Preliminary Experiments on the Orientation of Nocturnal Migrants under an Artificial Starry Sky

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(Med et dansk resumé: Koordinatnavigation hos trækfuglene)

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INTRODUCTION

It is generally supposed that birds are able to find their way towards a goal or home position using a bicoordinate navigation system (e.g. Walraff 1974, Emlen 1975). However, the environmental variables constituting the navigatory coordinates have not yet been discovered.

In principle, the coordinates might be identified by experimental shifts in the values (intensities) of the supposed coordinates. The orientation is investigated before and after the shift(s), on the assumption that the bird perceives the shift as a geographical displacement and compensates for the »displacement«.

As a world-wide navigation system is to be expected for long-distance migrants we guessed that the starry sky might provide the birds with at least one of the navigational coordinates. Consequently, the caged birds were exposed to N-S and E-W shifts on the artificial starry sky of a planetarium.

Such experiments have already been carried out with long-distance migrants (Sauer 1957, Sauer and Sauer 1960), but the interpretations of the results are conflicting. At least some of Sauer's results arising from longitudinal shifts could be taken as an indication of star navigation, but they could also be interpreted as indicating fixed one-direction orientation to stellar patterns in the southern sky (Emlen 1975). Obviously, more experiments are needed in order to find out whether the starry sky provides the birds with bicoordinate navigational information.

MATERIAL AND METHODS

The experiments were carried out at Christiansø in the Baltic Sea during May-June 1977 and 1978. We made a total of 100 experiments with freshly trapped migrants, mostly Redstarts *Phoenicurus phoenicurus* (50) and Garden Warblers *Sylvia borin* (24). We have not distinguished between the orientations of the different species, as no significant differences seem to occur. The presumed »standard direction« of the birds is NNE, but of course this should only be considered as the mean direction towards the actual goal area and/or final goal (home) of the birds. It should be noticed that we deal with experienced birds, all of which have had the opportunity to be imprinted with the coordinate values of the breeding ground, nesting area, and first part of the autumn migratory route.

Orientation was registered in 30 cm plastic funnels as foot scraping on 12 pieces of »Lettex« typewriter correction paper, which were mounted 30° apart on the inner slope of the funnel (Fig. 1). The experimental time was 1.5–3 hours, mostly before or just including the midnight. The mean direction – or the two peaks in a bimodal activity – was estimated by eye (Rabøl 1979). The orientation was designated as: disorientation, unclear, fairly clear, clear or bimodal (Fig. 3). The amount of activity was labelled as zero, low, medium, or high.

The funnels were placed inside the planetarium (Fig. 2), which consisted of a hemispherical dome 4 meter in diameter with the

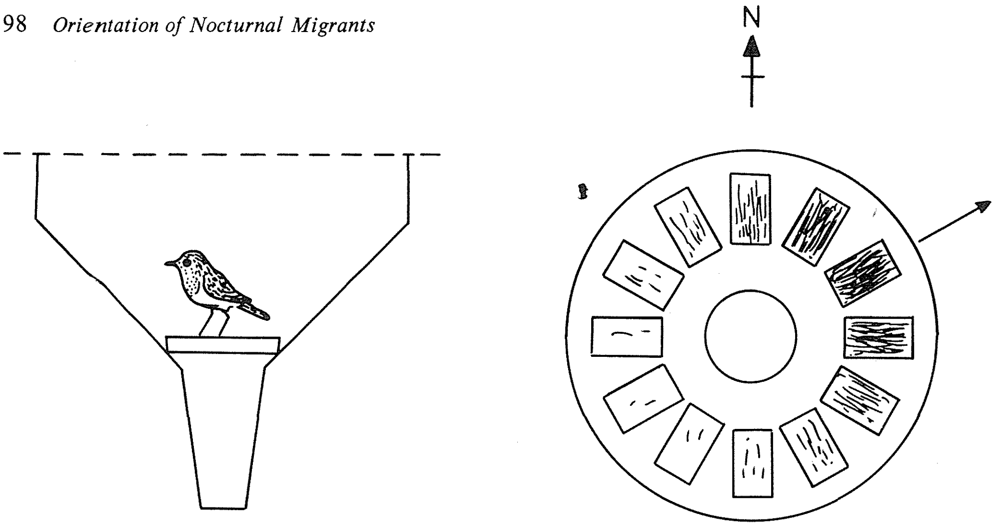

Fig 1. To the left is shown a Robin *Erithacus rubecula* in an orientations-funnel, covered by wirescreen. To the right the funnel is seen from above. 12 pieces of typewriter correction paper are mounted on the inner side of the funnel. The jumping of the bird – which is an expression of the migratory restlessness – produces a foot-scraping pattern on the soft surface of the paper. In the case shown a mean direction of 60° (NE-ENE) is registered.
Orienteringstragt. Til venstre ses tragten fra siden. Foroven er tragten dækket med trådnet. Til højre ses tragten fra oven – uden fugl i. På tragtens indersider er fastgjort 12 stykker skrivemaskine korrektionspapir. Den trækurolige fugl springer op ad tragtens sider, og dens kløer skraber i papirets overflade. Herved fremkommer et mønster, der giver oplysninger om den gennemsnitlige opspringsretning. I det viste eksempel er orienteringen (= den gennemsnitlige opspringsretning) 60° (NØ-ØNØ).

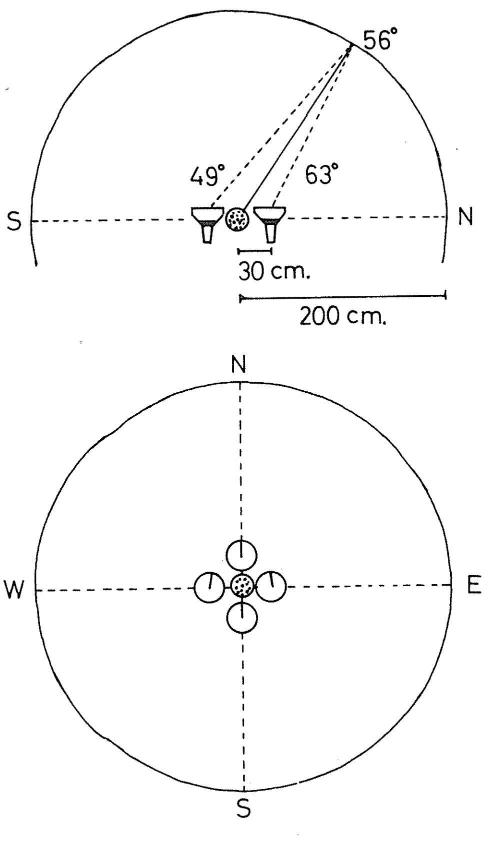

Fig. 2. The planetary dome, the star projector (in the middle), and the funnels shown from the side and from above. When the Polaris altitude of the projector is 56°N, the star latitudes in the middle of the N- and S-funnels are about 63° and 49°, respectively.
Den øverste figur viser stjerne-planetariet fra siden, og den nederste figur stjerne-planetariet fra oven. I midten ses stjerne-projektoren, og uden om den er tragtene anbragt. Stjerneprojektoren er en hul metalkugle med en elektrisk pære i midten. Gennem fine huller i kuglen kommer lyset ud og kastes op på »planetarie-himlen«, der har form som en halvkugle med diameter på 4 meter. Lyspletterne på »himlen« forestiller stjerner på en rigtig himmel. Man kan efterligne en hvilken som helst stjernehimmel her på jorden. Man kan f.eks. præsentere en fugl for den øjeblikkelige stjernehimmel over Moskva. Hvis fuglen nu bruger stjernehimlen til positions-bestemmelse i forhold til et mål, kan man måske få fuglen til at tro, at den er blevet flyttet til den geografiske position svarende til Moskva. Gennem sin orientering i tragten giver fuglen os oplysninger, om den bruger stjernehimlen til bestemmelse af sin aktuelle position.

Table 1. The orientation in the N- and S-funnel in 1977, cf. Fig. 2. All orientations are included in the number to the left, whereas the number in brackets to the right shows the orientations without the minor peaks of the bimodal distributions. We tested the difference between the orientations in the N- and S-funnel by means of two 2×2 Chi square tests (the E-W-orientations are omitted) which gave Chiysquare = 5.13 and 4.99, resp. ($p < 0.05$). The conclusion should be that the orientation in the S-funnel is more northerly than in the N-funnel.
Orienteringen i N- og S-tragten i 1977. Vi ser på antallet af gennemsnitretninger, der er N og S for Ø-V-linien, samt nederst for dem der ligger eksakt i Ø eller V. Der er en tydelig tendens til, at orienteringen i S-tragten er N-ligere end i N-tragten.

	N-funnel	S-funnel
Orient. N of E-W	6 (4)	10 (8)
Orient. S of E-W	11 (8)	3 (2)
E-W orient.	2 (2)	2 (1)

star projector (22 cm in diameter) situated in the centre. The artificial stars seen on the »sky« were all of the same light intensity per unit of area, but the naturally brighter stars were larger in size producing the well-known major star patterns. The projector could simulate a starry sky corresponding to any time, latitude and longitude all over the world. The rotational speed was the normal one for a starry sky, 15° counterclockwise per hour. In all experiments (except 4 in 1978) the rotational axis (Polaris altitude, latitude) was fixed at 55°-56°, corresponding to the latitude of Christiansø. The star time or longitude was set in relation to the azimuth of some of the outside stars in Cassiopeia, which stood exactly below the Polaris star in the northern sky.

The planetarium was placed inside a stone building, and star N was 340° (1977), and 360° (1978). As shown in Fig. 2 the funnels were placed a little N and S of the projector producing star latitudes of about 63° and 49° for the N- and S-funnels respectively. In 20 of the 58 1978-experiments funnels were also set up E and W of the projector.

The intended procedure was to show the birds the Christiansø longitude during the first night, and then simulate an eastward or west-

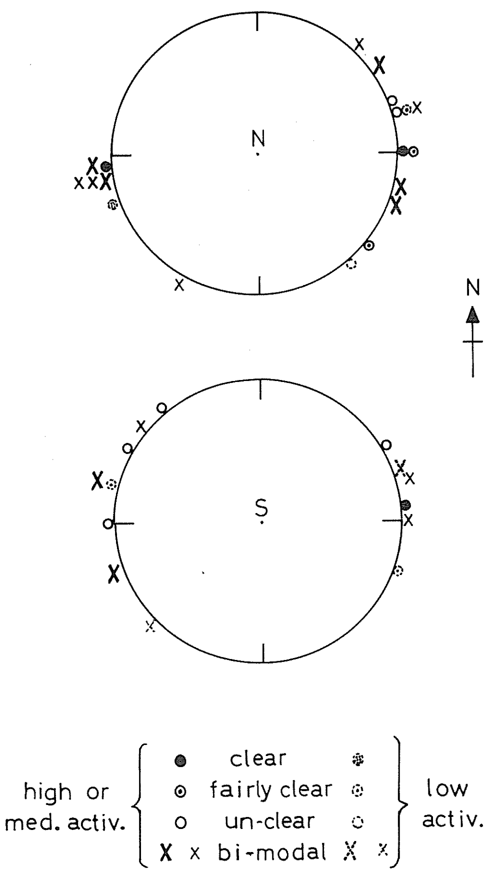

Fig. 3. The orientation in the N- and S-funnel in 1977. Both patterns are bimodal with about 180° between the easterly and westerly peaks. There seems to be a weak tendency towards a more northerly orientation in the S-funnel compared to the N-funnel (Table 1). If the two figures are combined and the minor peaks of the bimodal distributions are omitted the mean of the easterly orientations is 91° ($n = 14$), and the westerly mean is 275° ($n = 10$). By means of doubling angles (Batschelet 1965) we calculated the mean orientational axis to be 92°-272°. The mean vector length (r) for the doubled angle distribution was as high as 0.691, producing a very low probability for a uniform distribution ($0.001 < p < 0.01$, Raleigh test).
Orienteringsforsøg Christiansø maj 1977. Den øvre cirkel viser orienteringen i N-tragten, den nedre cirkel orienteringen i S-tragten (se Fig. 2). Vedrørende tegnforklaringen se Fig. 6.

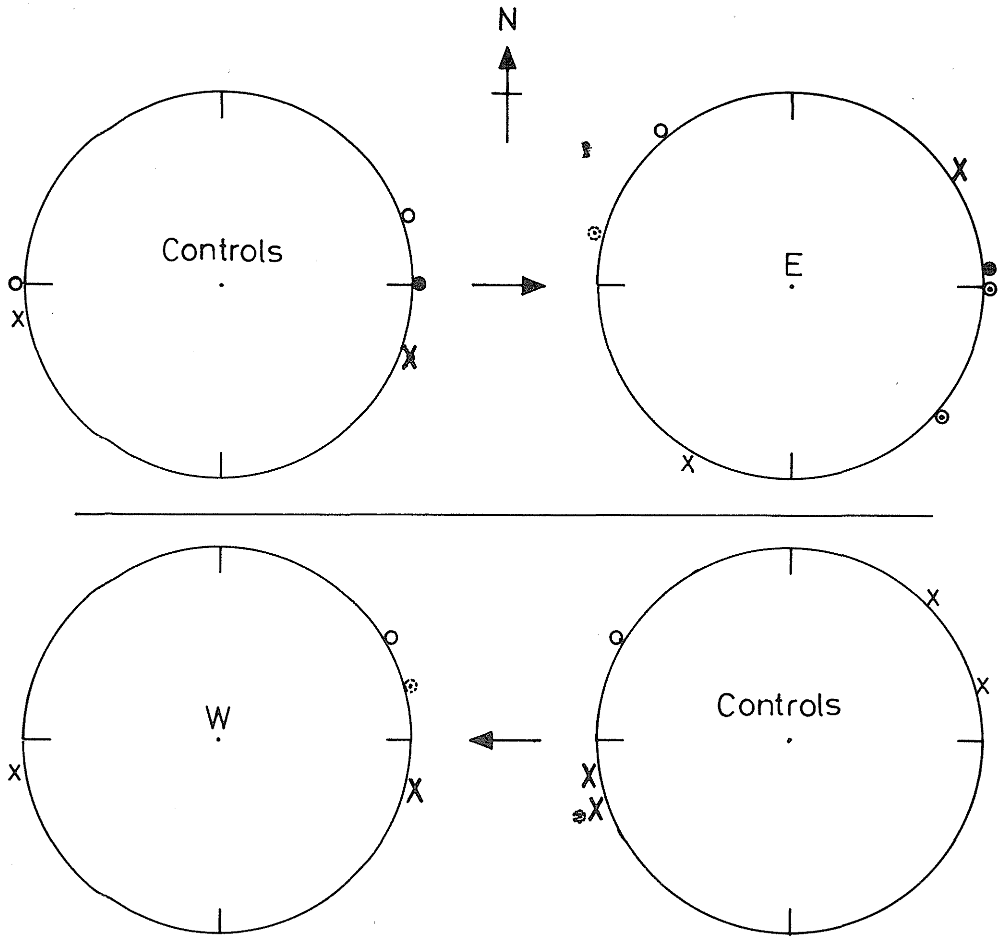

Fig. 4. Stellar »displacements« 1977. The upper figure shows »displacements« 1-1.5 hours towards E, and the lower figure 1-1.5 hours towards W. On the first night the birds experienced the star longitude of Chr.ø (controls), and were then »displaced« the following night. There seems to be a compensation for a westward displacement. The sample mean vector of the control birds is 265° – 0.937 (n = 4, p⟨ 0.05), and of the »displaced« birds 80° – 0.947 (n = 3, p⟩ 0.05). The difference between the two sample mean vectors is highly significant (p⟨ 0.001, Wheeler-Watson-test, Batschelet 1965).
Kunstige Ø-V-»forflytninger« i maj 1977. Efter et forudgående forsøg (»controls«) under en kunstig »stjernehimmel«, der i udseende svarer til den virkelige stjernehimmel over Christiansø, »flyttes« fuglene mod Ø (»E«) eller V (»W«) på den kunstige »stjernehimmel«. Hvis de opfatter dette som en virkelig geografisk forflytning, skal orienteringen efter »forflytningen« være mere eller mindre modsat rettet orienteringen i det første forsøg.

ward displacement of 1-2 hours (15°-30°) the following night. If, during the first night, the group of birds showed an easterly orientation they were »displaced« eastward by a longitudinal shift the following night in order to see whether they compensated for the »displacement« by a westerly orientation. Of course, the procedure was the reverse, if during the first night the birds showed a westerly orientation. In all experiments using the N- and S-funnel, the birds were latitudinally »displaced« already during the first night.

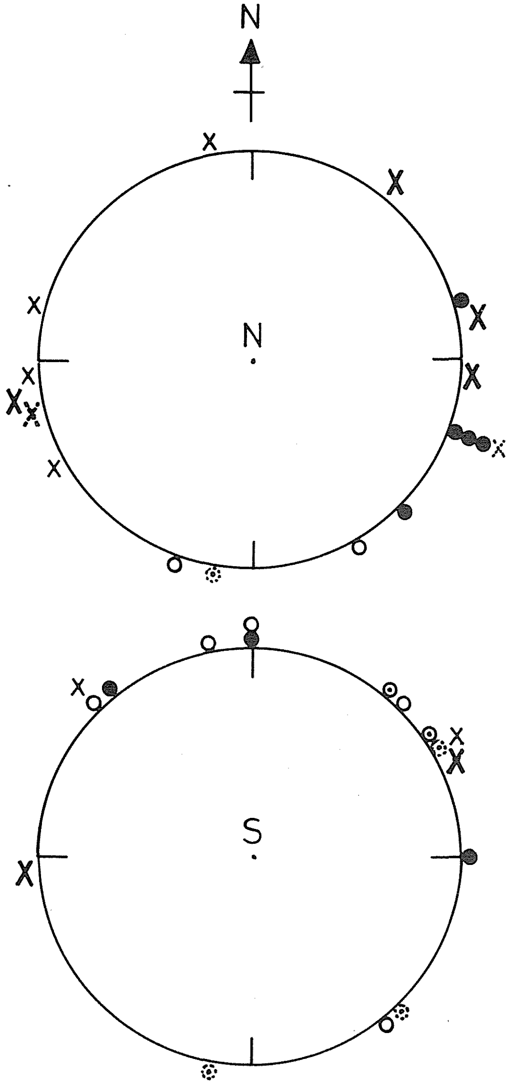

Fig. 5. The orientation in the N- and the S-funnel 1978. We have calculated two sorts of sample mean vectors: 1) On the basis of only unimodal orientations, and medium or high activities. 2) On the basis of all individual orientations except the minor peaks in the bimodal distributions. For the N-funnel we calculated the following sample mean vectors: 1) 125° – 0.813 (n = 7, $p < 0.01$), and 2) 127° – 0.494 (n = 13, $0.01 < p < 0.05$). For the S-funnel we calculated: 1) 22° – 0.626 (n = 10, $0.01 < p < 0.05$), and 2) 37° – 0.416 (n = 15, $p > 0.05$). The statistical differences between the mean vectors are both significant: 1) $0.001 < p < 0.01$, and 2) $0.01 < p < 0.025$ (Wheeler-Watson test, Batschelet 1965).
Orienteringen i N- og S-tragten i 1978. Orienteringen i S-tragten er klart nordligere og mere entydig end i N-tragten, hvor orienteringen fremtræder med to toppe, en større i ØSØ og en mindre i VSV-V.

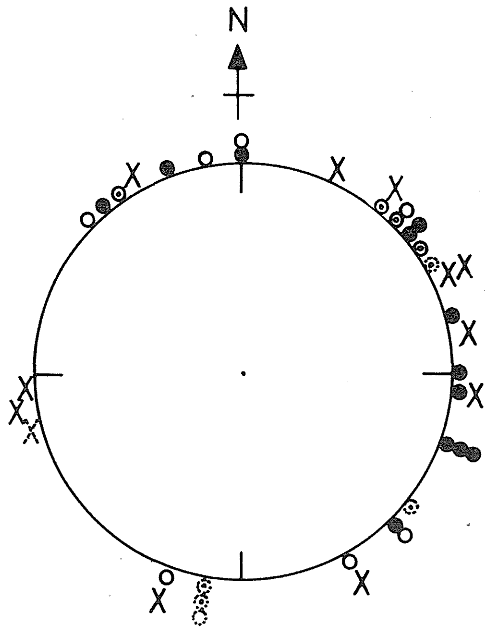

Fig. 6. The orientation in the N-, E-, S-, and W-funnel 1978. Only the major peaks in the bimodal distributions are shown. Following the procedure outlined in Fig. 5 we calculated the following two sample mean vectors: 1) 56°-0.486 (n = 23, $p < 0.01$), 2) 71°-0.318 (n = 40, $0.01 < p < 0.05$).
Orienteringen i N-, Ø-, S-, og V-tragten i 1978. Gennemsnitretningen er ca. NØ-ØNØ, hvilket er noget sydligere end den formodede NNØ-lige normaltrækretning.
Tegnforklaring: En prik står for gennemsnitretningen af een fugl pr. nat. Krydserne hører sammen to og to og viser en to-toppet orientering, d.v.s. fuglen har lavet opspring i to forskellige afsnit af tragten, der ligger så tilpas langt fra hinanden, at de lader sig adskille. Det er ofte sådan, at et stort og et lille kryds hører sammen. Det store kryds viser, i hvilket afsnit aktiviteten har været størst. Stiplede prikker og kryds viser forsøg med en så lav aktivitet, at man skal være forsigtig med at lægge for meget vægt på retningen. Jo mere udfyldt en prik er, og jo kraftigere et kryds, desto mere kan man stole på retningen.

RESULTS

The results are presented in Figs. 3-7 and Table 1.

The two years should be considered separately:

1977: The orientation in both the N- and S-funnel is clearly bimodal with the peaks around E and W (Fig. 3). The orientation in the S-funnel, however, is significantly more northerly than in the N-funnel (Fig. 3, Table 1). Fig. 4 shows the orientation following longitudinal »displacements« towards E or W. There is no obvious response to the eastward »displacement«, but the orientation following the westward »displacement« is suggestive of a compensatory reaction.

1978: The overall orientation is to the ENE and unimodal compared to the bimodal E-W-orientation in 1977 (Fig. 6). Again – and this time much more clear – the orientation in the S-funnel is more northerly than in the N-funnel (Fig. 5). There is no clear compensation for an eastward »displacement« (Fig. 7). Two Redstarts which showed a westerly orientation during the first night (No. 1) 325° and (No. 2) 200°) and then »displaced« westward perhaps showed a compensation during the following night (No 1 bimodal 200°/30° and No. 2 40°/240°).

DISCUSSION

The question is whether the (artificial) starry sky provides the birds with longitudinal and/or latitudinal information. If so, the orientations following the stellar »displacements«, may be predicted as shown in Fig. 8. Obviously, the orientations are in fairly good accordance with the predictions, and could be considered as compensatory reactions towards a goal (1) relatively close to the actual position (Chr.ø).

Particularly the 1977 orientations are, however, too »flat« in the E-W. direction. This pattern could perhaps be understood by the zero-axis navigation hypothesis of Wallraff (1974). The zero-axis runs (more or less) E-W, and the »nonsense«-direction should be E (Fig. 9).

The more westerly orientations in 1977 compared to 1978 could (also) be ascribed to the more variable wind direction in 1977. In 1978 the wind was easterly during the whole period and presumably the birds had been drifted by the wind, and then compensated for the drift during the next night by a delayed »headwind« component in their orientation (Rabøl 1975).

In conclusion, we seem to have demonstrated the influence of the starry sky on a N-S-component in the orientational mechanism of the birds. There is a weak indication of an influence on an E-W-component, but the observed patterns are at least partly open to other interpretations not involving stellar bicoordinate navigation at all. It seems wise to wait for more experiments before further hypotheses are proposed.

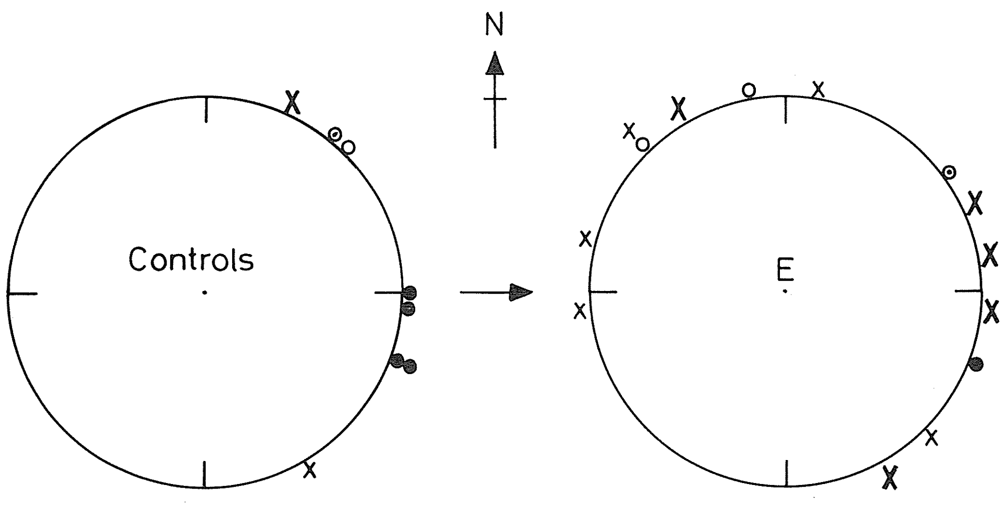

Fig. 7. The orientation following an eastward »displacement« 1978, cf. Fig. 4. The orientation in the eastern group is somewhat bimodal, and the NW-»peak« could be taken as an indication of a compensatory orientation.

Kunstig »forflytning« mod øst i 1978. Sammenlign Fig. 4. Der er intet entydigt svar på »forflytningen«. De fleste fugle fortsætter med at være Ø-orienterede, men en svagere tendens til orientering mellem V og N kan tolkes som en korrektion for »forflytningen« hos nogle af fuglene.

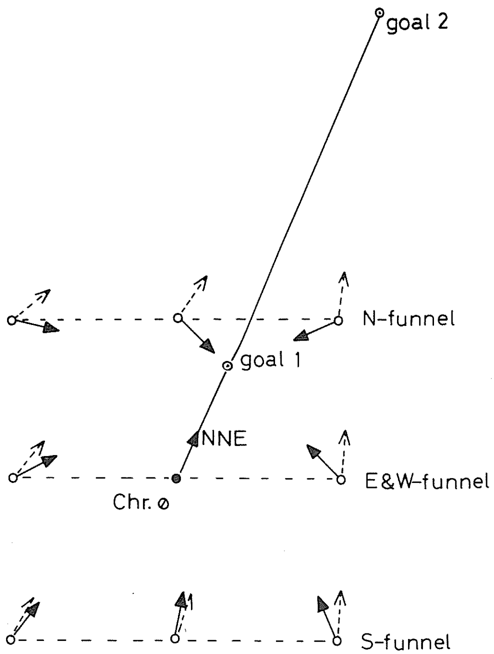

Fig. 8. The goal is presumed to be situated NNE of Chr.ø – either a relatively short distance (1) or a longer distance (2). The orientations in the N, E, S, and W-funnel should follow the pattern shown. The middle column shows the orientation without a longitudinal »displacement«, whereas the right and left columns show the orientations following an eastwards or westwards »displacement« respectively. *Vi forestiller os, at fuglens øjeblikkelige mål ligger i retningen NNØ for Christiansø. Afstanden til målet kan være kort (»goal 1«) eller lang (»goal 2«). Hvis en fugl bruger stjernehimlen til positionsbestemmelse og korrigerer for »forflytningen«, så burde den , afhængigt af tragtens placering og »forflytningens« retning, vise en orientering som pilene indicerer. Hvis målet ligger langt væk, vil orienteringen (de stiplede pile) blive stort set i samme retning i alle tilfælde. Hvis målet ligger tæt på (de fuldt optrukne pile) vil den korrigerende orientering for især »forflytninger« mod øst og nord kunne afvige særdeles meget fra den NNØ-lige normaltrækretning.*

DANSK RESUMÉ

Koordinat-navigation hos trækfuglene

Man antager almindeligvis, at trækfugle er i stand til at koordinatnavigere: De kender beliggenheden af deres mål, og de kan bedømme deres aktuelle position i forhold til målet. Er der forskel på de to positioner, orienterer de sig så mod målet.

Man kan forestille sig adskillige navigationskoordinat-systemer baseret på intensitets- eller retningsforskelle i diverse astronomiske eller geofysiske felter, mønstre eller faktorer. Der er muligheder i f.eks. sol- og stjernehimlen, jordmagnetismen, coriolis-kraften, lavfrekvente lydbølger (Kreithen 1978) og dufte (Schmidt-Koenig 1979). Indtil videre kender man ikke koordinaterne i trækfuglenes og brevduernes navigations-system.

Hvordan kan vi finde frem til dem? Det kan gøres ved at gætte på, hvad der danner koordinaterne, og så ændre på værdierne af en eller begge koordinater. Jeg gættede på, at de nødvendige informationer i så henseende måtte stamme fra stjernehimlen.

Stjernehimlen giver oplysning om længde- og breddegrad, og det er et verdensomspændende system i modsætning til flere andre mulige navigations-systemer. Stjernerne roterer om Nordstjernen som viserne i et ur, men de drejer rundt venstre om, og en omdrejning tager ikke 12, men 24 timer. Jo længere østpå man kommer, desto længere er stjernerne fremme i deres rotationsfase – jo mere er tiden fremskreden. Går vi f.eks. 30° østpå, er tiden 2 timer forud for her. Går vi 45° mod vest, er tiden 3 timer bagud i forhold til her. Kender fuglen tiden (omdrejningsfasen) i målet, og kan den ud fra observation af stjernernes omdrejningsfase vurdere tiden i sin aktuelle position, så kan den afgøre, om den er øst eller vest for sit mål – og hvor meget øst eller vest. Hvis fuglen kender Nordstjernens højde over horisonten i sit mål, kan den yderligere afgøre om den i sin aktuelle position er nord eller syd for målet. Nordstjernens højde er nemlig identisk med og skifter som breddegraden. Er Nordstjerne-højden i målet f.eks. 60°, medens den er 55° i fuglens aktuelle position, så skal fuglen bevæge sig 5° mod nord svarende til 555 kilometer.

Ved hjælp af et stjerne-planetarium kan man lave kunstige »forflytninger« på stjernehimlen. På Fig. 2 ses det planetarium som jeg anvendte i en række orienteringsforsøg, der fandt sted på Christiansø i forårene 1977 og 1978. Det består af en stjerne-projektor, der roterer en gang rundt i døgnet, og hvor man vilkårligt kan stille ind på en ønsket position i længde- og breddegrad. Det er kun et lille planetarium. Afstanden fra stjerne-projektoren og til »himlen« er blot 2 meter. Rundt om projektoren og så tæt som muligt ved denne blev anbragt to eller fire tragte. I hver tragt befandt sig en trækfugl i 2-3 timer midt på natten, og fuglens retningsvalg blev registreret ved hjælp af fodskrab i tolv stykker skrivemaskine korrektions papir (Fig. 1).

Projektoren var normalt indstillet på en højdevinkel på 55° af den kunstige stjernehimmels rotationspunkt (Nordstjernen) – hvad der svarer til breddegraden på Christiansø. På grund af planetariets små dimensioner, bliver de samtidige højdevinkler i N- og S-tragtene henholdsvis 61° og 49°. Da højdevinklen som nævnt er et mål for breddegraden, har fuglen i N-tragten modtaget en kunstig »forflytning«, på ca. 6° nord, og fuglen i S-tragten ca. 6° S. Tragtene anbragt øst og vest for projektoren får en breddegrad

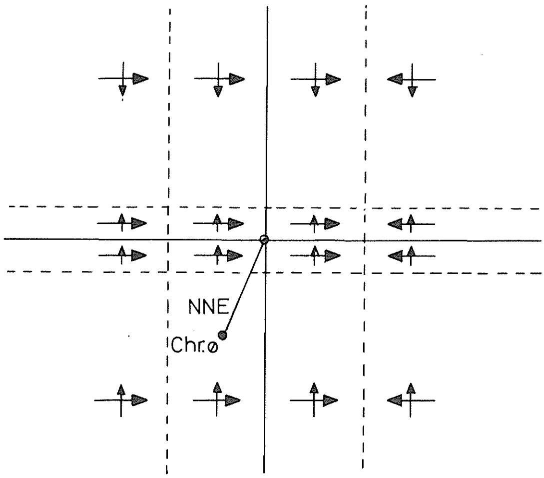

Fig. 9. Navigation coordinate system with threshold zones around both coordinates (hatched lines) – following the model of Wallraff (1974). The figure is shaped for spring migration, for a standard direction between N and E, and for an application of the present results. Within the common threshold zone the birds orient stereotypically towards E and N. The threshold zone is broader around the longitude compared to the latitude, and in most situations the tendency to be oriented E(W) is relatively stronger than the tendency to be N(S)-oriented.
Wallraff's navigations-model.

svarende til Christiansøs (55°) – og længdegraden i samtlige tragte kommer til at svare til Christiansøs længdegrad.

Jeg har nu især undersøgt, om der var forskel på orienteringen i N- og S-tragten – d.v.s. om fuglene korrigerede for en breddegrads-»forflytning«.

Som vist på figurerne og i tabellen er der klar tendens til at fuglene i S-tragten er N-orienterede, medens fuglene i N-tragten er mere to-toppet orienterede mod ØSØ og VSV-V. Dette er især tydeligt i 1978 (Fig. 5), og stemmer godt overens med forventningen vist i Fig. 8 – især hvis målet (»goal 1«) ligger tæt ved Christiansø. Alt ialt kan resultaterne godt tolkes som udslag af stjerne-navigation. Det er dog åbenbart, at der skal flere forsøg til – og også efterårs-forsøg – før man kan udtale sig med større sikkerhed om en tilstedeværende stjerne-navigation. Sådanne forsøg vil jeg foretage i de næste år.

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