.4.	15	0
D	19.4.	6	8
E	20.4.	14	0
F	21.4.	7	0
G	22.4.	8	0
H	23.4.	14	0

Included in the »Number« are also birds showing no or a disoriented activity. The ratio in connection with the index shows the presumed ratio of experimental birds which had arrived to Hesselø within 24 hours of the experiments.

Fig. 2. Rødhals, Hesselø, forår 1971. De 8 forsøgsdage i april 1971 (se ovenstående tabel).

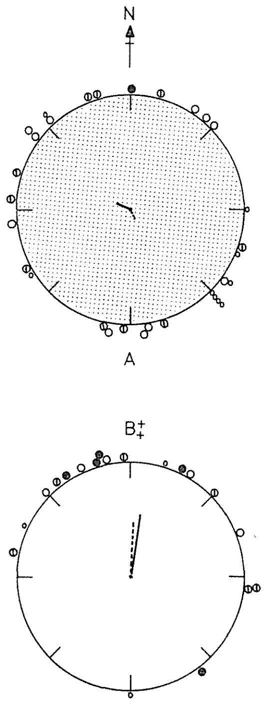

Fig. 3. Garden Warbler *(Sylvia borin)* and Redstart *(Phoenicurus phoenicurus)*, Hesselø, spring 1969. A and B show the orientation on overcast and starry nights, respectively. A is the sum of Figs 4A, B and C, whereas B is the sum of Figs 4D and E. The experimental time is 2–2½ hours.

Fig. 3. Havesanger og Rødstjert, Hesselø, forår 1969. A og B viser retningsvalgene i overskyet og stjernklart. A er summen af Fig. 4A, B og C, B er summen af Fig. 4D og E.

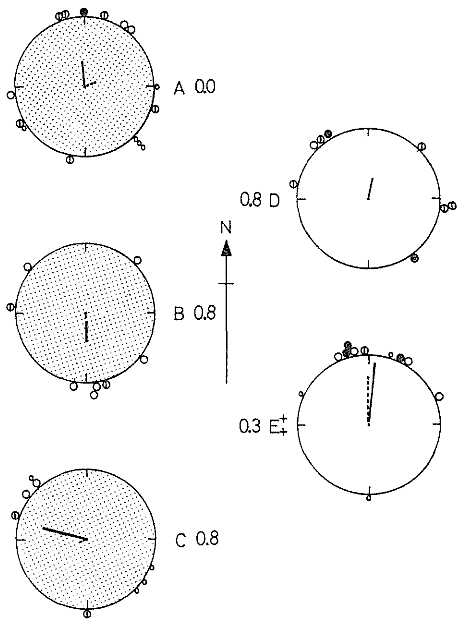

Fig. 4. Garden Warbler *(Sylvia borin)* and Redstart *(Phoenicurus phoenicurus)*, Hesselø, spring 1969.

Index	Date	Number	Cloudiness
A	17.5.	15	8
B	18.5.	12	8
C	19.5.	12	8
D	20.5.	12	0–1
E	21.5.	15	8–4–3

Fig. 4. Havesanger og Rødstjert, Hesselø, forår 1969. De 5 forsøgsdage i maj 1969 (se ovenstående tabel).

little higher, but the difference is not significant ($p = 0.40$).

The starry sky experiments are presented — in a slightly different way – in Rabøl (1970b).

3) Lesser Whitethroat *(Sylvia curruca)*, Ottenby, autumn 1968 (Figs 5–6).

The concentration in the individual mean vectors is a little higher in the starry sky group, but the difference is not significant ($p = 0.30$).

However, the activity is much higher in the starry group ($p < 0.00003$).

Fig. 5A is presented in another way in Rabøl (1969).

4) Garden Warbler, Hesselø, autumn 1969 (Fig. 7).

The concentration is a little lesser ($p = 0.234$) and the activity a little higher ($p = 0.521$ on the single overcast night compared with the four starry nights.

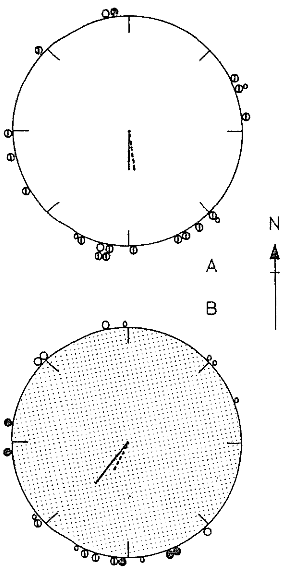

Fig. 5. Lesser Whitethroat *(Sylvia curruca)*, Ottenby, autumn 1968. A and B show the orientation on starry and overcast nights, respectively. A is the sum of Figs 6A, C, D, E, and F, whereas B is the sum of Figs 6B and G. The experimental time was $2^1/_2$–3 hours.

Fig. 5. Gærdesanger, Ottenby, efterår 1968. A og B viser retningsvalgene, når det er henholdsvis stjerneklart og overskyet. A er summen af Fig. 6A, C, D, E og F, B er summen af Fig. 6B og G.

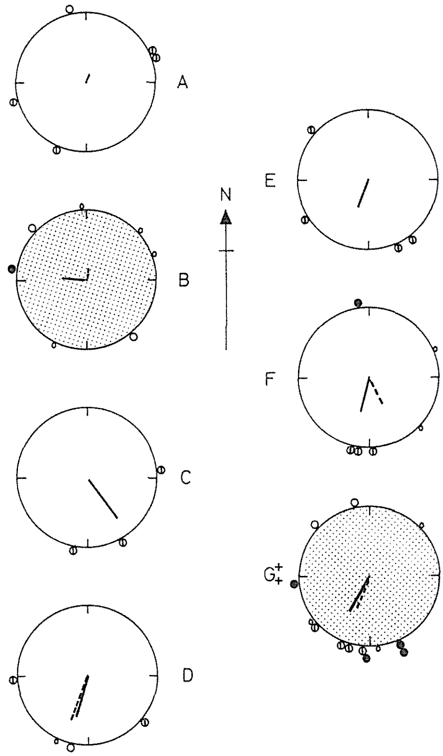

Fig. 6. Lesser Whitethroat *(Sylvia curruca)*, Ottenby, autumn 1968.

Index	Date	Number	Cloudiness
A	20.8.	5	0–1
B	21.8.	7	(7)–8
C	22.8.	5	0
D	23.8.	5	0
E	24.8.	4	0
F	25.8.	6	0
G	30.8.	13	7–8

Fig. 6. Gærdesanger, Ottenby, efterår 1968. De 7 forsøgsdage i august 1968 (se ovenstående tabel).

Making use of population mean vectors the same material is presented by RABØL and PETERSEN (1971).

5) Garden Warbler, Ottenby, autumn 1968 (Fig. 8).

The birds were trapped at Blåvand and displaced to Ottenby 26. 8. (RABØL 1969).

The concentration is higher (p just above 0.05) and the activity much higher ($p = 0.0007$) in the starry sky group.

6) Blackcap *(Sylvia atricapilla)*, Hesselø, spring 1970 (Fig. 9).

13 out of 16 birds were oriented in the starry group, whereas only 7 out of 13 were oriented in the overcast group. The difference is, however, not statistically significant ($0.10 < p < 0.15$, x^2-test).

The individual activities were classified (ranked) in six groups: 0, 1, 2, 3, 4, and 5. The arithmetic means for the overcast and starry sky groups were 3.4 and 3.3,

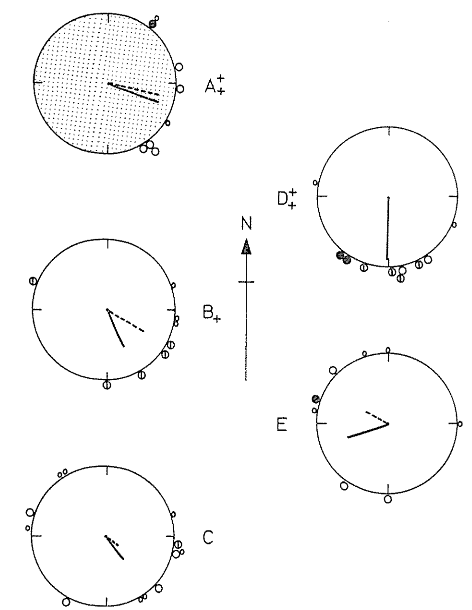

Fig. 7. Garden Warbler *(Sylvia borin)*, Hesselø, autumn 1969.

Index	Date	Number	Cloudiness
A	4.9.	8	8
B	5.9.	8	2
C	6.9.	12	0
D	7.9.	10	0
E	9.9.	8	0

The experimental time was 1¹/₄ hours.

Fig. 7. Havesanger, Hesselø, efterår 1969. Se ovenstående tabel.

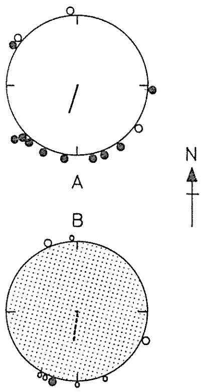

Fig. 8. Garden Warbler *(Sylvia borin)*, Ottenby, autumn 1968.

Index	Date	Number	Cloudiness
A	26.8.	8	0
	29.8.	9	0
B	27.8.	9	8
	28.8.	2	8

The experimental time was 2¹/₂ hours.

Fig. 8. Havesanger, Ottenby, efterår 1968. Forsøg under en stjerneklar (A) og en overskyet himmel (B). Se ovenstående tabel.

respectively, thus indicating no differences between the groups. (Of course, these arithmetic mean calculations are nonsense in a strictly mathematical sense.) The material is also presented in TØNDER and RABØL (1972).

7) Chaffinch *(Fringilla coelebs)* and Brambling *(Fringilla montifringilla)*, Hesselø, spring 1969 (Fig. 10).

A total of 242 experiments with finches were carried out at Hesselø in the period of April 12 – May 5, 1969. More than 200 experiments were diurnal and most of these were carried out in the morning hours.

For both species an »anti-sun-taxis« was obvious, i. e., the activity was often concentrated on the sunny spot at the innerside of the funnel. Of course, such an activity has nothing to do with the »true« migratory activity but should be considered as a directed escape reaction. Both with and without (Fig. 10) the sun at the sky, an »SW« (esp. the Brambling) and a weaker »SE« (esp. the Chaffinch) tendency

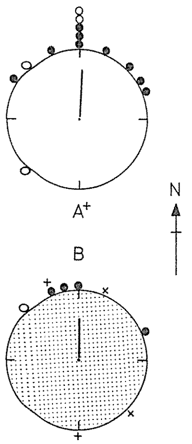

Fig. 9. Blackcap *(Sylvia atricapilla)*, Hesselø, spring 1970.

Index	Date	Number	Cloudiness
A	29.5.	9	0–7
	31.5.	7	6
B	25.5.	6	8
	30.5.	7	8

The experimental time was 1 1/4 hours.

The individual directions are estimated. Black and white dots denote high and low concentration, respectively. Crosses mean a bimodal distribution. Each of the directions in a bimodal distribution is weighed to 1/2 in the sample mean vector calculation.

Fig. 9. Munk, Hesselø, forår 1970. A og B viser retningsvalgene i henholdsvis stjerneklart og overskyet (se ovenstående tabel).

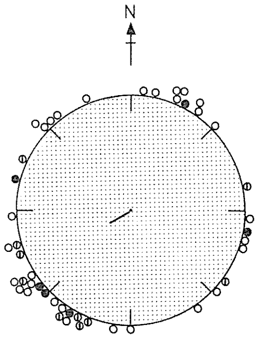

Fig. 10. Chaffinch *(Fringilla coelebs)* and Brambling *(Fringilla montifringilla)*, Hesselø, spring 1969. Experiments in the morning hours under condition of an overcast sky. The concentration of the sample mean vector is 0.219 and p is just above the 0.05 level. The experimental time was 3/4 hour.

Fig. 10. Bog- og Kvækerfinke, Hesselø, forår 1969. Forsøg morgen og formiddag i overskyet.

were also often present. A clear N–NE »standard direction tendency« was not observed.

8) In summary:

The *sample mean vectors* in the corresponding overcast and starry sky groups are normally directed close to each other. For the whole material the concentration of the single night sample mean vectors is a little higher in the starry sky group (the arithmetic means for the concentration in the starry and overcast sky groups are 0.54 and 0.47, respectively), but the difference is not statistically significant ($p = 0.11$, Mann-Whitney).

Concerning the concentration of the *individual mean vectors* in the overcast and starry sky group: If the number of experiments in the three concentration intervals: 0.10 – 0.29, 0.30 – 0.49, and > 0.50 are summed up for the Figs 2, 4, 6 and 7, these are 25, 16, and 7 in the overcast group, and 33, 61, and 17 in the starry sky group. The concentration is thus higher in the starry sky group, and the difference is statistically significant ($0.01 > p > 0.001$, x^2-test).

Concerning the *individual activities* these are normally higher in the starry sky group.

DISCUSSION

Our experiments clearly suggest that the birds are able to take up a compass direction (and/or navigate?) under condition of an overcast sky.

Concerning the individual mean vectors and activities our experiments agree well with the results of WILTSCHKO et al. (1971). The concentration of the sample mean vector of WILTSCHKO et al. (1971) was, however, higher under condition of an overcast sky.

On nights following a great immigration to the trapping area the sample mean vector often seems to be either reversed, or the concentration is very small (Fig. 2E, Fig. 4B, C and D, and Fig. 6A). Perhaps such birds either had overshot their »goal area« (RABØL 1970a, 1972) or are »within« their »goal area«, thus producing random or »reverse« orientation. Certainly, the evidence for this view is not very convincing, and should be looked for in future investigations.

Very often the orientation under condition of a starry sky are not in good accordance with the concept of »standard direction« (or the »reverse« direction), e. g., Fig. 1B (where the »standard direction« should be N–NE). The same seems to hold true for some of the overcast experiments mentioned in this paper, e. g., Fig. 7A and Fig. 6G. The »standard directions« in these two cases should be »S« and »SSE«, respectively.

SUMMARY

The migratory restlessnes of nightmigrants were recorded in Emlen-funnels, and the mean vectors from starry and overcast night experiments were compared.

The sample mean vectors in the two groups were normally directed close to each other, whereas the concentration of the sample mean vectors under condition of an overcast sky was normally lesser than in the case of a starry sky.

Both the concentration in the individual mean vectors and the individual activities was normally higher in the starry sky group.

Apart from the concentration of the sample mean vectors, our results thus agreed well with the results of WILTSCHKO et al. (1971).

DANSK RESUMÉ

Sammenligning af retningsvalgene hos nattrækkere under en overskyet og en stjerneklar himmel.

Det har ofte været diskuteret, om trækfugle kan orientere sig, når himlen er overskyet. At orientere sig vil her nærmest sige at præstere et klart retningsvalg (der så yderligere helst skal være i overensstemmelse med ens forudfattede meninger om, hvad fuglen bør gøre – hvilket (igen) er ensbetydende med en reaktion i normaltrækretningen).

Når nogle mener, at fuglene ikke kan orientere sig, når det var overskyet, skyldes det bl. a.:

1) I både udendørs og planetarie-forsøg med »Kramerbure« og »Emlen-tragte« (f. eks. SAUER og EMLEN) viser forsøgsfuglene helt generelt god orientering med stjerner på himlen og manglende orientering uden stjerner på himlen. Den samme tendens er åbenbar i løsladelses-forsøg med ænder og brevduer (bl. a. MATTHEWS og WALLRAFF). Når der er sol eller stjerner på himlen, forsvinder alle fuglene stort set i samme retning. Når det er overskyet, forsvinder fuglene derimod tilfældigt i alle retninger.

2) Fra 1950 og i årene derefter fremkom en masse forsøg og observationer, der klart viste, at fuglene kunne orientere sig efter solen og stjernerne. Det var man selvfølgelig meget glad for at have fundet ud af. Det forklarede en hel masse, man ikke tidligere havde kunnet forstå. I denne, man fristes til at sige, »himmel-legemernes jubel-fase« var der ligesom ikke plads til at tro på tilstedeværelsen af andre kilder for orienteringen – såsom f. eks. jordmagnetismen. Og derfor troede man heller ikke på, at fuglene kunne orientere sig, når det var overskyet.

3) Kloge folk havde regnet ud, at fuglenes sanseorganer ikke var nær nok følsomme til at kunne opfatte jordmagnetiske påvirkninger. Sådanne udregninger er imidlertid altid farlige. Man skal meget hellere undersøge, om fuglene rent faktisk reagerer på de magnetiske påvirkninger.

Ovenstående formeninger og forsøg taler således mod eksistensen af en orienterings-mekanisme, der træder i funktion, når det er overskyet.

Der er imidlertid også en del observationer og forsøg, der viser klar orientering under en overskyet himmel:

1) Feltobservationer af trækkende fugle. Her vil trækket ofte forløbe meget ensidigt i en bestemt retning – selv efter flere dage med helt overskyet himmel. Dette gælder også for indlands-observationer af fugletræk.

2) Ænder og brevduer løsladt i overskyet vejr finder normalt hjem til andedammen eller dueslaget med lige så stor eller næsten lige så stor fart som deres frænder løsladt under en sol- eller stjernehimmel. Nyere løsladelses-forsøg med brevduer (KEETON) viser også, at bortflyvnings-retningerne i overskyet ofte er ret entydige og peger i den »rigtige« retning.

3) Allerede først i 1960-erne begyndte tyskerne MERKEL og FROMME at berette om klar orientering af bl. a. Rødhals i indendørs forsøg – og den retning fuglene orienterede sig i var stort set identisk med årstidens normal-trækretning. De mente og sandsynliggjorde også, at deres fugle orienterede sig efter jordmagnetismen. Både PERDECK og WALLRAFF eftergjorde deres forsøg, men kunne *ikke* finde nogen indendørs orientering uden tilstedeværelse af sol eller stjerner.

Ingen troede rigtigt på MERKEL og co. Man rystede sågar en del på hovedet af dem.

Fra 1968 og frem til i dag har MERKEL og især hans medarbejder, WILTSCHKO, dog »produceret« så mange beviser på magnetisk orientering, at man ikke rigtigt kan benægte eksistensen af det længere. Det gør de fleste da så heller ikke. WILTSCHKO kunne bl. a. vise, at hvis han (kunstigt) flyttede retningen af den horisontale komponent i jordens magnetfelt et vist antal grader, så flyttede fuglenes retningsvalg et tilsvarende antal grader med. Han kunne også vise, at hældningen (inklinationen) af de magnetiske felt-linier var essentielle for fuglenes retningsvalg.

I en nylig publiceret artikel kunne WILTSCHKO et al. (1971) fremlægge forsøgsresultater, der viste, at Rødhalse var lige så godt – i nogle henseender endda bedre – orienterede under en overskyet sammenlignet med en stjerneklar himmel. De kunne også vise, at orienteringen i deres udendørs forsøg under en overskyet himmel fandt sted gennem påvirkning af jordmagnetismen.

Umiddelbart stemte disse resultater ikke ret godt overens med *vore* – ret løse formeninger – om retningsvalgene i vore orienteringsforsøg under overskyet og stjerneklar himmel. Vi havde dog aldrig undersøgt spørgsmålet til bunds. Det har vi gjort nu, og resultaterne af vore beregninger er vist på Figs. 1–10.

Den konklusion, vi hermed når frem til, ligger nærmest et sted mellem vor oprindelige formening og WILTSCHKO et al.'s resultater: 1) Fuglene er gennemgående ganske godt orienterede under en overskyet himmel, og 2) de natlige gennemsnitretninger er stort set ens i overskyet og stjerneklar, men 3) koncentrationen af de enkelte fugles aktiviteter og koncentrationen af den enkelte nats gennemsnit-vektor er normalt noget større på de stjerneklare nætter.

Med disse forsøg har vi altså bidraget med ny evidens for, at trækfugle kan orientere sig under en overskyet himmel. Vi har derimod ikke vist noget om, hvad de orienterer sig efter. Med de omtalte forsøg af WILTSCHKO og andre in mente er det dog nærliggende at tro, at vore »overskyede« fugle har orienteret sig efter jordmagnetismen.

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