Orientation Experiments with Whitethroats Sylvia communis and Lesser Whitethroats Sylvia curruca

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(Med et dansk resumé: Orienteringsforsøg med Tornsanger Sylvia communis og Gærdesanger Sylvia curruca)

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INTRODUCTION

This paper describes some orientation experiments with a group of juvenile Sylvia-warblers trapped in the breeding area, and experiments in the trapping area running from the pre-migratory period through the whole autumnal migratory season. Furthermore, experiments in Denmark with the same birds were also carried out on a single night in the following spring migratory season.

The *expected development* in the orientational reactions in the course of the experimental period was:

1) Weak and randomly oriented activity in the premigratory period.

2) Then a more or less south-directed activity.

3) Maybe slight directional shifts during the autumn – either following the course of the migratory route (compass orientation) or directed towards goal areas shifting down the migratory route (navigation). The »standard direction« of the Whitethroat *Sylvia communis* is supposed to shift from SSW to SE in the course of the autumn. The corresponding shift in the Lesser Whitethroat *Sylvia curruca* should be from SE to S (e.g., WILLIAMSON 1964).

4) Concerning the spring experiments: If the homeward orientation from the wintering ground is program-

is involved, the March goal area should be in between Denmark and the African wintering ground – and thus produce a southerly orientation. MATERIAL AND METHODS

med as a compass reaction, the Marchdirections should be more or less northerly. On the contrary, if goal navigation

The experimental birds were Whitethroats and Lesser Whitethroats trapped at Blåvand, Western Jutland (Denmark). They were all supposed to be local juveniles – i.e., offspring of breeding birds in the trapping area. All experiments except the spring experiment – and the autumn experiments presented in Fig. 10 – were carried out at Blåvand.

The birds were trapped in mistnets from July 27 to August 23, 1971 (Table 1). Until September a few birds died and several escaped, but from September 13 only 10 Whitethroats and 1 Lesser Whitethroat were in experiment. Apart from a single escape, these birds were kept in captivity and survived to the following spring in May when they were released.

At Blåvand the birds were kept in indoor cages in the natural (outer) light: dark rhythm – and at the outer temperature. Except for the short ex-



- r<0.10 or ≤5jumps
- r = 0.10 0.29
- r = 0.30-0.49
- r≥0.50

Fig. 1: Blåvand, July 31. Each dot denotes the direction and concentration (r) of an individual mean vector. On the basis of the individual directions two sample mean vectors are constructed. The hatched sample mean vector ($350^\circ - 0.474$) includes all individual directions, whereas the full-drawn sample mean vector ($354^\circ - 0.596$) omits the lower category of individual mean vectors (r > 0.10, or < 5 jumps). The full-drawn and dotted cross bars within or ahead the sample mean vectors show the 0.01 and 0.05 significance border of the Raleigh-test.

Blåvand, 31/7. Hver prik viser retningen og koncentrationen af én forsøgsfugls opspring. På basis af disse enkeltretninger er der konstrueret 2 slags gennemsnitvektorer, hvoraf den stiplede vektor inkluderer alle enkeltretningerne, medens den fuldt optrukne vektor udelader den mere problematiske del af enkeltretningerne (de små pletter).

perimental periods the birds were not able to see the starry sky.

On November 1 the 10 birds were transported to Copenhagen where they were kept in a 12-hour light: 12-hour dark rhythm (light 0600 - 1800) and at $25^{\circ}C$ – in order to simulate the conditions of their African wintering ground as much as possible. Already on February 24 1972 several birds displayed migratory restlessness during the night, and nocturnal activity was frequently recorded until March 17, when outdoor experiments were carried out at Tisvilde (60 km NNW of Copenhagen). No other spring experiments were carried out due to the very few suitable nights (starry sky, and no moon) from the end of February to the beginning of May when the birds under natural conditions should have arrived at the Danish breeding ground.

The birds were fed on mealworms, bananas and dried food. They were fat and lively, but their tail and wing feathers became fairly worn. In several of the birds the tail feathers were moulted several times during the winter.

The nocturnal activity was recorded by means of our modification of the Emlenfunnel (RABØL 1972, PETERSEN & RABØL 1972). The estimated number of independent jumps in the sixteen $221/2^{\circ}$ sectors follows the transformation: Jumps = 0.4 x 2 c.d.-1.



Fig. 2: Blåvand, Aug. 18 and 19. The sample mean vectors are $45^{\circ} - 0.204$, and $51^{\circ} - 0.094$ respectively.

Blåvand, 18-19/8.

For every bird is calculated an individual mean vector which informs about the mean direction and the concentration (r) of the activity. At the figures the individual mean vectors are put in four groups (Fig. 1) - a fifth group, the zero vector, is of course not shown (only 3 out of 123 experiments produced a zero vector). Sample mean vectors are constructed on the basis of the individual mean directions. A hatched sample mean vector includes all directions, whereas a fulldrawn sample mean vector omits the lower category of individual mean vectors. The 0.01 and 0.05 significance borders of the Raleigh test (BATSCHELET 1965) are drawn in connection with the sample mean vectors as a fulldrawn and a dotted cross bar.

The duration of the experiments was always one hour, and all experiments started $1\frac{1}{2} - 3$ hours after sunset – except on October 30, when the experiments first started 01.55 due to the presence of the moon until that time. There were no or very few clouds on the sky any night except on August 22 and September 21, when the sky was partly overcast. The experimental nights and the number of experiments are shown in



Fig. 3: Blåvand, Aug. 21, 22 and 23. The sample mean vectors are $34^{\circ} - 0.641$, and $40^{\circ} - 0.605$ respectively.

Blåvand, 21-22-23/8.



Fig. 4: Blåvand, Aug. 24. The sample mean vectors are $120^{\circ} - 0.345$, and $158^{\circ} - 0.418$ respectively.

Blåvand, 24/8.

Table 1. As seen from the figures some of the nights are put together in groups.

In addition to the Blåvand experiments in August similar experiments are shown at Hjelm with local juvenile Whitethroats (Fig. 10). The same northern tendency as seen at Blåvand until August 23 is obvious.

RESULTS

The individual mean vectors and the sample mean vectors from different nights (or groups of nights) are shown at the figures.

In the course of the autumn there is a tendency to a shift in the sample mean vector from north over northeast to southeast and then to random. Making use of the parametric two-sample test mentioned in BATSCHELET (1965, p. 33) the statistical probabilities of coincidence for the following fulldrawn sample mean vectors are found to be: July 31: August 21 + 22 + 23, p > 0.10 (F = 2.85, and p = 0.10 corresponds to F = 2.99). August 21 + 22 + 23: September 21. 0.001 . The random orientationin Figs 5 and 7-8 may, however, also be perceived as 180° bimodal distributions (with small concentrations) towards ESE-

88 Orientation Experiments

Table 1: The date of trapping for the experimental birds. The right column shows the number of experiments on the single nights. The number of Lesser Whitethroats is mentioned in the paranthesis.

Fangstdatoen for forsøgsfuglene. Den højre søjle viser antallet af forsøg på de enkelte nætter. Tallet i parentes viser antallet af Gærdesangere i forsøg.

Date of experiment	Date of trapping										Total
······	27/7	30/7	31/7	10/8	12/8	17/8	19/8	21/8	22/8	23/8	
31/7 18/8 19/8 21/8 22/8 23/8 24/8 13/9 14/9 21/9 14/10 30/10 17/3 Total	5 2 1 1 3 3 2 3 2 3 5	4 3 1 2 1 1 2 2 1 1 3	3 1 1 1 2 2 1 2 3	1 1 1 1 1 1 1	1	1 1 2 1 1 2 2 2 2 2 2 2	4 1 1 4	1	4	1 1 1 1 1 1 2	12 (3) 8 (1) 7 2 (1) 4 8 (2) 3 8 (1) 10 (1) 11 (1) 8 10 (1)

WNW, SSW-NNE, and E-W, respectively. Two single birds on October 14 and October 30 thus showed bimodal activity patterns towards NNE-S-SSW, and ESE-SE – WNW-NW, respectively.

There seems to be a general tendency to decreasing concentration (r) in the sample mean vectors in the course of the autumn. However, this tendency cannot be »proved« statistically due to the small sample size.

The concentration of the individual mean vectors also seems to be decreasing through the season. Arithmetic means for the concentration of the individual mean vectors at Figs 1-8 are (r based on 5 jumps omitted): July 31 (0.43), Aug. 18+19 (0.52), Aug. 21+22+23 (0.41), Aug. 24 (0.40), Sept. 13 + 14 (0.36), Sept. 21 (0.46), Oct. 14 (0.29), and Oct. 30 (0.29). The corresponding value for March 17 is 0.43. If the con-



Fig. 5: Blåvand, Sept. 13 and 14. The sample mean vector is 178° – 0.080. *Blåvand, 13-14/9.*



Fig. 6: Blåvand, Sept. 21. The sample mean vectors are $144^{\circ} - 0.524$, and $147^{\circ} - 0.475$ respectively. *Blåvand*, 21/9.



Fig. 7: Blåvand, Oct. 14. The sample mean vectors are $190^{\circ} - 0.203$, and $214^{\circ} - 0.171$ respectively. *Blåvand*, 14/10.

centrations in the two periods Aug. 18-Sept. 21: Oct. 14-Oct. 30 are compared (Mann-Whitney U-test, one-tailed, SIEGEL 1956) the difference is highly significant (p = 0.0015).

Apparently, also the *activity* (number of jumps) is decreasing with the time. The mean number of jumps for the following



Fig. 8: Blåvand, Oct. 30. The sample mean vector is 79° – 0.297. *Blåvand, 30/10.*

nights or periods is: July 31 (352.9), Aug. 18-Sept. 21 (204.0), Oct. 14+30 (72.3), and March 17 (17.6). The most relevant comparison should be *Aug.* 18-Sept. 21: *Oct.* 14+30. The difference between these two groups, however, is not significant (p = 0.12, Mann-Whitney).



Fig. 9: Tisvilde, March 17. The sample mean vectors are $166^{\circ} - 0.153$, and $108^{\circ} - 0.103$ respectively. *Tisvilde*. 17/3.

In a material like that presented, seasonal trends in groups of individual mean vectors or activities are extremely difficult to demonstrate. The number of experimental nights is small, and the variations from night to night are not only dependent on the season, but also varies according to, e.g., time of the night and the weather. Furthermore, the number of birds is not the same on all nights. The application of a Mann-Whitney U-test with *one bird* as the statistical unit is thus not very appropriate.

DISCUSSION

1) The northern orientation.

The dominance of northern directions in July and August can hardly be considered as an accident. Furthermore, in some of our earlier experiments with autumn migrants trapped en route, clear northern tendencies were also observed in the very beginning of the migratory season (RABØL 1970, RABØL and PETERSEN 1971).

A more or less northern orientation in the autumn is normally designated reverse orientation (migration). Reverse means 180° displaced (opposite) the »standard direction«. Many species of chats and warblers are known to perform reverse migration. The following examples could be mentioned: Redbreasted Flycatcher Siphia parva (NISBET 1962, RABØL 1969a, GATTER 1972), Barred Warbler Sylvia nisoria (NISBET 1962, RABØL 1969b), Blackcap Sylvia atricapilla (HILDEN 1969). and several Phylloscopuswarblers (RABØL 1969c, SHARROCK 1972). Normally, adult birds constitute a very small part of these »reverse birds«. Sometimes, as in the case of Barred Warbler in Great Britain (DAVIS 1967) only juveniles seem to be involved. It is not known how great a proportion of the total juvenile population of one species or another actually does perform reverse orientation, and how long time this migration normally lasts. reverse However, reverse migration to Western Europe probably involved a significant part of the West-Sibiric populations of Yellowbrowed Warblers Phylloscopus inornatus and Richard's Pipit Anthus novaeseelandiae in the autumn of 1967 (e.g., FERGUSON-LEES and SHARROCK 1967, SHARROCK and FERGUSON-LEES 1968, and SMITH 1968). Sometimes the reverse migration continues for months covering of several thousands distances of kilometres - e.g., in the case of Pallas Leaf Warbler Phylloscopus proregulus (ROOKE 1967, RABØL 1969c).

Maybe it is typical that many (most?) of the young chats and warblers in the very beginning of the autumn are reversely oriented. Certainly, a 180°-mistake in the establishment of the »standard direction« could not be the single (or even a good) explanation of the bulk of northward orientation at Blåvand and Hjelm in July-August. A possible *function* could be extension into and exploitation of areas suitable for resting and feeding in the end of the summer and in the beginning of the autumn before the start of the migration. »true« autumn Possible parallels could be 1) the northward moult migration of juvenile palaearctic and nearctic geese (SALOMONSEN 1968), 2) the reverse orientation and movements of Chaffinch Fringilla coelebs at the Kurisches Nehrung in the automnal premigratory period (DOLNIK and BLYUMENTAL 1967), and 3) the northward »Zwischenzug« of the Starlings Sturnus vulgaris of Switzerland (Studer-Thiersch 1969).

WILTSCHKO and HÖCK (1972) describe a NNW-»nonsense«-orientation in caged Robins *Erithacus rubecula* in the evening, i.e., just before the »true« nocturnal migratory restlessness. This reaction occurred, however,





Fig. 10: Hjelm, Aug. 17-18, and 24. Hjelm is a little island in Kattegat, and all experimental birds – being juv. Whitethroats from the local breeding stock – were trapped on Aug. 17-18. The number of experiments were: 17/8 (13), 18/8 (5), and 24/8 (6). 4 of the 24/8 – birds were also in experiment on 17/8. In the uppermost figure the two sample mean vectors are 352° – 0.270, and 0° – 0.207 respectively. Obviously, the sample mean vectors offer poor descriptions of the distribution of the individual mean

both in the spring and autumn and was tentatively interpreted as being directed by the handling of the birds. Otherwise, there could be a motivational relationship between the reactions prior to the period of nocturnal migratory restlessness and the reactions in pre-migratory period and in the beginning of the migratory season.

The exact departure period of the Sylviawarblers from their breeding area at Blåvand is not known. At Hesselø the great majority of local Whitethroats left the island in the period Aug. 8-16 in 1964 and 1965 (RABØL and PETER-SEN unpubl.). In the period of July 24 – Aug. 17 1972 outdoor experiments on the nocturnal acin 3 Whitethroats and 3 Lesser tivitv Whitethroats were carried out at Blåvand. All the birds were juveniles and offspring of local breeding birds. One bird displayed nocturnal restlessness on the night of July 28-29, and on most of the following nights from Aug. 4-5. A second bird sometimes showed a nightly activity from Aug. 9-10 and onwards. Three of the other 4 birds never showed any significant nocturnal activity in the period. At least July 31 should thus be well before the normal time of departure.

2) The development in the sample mean vector.

The shift in the sample mean vector in the course of the autumn from north over northeast to southeast and then to random is not easily explained – neither as a compassdirection shift (following the migratory route) nor as navigation towards a wandering goal area in the migratory route.

The random orientation in October could be a result of the long-lasting captivity in which the birds were prevented from seeing the starry sky. However, e.g., EMLEN and WILTSCHKO report on clear (»standard«) orientation in birds kept in captivity for a much longer time.

vectors, which seem to be grouped around two peaks (20° and 210°) roughly displaced 180° from each other. The observed distribution is, however, not significantly different from a uniform distribution (> 0.10, p. 26-27 Kuiper's modification of Kolmogorov, BATSCHELET 1965). The sample mean vectors of the bottom figure are 326° - 0.680, and 312° - 0.454 respectively.

Hjelm, 17-18/8 og 24/8. Forsøg med unge Tornsangere fra den lokale ynglepopulation.



Lesser Whitethroat Sylvia curruca at nest. Photo Benny Génsbøl. Gærdesanger Sylvia curruca ved rede.

EMLEN (1969) suggest that the sight of the starry sky in the pre-migratory period is necessary for the establishment of the southward »standard« orientation in the autumn migratory season in the Indigo Bunting Passerina cyanea. Probably, all the birds used in our experiments were, however, fledged at least 2-5 weeks before the capture. Thus »stardeprivation« should not be an obvious reason for the weak reactions in the »standard direction«.

The random orientation at Blåvand on October 14 and October 30, and at Tisvilde on March 17 could also be caused by the great distance between the actual position and the actual goal area (the place where the bird »should be« at the present time). This view seems at first sight not very rewarding but the following examples could support it.

a) SAUER and SAUER (1960) investigated the orientation of Blackcaps and Garden Warblers *Sylvia borin* in a planetary. In a single Blackcap, *dis-orientation* (random orientation) occurred when the starry sky was »displaced« 4-11 hours towards E or W, whereas com-

pensation occurred within 1-6 hours displacements, and migration-conflict (i.e., bimodal standard – reverse orientation) occurred when the stars were displaced 10-12 hours.

b) At the end of September 1970, 16 migrant chats and warblers were transported from Denmark to Ithaca, New York, USA, i.e., the birds received a western displacement in the order of magnitude of 5 hours. Few days after the arrival S.T. EMLEN performed outdoor experiments with the birds under a starry sky. All 16 birds were tested on 5 different nights, but »none of them displayed any strong directional tendencies at all« (EMLEN in litt.). This presumably (also) means that the sample mean vectors were small and insignificant. Unfortunately, none of the USA-transports were in experiment at the trapping place in Denmark (Christiansø), but 13 out of 15 birds of the same species trapped and tested here a week later displayed clear orientation in the southern sector between SE and SW (RABØL unpubl.).

In both examples mentioned above disorientation seemingly occurred (quite unexpected) following several hours of displacement. The distances covering these displacements are roughly the same as the distance from Blåvand, Denmark, to the presumed normal position of Whitethroats in the northern part of Africa in the second half of October (and in March).

The random (or bimodal) orientation in October could also be interpreted as due to cessation of »true« migratory activity (the birds have »arrived« at their African wintering ground).

Possibly, all this discussion originating from three obscure October and March experiments is not at all very rewarding – at least not as attempts to an explanation of the present results.

3) The March experiment.

The obscure spring experiment could be »explained« as outlined above. None of the expectations mentioned in the »Introduction« are met.

SUMMARY

Orientation experiments with a group of juvenile Sylvia-warblers trapped and experimented with in the breeding area are presented. The experimental time covers both the pre-migratory period and the whole autumnal migratory season. Furthermore, some experiments were also carried out in the following spring.

The orientation in the pre-migratory period and in the very beginning of the migratory season was *northerly* and then shifted in the course of the autumn over northeast towards southeast and then to random. The spring experiments also showed a random orientation.

The phenomenon and significance of the northern (reverse) orientation is discussed – as is the random orientation. Reverse orientation (migration) is of common occurrence in the Passerines in the autumn. However, the bulk of reverse migration in the present experiments was surprising. A possible function could be exploitation of areas »north« of the breeding area before the »true« migration goes on. The random orientation could be considered as a breakdown of the orientational system due to the long time in captivity and the increasing discrepancy between actual and »programmed« position.

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DANSK RESUME

I juli-aug. 1971 indfangede vi unge Torn- og Gærdesangere af den lokale ynglefugle-population ved Blåvand Fuglestation. Disse fugle blev nu anvendt i en række orienteringsforsøg ved Blåvand i tiden frem til 30/10 (Tabel 1). I det følgende forår udførtes endnu 10 forsøg ved Tisvilde, efter at fuglene havde tilbragt en melorme og banan-rig vinter på Zoologisk Laboratorium i København. Først i maj 1972

Formålet med forsøgene var at registrere eventuelle retningsændringer i efterårets løb, samt orienteringen om foråret. Da nogle af forsøgene blev udført sidst i juli og midt i aug. før eller lige i begyndelsen af det forventede efterårs-borttræk fra Blåvand, havde vi regnet med, at den natlige aktivitet her ville være svag og u-orienteret. Efterhånden skulle denne (forventede) u-orienterede aktivitet så gå over i noget mere eller mindre SE-SSW-rettet, d.v.s. forløbe i »normaltrækretningen«. For forårsorienteringens vedkommende havde vi ventet (håbet på) enten: 1) »Nordlige« retninger hvis trækket var programmeret som et »nord«gående kompas-træk fra det afrikanske vinterkvarter »hjem« mod Danmark, eller 2): »Sydlige« retninger - hvis trækket var programmeret som navigation mod et bevægeligt »målområde«, der i så fald skulle være et sted (mod »syd«) mellem Afrika og Danmark.

Ingen af disse smukke forventninger slog rigtigt til, og i stedet optrådte to ret så uventede reaktioner:

1) Nordlig (omvendt) orientering i slutningen af sommeren og i begyndelsen af efteråret (se Figs. 1-3, 10). Islættet af omvendt træk er her så dominerende, at man ikke bare kan betragte det som en 180°-fejl i orienterings-mekanismen. En mulig funktion kan være en fødemæssig udnyttelse af områder, hvor arten yngler mere sparsomt eller slet ikke yngler. I så fald kan det betragtes som en parallel til det nordgående fældningstræk af diverse gåsearter (SALOMONSEN).

Omvendt træk (om efteråret) er iøvrigt et hyppigt forekommende fænomen hos spurvefuglene – det kendes bl.a. hos Høgesanger og Lille Fluesnapper (se bl.a. RABØL 1969a og 1969b). Sådanne »omvendte fugle« – og dette gælder naturligvis endnu mere udpræget Fuglekonge sangere o.l., der kommer helt fra Sibirien – er dog ganske indlysende på afveje. Hvad der muligvis begyndte som en mindre og måske formålstjenlig bevægelse i den omvendte retning er her endt som et fejlslagent træk, hvor endestationen sikkert som oftest hedder Atlanterhavet.

2) Den nordlige (omvendte) orientering kører i løbet af aug. over NØ til SØ – hvorefter den i oktober ender med at blive *u-orienteret* (Fig. 1-8).

Årsagen til den u-orienterede adfærd sidst på efteråret – og igen i marts – skyldes rimeligvis nedbrydning af orienterings-mekanismen. Denne bryder næppe bare sammen som følge af det lange fangenskabs-ophold i sig selv, men snarere fordi fuglen så at sige ikke er i stand til at være i overensstemmelse med sit program. Man kunne således tænke sig, at uoverensstemmelsen mellem fuglens aktuelle position i Vestjylland og dens naturlige position for årstiden (Sydeuropa -Nordafrika) efterhånden blev for stor - med en orienteringsmæssig kollaps som følge. Dette lyder måske lidt søgt. Umiddelbart bedømt skulle det nærmest være lettere at navigere mod et punkt jo længere dette er væk. Hvis vi f.eks. flyver til New York opfatter vi meget let ved hjælp af vort »indre ur« den vestlige forflytning, der bl.a. giver sig udslag i at det bliver 5 timer »for sent« mørkt om aftenen. Vi er således ganske klar, at vi skal »trække« mod Ø for at komme hjem til Danmark igen. Flyver et menneske derimod fra Chr.ø til Blåvand skal vedkommende have et godt »indre ur« for at kunne opfatte, at solnedgangen her sker 25-26 min. senere end på Chr.ø. Tidligere forflytningsforsøg med fugle viser at fuglene vil kompensere tydeligt for en forflytning af vejlængden Chr.ø – Blåvand. I sept.okt. 1970 forflyttede vi 16 fugle fra Chr.ø til New York. Vi forventede naturligvis en kraftigt og entydig kompensation mod ØNØ - ØSØ. Det helt uventede skete imidlertid. Fuglene var komplet u-orienterede. Åbenbart opfatter mennesker og trækfugle ikke forflytninger på samme måde.

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