Star navigation in Pied Flycatchers *Ficedula hypoleuca* and Redstarts *Phoenicurus phoenicurus*

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(Med et dansk resumé: Stjernebaseret navigation hos Broget Fluesnapper Ficedula hypoleuca *og Rødstjert* Phoenicurus phoenicurus*)*

Introduction

In recent years, the influence of a star-based (coordinate) navigation system in bird migration has been investigated in only few experiments (Able 1995; see, however, Rabøl 1992, 1994, Åkesson et al. 1995). Accordingly, indications of such a navigation system are found only sporadically in papers (Sauer 1957a, 1957 b; Sauer & Sauer 1960; Rabøl 1981, 1988, 1990, 1992, 1994, 1995), and even though Emlen (1975) acknowledged the possibility of stellar based coordinate navigation in migrant birds (including juvenile and inexperienced birds), his experimental design was not optimal for such a demonstration (Emlen 1967, see Rabøl 1997).

Two kinds of orientation experiments form the most appropriate procedures for demonstration of star navigation: 1) under a natural starry sky following a real geographical displacement, and 2) a simulated geographical displacement under the "starry sky" of a planetarium (in the following defined by quotation marks). According to the clock-and-compass hypothesis, no directional shifts in relation to the compass reference(s) should follow a real or simulated displacement (Rabøl 1992). Conversely, compensatory orientation, especially following a simulated displacement, should be strongly indicative of star navigation.

The following is an extension of the Tycho Brahe Planetarium experiments (Rabøl 1992). An extensive report (Rabøl 1997) gives more details and information about procedures, results, and the interpretations of these, as well as of other relevant experiments in the literature.

Material and methods

Funnel experiments were carried out in the Tycho Brahe Planetarium, Copenhagen, in September 1991 (Rabøl 1992), and in the star planetarium of the Steno Museum, Århus, in September 1994 (preliminary experiments to the latter were initiated in September 1993 and May 1994). The Steno experiments were carried out with two groups of birds designated Steno I and Steno II.

The birds were tested singly in plastic funnels (slope 45°, upper diameter 30 cm) with a 160° (or 140°, Tycho) vision of the "stellar sky". The orientation and amount of activity were estimated using the correction paper method (Rabøl 1979, 1993, 1994). Sample mean vectors for each night were calculated on the basis of the individual

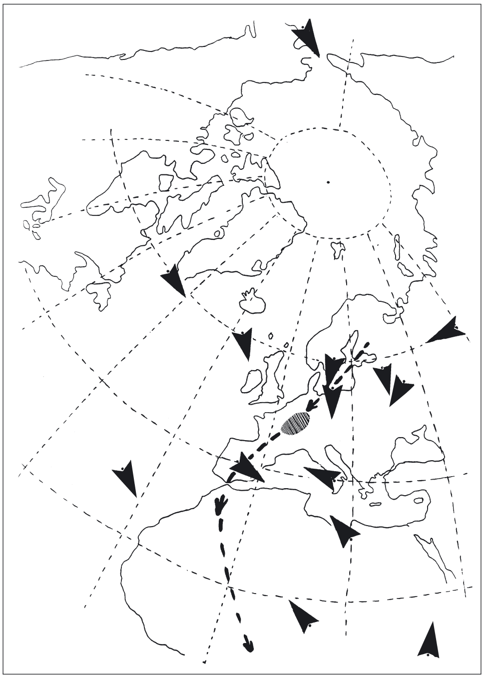

Fig. 1. The sample mean directions (compare Tab. 1-2) from the 14 positions to which the birds were "displaced" (the three "Christiansø" experiments are combined). Also shown are the autumnal migratory route (dotted line) and the presumed goal area (hatched) in NE France.
Den gennemsnitlige orientering på de 14 simulerede positioner. Den prikkede linie er efterårs-trækruten, og det skraverede felt i NØ Frankrig er det formodede målområde i forsøgsperioden.

mean directions of unimodal activities and the major peak directions in bimodal activities. Only activities above the score "low" were included.

The diameter of the Tycho dome is 23 m and about 9000 stars are displayed on the "sky". The floor slopes 30°, and this marked "downhill" effect makes shielding (collars) necessary. Magnetic N is 60° to the right of rotational N of the "starry sky".

The Steno dome is 11 m and shows about 2500 stars. The floor is horizontal and no shielding was deemed necessary. Magnetic N is 12° to the left of rotational N. Neither moon, planets, nor the Milky Way were shown in either planetarium. The rotation speed was 15° per hour.

Twelve funnels were used each night, six to the W and six to the E of the star projector. Funnel N/S was parallel to the projected stellar N/S axis. The deviations of funnel N from rotational N (on latitude 55° N in Steno) were 8°-18° to the left or right as seen from the funnels W or E of the projector, respectively. In Tycho these deviations were slightly higher (Rabøl 1997).

The Steno I experiments were performed on 6-11 September 1994, and the Steno II experiment on 12-16 September 1994. The birds in the two groups were trapped as migrants on Christiansø in the Baltic Sea on 28-30 August and on 9 September. When the initial orientations were tested on Christiansø, the sample mean vectors were 192° - 0.449 (n=11, sky partly covered) and 210° - 0.864*** (n=13, clear sky).

The Tycho experiments were performed on 22-26 September 1991 with birds trapped on Christiansø on 3-9 September 1991. The sample mean vector of the experiments on Christiansø on 8-9 September was 276° - 0.527* (n=12, clear sky).

The asterisks denote the significance of the sample mean vector concentrations using the Rayleigh test. (*), *, **, and *** denote $P < 0.10$, < 0.05, < 0.01, and < 0.001. The experimental sequences of the three series are shown in Tab. 1 and 2.

The general procedure was to expose the group to the "Christiansø sky" in the planetarium on the first night(s), and then "displace" the group to other "positions" on the following nights by adjusting the planetarium sky. Most of the birds were juvenile (1Y) Pied Flycatchers *Ficedula hypoleuca*, but some 1Y Redstarts *Phoenicurus phoenicurus* and a few adult (2Y+) Pied Flycatchers were included as no significant differences in orientation were found between the species or age groups.

Results

Tab. 1 and 2, and Fig. 1 show the sixteen experiments. Tab. 3 and Fig. 2 summarise the orientations in relation to 1) funnel N and 2) the direction towards a presumed goal area in NE France (Nancy/Mulhouse).

The 14 "positions" in Fig. 1 mimic the symmetrical release patterns most often used in pigeon homing experiments (e.g. Wallraff 1974): the sample mean vector of the 16 orthodrome directions from the "positions" towards the presumed goal area in NE France is 294° - 0.255 ($P = 0.36$), i.e., the WNW mean direction is not significant.

The pattern of Fig. 2A is bimodal with a major peak in "SSE" and a minor peak in "NW". Doubling the angles leads to modi in 135° and 315° and a concentration of 0.258, i.e. the concentration increases but is still far from significant at the 0.05 level.

The pattern of Fig. 2B is unimodal and significant: the sample mean vector is -11° - 0.755**.

In conclusion, the general pattern is significantly goal directed and not oriented in the standard direction (SW).

Tab. 1. Orientation experiments in the Steno Museum with two different groups of birds from Christiansø: Steno I, 6-11 September 1994, and Steno II, 12-16 September 1994. The second column shows the positions to which the birds were ”displaced”. The next column is the sample mean vector of the n birds showing directed migratory activity. The fourth column gives the orthodrome (great circle) direction from the ”displaced” position towards the presumed goal area in NE France. The asterisks in this column denote the significance of the goalward component of the sample mean vector using the V-test. The fifth column gives the great circle distance between the ”displaced” position and the presumed goal area. The rhumblines (loxodromes) from the ”Canary Islands” and ”Sudan” are 53° and 237°, respectively.
Steno-forsøgene. Med et eksempel skal tabellen forstås således: 10/9 ser de 12 fugle i forsøg en ”stjernehimmel” svarende til Skt.Petersborg. Otte af dem viser klar orientering og gruppe-gennemsnitsvektoren (178° - 0.535) er rettet ca mod syd. Storcirkel-retning og afstand til det formodede målområde i NØ Frankrig er ca vestsydvest (245°) og 1935 km.

Date	Position	Mean vector	Orthodrome	Distance, km	n
6.9	Christiansø 55°N, 15°E	232° - 0.201	222°	995	9
7.9	Christiansø 55°N, 15°E	142° - 0.468 (*)	222°	995	11
8.9	Libya 30°N, 20°E	313° - 0.383	333° (*)	2329	11
9.9	Canary Islands 30°N, 25°W	124° - 0.295	44°	3304	11
10.9	St. Petersburg 58°N, 30°E	178° - 0.535 (*)	245°	1935	8
11.9	Chad 15°N, 15°E	310° - 0.528 *	349° *	3759	11
12.9	Christiansø 55°N, 15°E	164° - 0.425	222°	995	0
13.9	Naples 40°N, 15°E	291° - 0.377	324°	1142	8
14.9	Madrid 40°N, 5°W	96° - 0.705 *	41° (*)	1248	8
15.9	Sudan 10°N, 35°E	10° - 0.514	333° (*)	5015	6
16.9	Moscow 55°N, 35°E	220° - 0.497	261° *	2132	10

(*) P < 0.10, * P < 0.05, ** P < 0.01, *** P < 0.001

Tab. 2. Orientation experiments in the Tycho Brahe Planetarium, 22-26 September 1991, summarised as in Tab.1. The rhumb lines (orthodromes) from ”Ural”, ”S Greenland”, and ”Alaska” are 249°, 112°, and 97° (264°), respectively.
Tycho-forsøgene.

Date	Position	Mean vector	Orthodrome	Distance, km	n
22.9	Sweden 60°N, 15°E	208° - 0.409	204° *	1482	9
23.9	N Atlantic 60°N, 15°W	127° - 0.617 *	124° **	1987	8
24.9	Ural 60°N, 60°E	287° - 0.584 *	272° **	630	9
25.9	S Greenland 60°N, 45°W	91° - 0.938 **	98° ***	3574	6
26.9	Alaska 60°N, 165°W	350° - 0.319	6°	8034	7

(*) P < 0.10, * P < 0.05, ** P < 0.01, *** P < 0.001

If the initial (outdoor) orientations on Christiansø are compared with the subsequent orientations on the ”position” of Christiansø in the planetarium (Tab. 1), the latter are rotated counter-clockwise and are less concentrated. This counter-clockwise rotation is more apparent when interpreted as great circle navigation towards a goal ”SSE” of Nancy/Mulhouse: the sample mean vector of the deviations between the sixteen sample mean vector directions and the great circle courses towards a goal at 35°N, 10°E (Tunisia) is 4° - 0.807, producing a goalward component of 0.805 (compared with 0.741 of the goalward mean vector of Fig. 2B).

Discussion

In the following, three questions are addressed:

1) Is the interpretation correct that stellar-based navigation is involved?

2) If so: a) are the results indicative of goal area navigation (e.g. Rabøl 1969, 1985, 1994), and b) is the apparent great circle navigation a real phenomenon or a spurious result?

Concerning 1, the reality of stellar-based navigation
As magnetic N and (stellar) rotational N do not coincide in the two planetaria, the possibility exists that the sixteen sample mean directions in Tab. 1 and

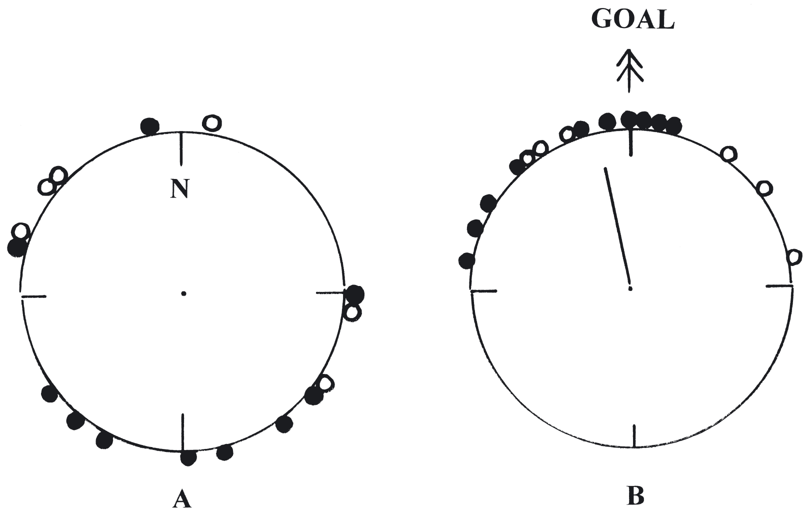

Fig. 2. The sixteen sample mean directions (Tab. 1-2). The six white dots refer to ”positions” at or south of 40°N, the ten black dots to ”positions” north hereof. A) Directions in relation to funnel-N. The sample mean vector is 197° - 0.154. B) Directions in relation to great circle courses from the displaced ”positions” towards a goal in NE France. The sample mean vector is -11° - 0.755**, and the sample mean vector of the black and white dots separately is -23° - 0.840** and 13° - 0.704*, respectively.
Prikkerne i A) viser gennemsnitsorienteringen de 16 forsøgsnætter i forhold til verdenshjørnerne (N), B) i forhold til storcirkel-kursen fra de simulerede positioner mod det formodede målområde i NØ Frankrig.

2, when transferred to magnetic N as the compass reference, describe better in terms of a (more) significant sample mean vector component in the standard direction (SW). However, the ”magnetic N” sample mean vector is insignificant (210° - 0.134).

For longitudinal displacements – or ”displacements” – an uncalibrated stellar S compass produces compensatory orientation which may be designated pseudo-navigation. Able (1995) interprets the compensatory orientation of Sauer’s famous Blackcap 632 (Sauer & Sauer 1960) as such pseudo-navigation, and Emlen (1975) also mentions this possibility.

A stellar S compass is a star (pattern) in the southern sky which displays a clockwise azimuth movement approx. 15° per hour from E over S to W. A biological clock is necessary if stellar S is to be used as a compass, for compensation of the movement of the star (pattern) across the sky. A stellar S compass is designated uncalibrated if an E or W displacement or ”displacement” is not appreciated through calibration of stellar S from rotational N (or magnetic N).

Using an uncalibrated stellar S compass produces counter-clockwise or clockwise rotated orientation of the same angle as the bird is displaced W or E, respectively.

The sixteen mean directions of Tab. 1-2 could be calibrated to the same longitude – e.g. 15°E – as if an uncalibrated stellar S compass were in operation. The degree of description then increases compared with Fig. 2A. For the ten ”displacements” on latitudes 55° through 60°, the sample mean vector component in the standard direction (0.610) describes almost as well as does the goalward component (0.773) of the same ten ”displacements” in terms of great circle navigation towards a goal in NE France (Fig. 2B). However, the description of the six ”displacements” at or south of 40°N is insignificant (0.033) compared with 0.686, which is the goalward component of the same six ”displacements” in terms of great circle navigation.

Besides comparing such third order sample mean vectors, we investigated the shifts from one night to the next on a) the same longitude, but different latitudes; and b) the same latitude, but different longitudes (Fig. 14, Rabøl 1997). In a), all shifts were larger than 90° (where an uncalibrated stellar S compass predicts no shifts). In b), all cases produced much larger directional shifts than expected if pseudo-navigation and an uncalibrated stellar S compass were responsible.

Tab. 3. The number of experiments (n) and the combined sample mean vectors in relation to funnel-N (upper row) and the great circle direction from the "displaced" positions towards the goal area in NE France (lower row; negative directions deviate to the left of the goal direction). The asterisks denote the statistical significance of the concentration of the sample mean vectors (Rayleigh test). The V-test was also applied in the four lower row conditions. Steno I was significant at the 0.01 level, and the three other constellations at the 0.001 level.
Resumé af de 39, 61 og 41 forsøg med klar orientering i henholdsvis Tycho, Steno I og Steno II forsøgene. Den øverste række viser retningen af gruppe-gennemsnitsvektoren i forhold til verdenshjørnerne (N), den nederste række i forhold til det formodede mål i NØ Frankrig.

	Tycho Brahe Planetarium 1991 n = 39	Steno Planetarium 1994 I n = 61	Steno Planetarium 1994 II n = 41	Total n = 141
Orientation, N=0°=360°	136° - 0.091	212° - 0.090	160° - 0.098	175° - 0.078
Orientation towards NE France	1° - 0.549***	-38° - 0.283**	-5° - 0.348**	-13° - 0.358***

(*) P < 0.10, * P < 0.05, ** P < 0.01, *** P < 0.001

In conclusion, pseudo-navigation cannot describe the directional shifts following the "displacements", and the influence of an uncalibrated stellar S compass in the ten longitudinal "displacements", treated as a third order sample mean vector (see above), may be a spurious result of a positive coupling with the outcome of stellar navigation. The most obvious explanation of the orientation following the "displacements" thus is stellar-based navigation.

Concerning 2a, the reality of goal area navigation
The compensatory stellar-based orientation reported in this paper does not prove that stellar-based goal area navigation takes place. Three other possible orientational systems may account for the compensatory orientation (see Fig. 1 in Rabøl 1994): a) coordinate navigation towards a goal area in the migratory route; b) a resultant vector between a standard direction component (established by means of clock-and-compass) and a vectorial component of coordinate navigation towards the site of trapping or any other previously experienced position; or c) cross-axis orientation. c) implies that the compensatory orientation is the outcome of a non-navigatory response based on the appropriate compositions and strengths of the standard, reverse, and right angle vectors.

However, the distinction between a), b), and c) may be academic. b) could be considered a variety of a), and the same is true of c) since the sense used by the birds to detect the vectors probably can be understood in navigatory terms only.

In my opinion, the results are outcomes of a), but they still only indicate that birds are able to use the stellar sky for navigation if "displaced" far from the trapping site. However, the results emphasize the possible existence of stellar navigation and the significance of displacement and "displacement" experiments.

Concerning 2b, the reality of great circle navigation
Obviously, birds do not navigate by great circles (or rhumb-lines) following formulas as developed by humans (e.g. Rabøl 1988). Migrant birds probably orient in terms of cross-axes orientation and/or null-axes/zones-of-uncertainty navigation (Wallraff 1974, Rabøl 1985, 1988). Therefore we investigated the directions of the sixteen sample mean directions from the four cardinal directions NE, SE, SW, and NW in a simple sign navigation system with a "pseudo-goal" in Tunisia (35°N, 10°E) and straight N/S and E/W coordinates. The third order sample mean vector was -1° - 0.700***. In other words, the description is slightly poorer than that of the deviations of the sample mean vectors from the great circles towards Nancy/Mulhouse (Fig. 2B). However, such a sign navigation system may be too sketchy, and on Fig. 1-2 a general "SE"-tendency (or perhaps an axial "SE/NW" tendency) is apparent. This pattern may correspond to nonsense orientation or PCD (Matthews 1968, Wallraff 1974, Rabøl 1988) and be a basic response of a navigatory process – especially as it arises under the more or less deprived conditions in experiments.

Summary

Juvenile Pied Flycatchers and Redstarts were trapped on Christiansø as migrants on their way from Sweden or Finland towards the Iberian Peninsula. On Christiansø, under a starry sky, their orientation was about SW and very significant. One group was tested in the Tycho Brahe Planetarium, Copenhagen, in September 1991, and two other groups in the Steno Planetarium, Århus, in September 1994. 12, 12 and 12 birds were tested on 5, 6, and 5 nights, respectively, in 30 cm plastic funnels using the correction paper method. The birds were exposed to ”starry skies” for 1.5-2 hours per night on 14 different geographical ”positions”, determined by the Polaris altitude (latitude) and rotational phase (longitude). The stellar skies rotated 15° per hour. The compass directions of stellar and magnetic N were constant between nights, and in the Steno experiments, the two directions almost coincided. Clearly, the birds compensated for the ”displacements”, and some sort of stellar-based coordinate navigation must be responsible for the patterns observed. This does not prove that goal area navigation takes place, but the possibility merits more consideration than previously given.

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Resumé

Stjerne-navigation hos Broget Fluesnapper *Ficedula hypoleuca* **og Rødstjert** *Phoenicurus phoenicurus*

I 1992 publicerede jeg en artikel i DOFT vedrørende nogle orienteringsforsøg i Tycho Brahe Planetarium i efteråret 1991. Forsøgene tydede på, at Broget Fluesnapper og Rødstjert brugte stjernerne til at navigere efter. Hvis jeg simulerede en geografisk forflytning – ved at vise fuglene en kunstig stjernehimmel svarende til en anden position – skiftede fuglene retning på dramatisk vis. En sydlig orientering på ”positionen” 60°N, 15°Ø (mellem Oslo og Stockholm) ændrede sig til henholdsvis vest- og øst-orientering efter ”forflytning” til henholdsvis 60°N, 60°Ø (Ural) og 60°N, 45°V (Sydgrønland). Disse Tycho-forsøg er resumeret i Tab. 2.

Der var imidlertid tale om en meget lille forsøgsserie, så den blev udvidet til det tredobbelte med to ekstra serier (I og II) i efteråret 1994, denne gang i Steno Museums planetarium i Århus. Med sit vandrette gulv og horisont er Steno bedre egnet end Tycho til orienteringsforsøg med fugle i tragte. Steno forsøgene er resumeret i Tab. 1.

Tilsammen er der for de to planetarier tale om ialt 16 forsøgsnætter med 12 fugle testet pr nat. Tre af forsøgene fandt sted på ”positionen” Christiansø, hvor fuglene var blevet fanget på efterårstrækket. De andre ”positioner” fremgår af Tab. 1 og 2, samt Fig. 1.

Orienteringen skifter meget fra ”position” til ”position”, og det passer meget godt med, at fuglene på den pågældende årstid skal være sådan ca i det nordøstlige Frankrig. Det fremgår også af Fig. 2B, hvor orienteringen er angivet som afvigelsen mellem den fundne gennemsnitsretning og (storcirkel)kursen fra ”positionen” mod et mål i det nordøstlige Frankrig. Derimod viser Fig. 2A, at de fundne retninger ikke er i overensstemmelse med forventningen ud fra kalender-og-kompas hypotesen, nemlig en sydvestlig normaltrækretning uanset ”positionen”.

Det umiddelbare gæt er altså, at fuglene stjerne-navigerer efter et mål på trækruten. Af historiske årsager er der imidlertid udbredt skepsis mod tanken om stjernenavigation, og for at få overbevist skeptikerne må vi gøre meget nøje rede for, at den kompenserende orientering – udover at være statistisk signifikant – ikke skyldes noget andet og simplere, altså ikke være udslag af kalender-og-kompas orientering i en aller anden form.

Sagen er nemlig, at en kompensation for en *øst- eller vest-forflytning* i større eller mindre grad kan være resultatet af noget andet end stjerne-navigation, nemlig en ikke-kalibreret orientering i forhold til en stjerne (eller et stjernebillede) på sydhimlen. En sådan stjerne bevæger sig ganske som solen med 15° i timen fra øst over syd til vest.

Hvis fuglen vil fastlægge og fastholde en konstant trækorientering (f.eks. mod syd), sker det gennem medvirken af et ”indre ur”, der kompenserer for stjernens (solens) gang over sydhimlen: Hvis en stjerne således står i sydvest på Christiansø (på 15° østlig længde) kl. 03 lokal tid, og fuglen vil orientere sig mod syd, kan det ske ved, at den holder en kurs på 45° til venstre for stjernen. Hvis man nu forflytter – eller ”forflytter” i et planetarium – fuglen til Kap Farvel, og den ikke opdager det eller kalibrerer for det, vil den holde den samme kurs på 45° til venstre for stjernen, som den gør på Christiansø. Kap Farvel er på 45° vestlig længde, så her er klokken 23, og den samme stjerne står ca i sydsydøst (kl. 03 vil den stå i sydvest). Fuglen orienterer sig derfor (cirka) mod østsydøst og har således skiftet kurs 60° til venstre i forhold til orienteringen under Christiansø-stjernehimlen. Dens reaktion ligner altså kompensation baseret på stjerne-navigation, men det er en form for automatisk kompensation, der alene bunder i kompas-orientering.

En nøjere analyse af responserne på øst- og vest ”forflytningerne” i planetarierne – og det gælder også for virkelige forflytninger foretaget mellem Christiansø og Skallingen (Rabøl 1994, 1995) – viser imidlertid, at fuglene gennemgående kompenserer meget mere end hvad der kan tilskrives en ikke-kalibreret kompas-orientering.

Desuden kompenserer de også meget klart for ”forflytninger” mod *syd* på planetarie-stjernehimlen, og her er det vanskeligt at forestille sig en anden mekanisme end stjerne-navigation.

Endelig er det ukendt, om fuglene rent faktisk bruger et stjernekompas på sydhimlen. Det er nemmere at bruge rotationspunktet (Nordstjernen) på nordhimlen. For dette punkt står altid i nord og er derfor et bedre kompas at holde kurs efter. Man ved, at Indigo-værlingen om fo-

råret bruger et sådant nordligt stjernekompas, der også så at sige ligger "foran" den, mere eller mindre i trækretningen. Om efteråret ligger en stjerne på sydhimlen derimod "foran", så det forekommer ikke urimeligt, at et sådan sydhimmel-kompas bruges til at fastholde efterårskursen efter forudgående fastlæggelse og kalibrering ud fra det nordlige stjernekompas (eller magnetkompasset). Hvis et sådant sydhimmel-kompas kalibreres hver aften/nat i forhold til nordhimmel-kompasset, opstår der ingen automatisk kompensation for en øst- eller vest-forflytning/"forflytning". Kalibreres det kun en gang imellem sker der imidlertid en automatisk – og hensigsmæssig – kompensation for de forflytninger, som vinden eller mennesker måtte udsætte fuglene for.

Konklusionen af forsøgene i Steno og Tycho er således, at meget tyder på, at de nattrækkende småfugle i hvert fald delvist benytter sig af stjernenavigation, når de fastlægger deres trækorientering.

Om dette er en bekræftelse af målområde-hypotesen kan diskuteres. Ifølge denne hypotese navigerer fuglene mod et målområde, der i årets løb gennemløber trækruten (bl.a. Rabøl 1985, 1988). Fremtidige forsøg, baseret på kortdistanceforflytninger ("forflytninger") må vise, om målområde-hypotesen er den mest dækkende og korrekte måde at beskrive reaktionerne på.

References

Able, K.P. 1995: Orientation and navigation: A perspective on fifty years of research. – Condor 97: 592-604.

Emlen, S.T. 1967: Migratory orientation in the Indigo Bunting *Passerina cyanea*. Part II: Mechanism of celestial orientation. - Auk 84: 463-489.

Emlen S.T. 1975: Migration: Orientation and navigation. Pp 129-219 in D.S. Farner & J.R. King (eds): Avian Biology, Vol. 5. – Academic Press, New York.

Matthews, G.W.T. 1968: Bird navigation. – Cambridge University Press.

Rabøl, J. 1969: Orientation of autumn migrating Garden Warblers (*Sylvia borin*) after displacement from western Denmark (Blåvand) to eastern Sweden (Ottenby). A preliminary experiment. – Dansk Orn. Foren. Tidsskr. 63: 93-104.

Rabøl, J. 1979: Magnetic orientation in night-migrating passerines. – Ornis Scand. 10: 69-75.

Rabøl, J. 1981: The orientation of Robins *Erithacus rubecula* after displacement from Denmark to Canary Islands, autumn 1978. – Ornis Scand. 12: 89-98.

Rabøl, J. 1985: The moving goal area and the orientation system of migrant birds. – Dansk Orn. Foren. Tidsskr. 79: 29-42.

Rabøl, J. 1988: Fuglenes træk og orientering. – Bogan, Copenhagen.

Rabøl, J. 1990: Navigerer Broget Fluesnapper *Ficedula hypoleuca* ved hjælp af stjernerne? – Dansk Orn. Foren. Tidsskr. 84: 72-74.

Rabøl, J. 1992: Star navigation in night-migrating passerines. – Dansk Orn. Foren. Tidsskr. 86: 177-181.

Rabøl, J. 1993: The orientation system of long-distance passerine migrants displaced in autumn from Denmark to Kenya. – Ornis Scand. 24: 183-196.

Rabøl, J. 1994: Compensatory orientation in Pied Flycatchers *Ficedula hypoleuca* following a geographical displacement. – Dansk Orn. Foren. Tidsskr. 88: 171-182.

Rabøl, J. 1995: Compensatory orientation in juvenile Garden Warblers *Sylvia borin* and Redstarts *Phoenicurus phoenicurus* following a geographical displacement. – Dansk Orn. Foren. Tidsskr. 89: 61-65.

Rabøl, J. 1997: Star navigation in Pied Flycatchers *Ficedula hypoleuca* and Redstarts *Phoenicurus phoenicurus*. – Report from Department of Population Biology, University of Copenhagen.

Sauer, F. 1957a: Astronavigatorische Orientierung einen unter künstlichem Sternenhimmel verfrachteten Klappergrasmücke, *Sylvia c. curruca*. – Naturwissensch. 44: 71.

Sauer, F. 1957b: Die Sternenorientierung nächtlich ziehenden Grasmücken (*Sylvia atricapilla, borin* und *curruca*). – Z. Tierpsychol. 14: 29-70.

Sauer, E.G.F. & E.M. Sauer 1960: Star navigation of-nocturnal migrating birds. – Cold Spring Harbor Symp. Quant. Biol. 25: 463-473.

Wallraff, H.G. 1974: Das Navigationsystem der Vögel. – Oldenburg, München.

Åkesson, S., V. Ottosson & R. Sandberg 1995: Bird orientation: displacements experiments with young autumn migrating Wheatears *Oenanthe oenanthe* along the arctic coast of Russia. – Proc. R. Soc. Lond. B. 262: 189-195.

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