The orientation of Pallas's Leaf Warbler *Phylloscopus proregulus* in Europe

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(Med et dansk resumé: Fuglekongesangerens Phylloscopus proregulus *orientering i Europa)*

THE MIGRATORY PROGRAMME

One of the most puzzling problems in present orientational research is whether the routes of migratory birds are hereditarily programmed on the basis of *one-direction orientation* only, or whether *bi(multi)coordinate navigation* is also involved (e.g. Wallraff 1972).

Definitions

One-direction (or compass) orientation denotes orientation at a fixed angle determined by an extrinsic stimulus. This stimulus could be the azimuth of the sun (Matthews 1968) or the polar star (the axis of rotation, Emlen 1970), or the inclination of the earth's magnetic field (Wiltschko *et. al.* 1971), for example.

Bicoordinate navigation involves the measurement of the values of two parameters. Nothing is known about the nature of these parameters, but time and polar star altitude could be imagined, for example (Rabøl 1970). The two measured values are compared with the corresponding values at the actual goal (the bird 'knows' these parametric values of the goal). These values could be considered as coordinates in a system where the parameters constitute the axes. The bird is now able to calculate the direction from the actual position towards the actual goal. This direction is then settled in relation to one or more extrinsic stimuli and the process of one-direction orientation is carried out as the last step in the process of bicoordinate navigation.

The common view

The commonly accepted view seems to be that juvenile birds are capable only of one-direction orientation on their first autumn migration, whereas the adult (experienced) birds may also navigate. This view was apparently established through a generalization from the interpretation of displacement experiments carried out especially by Perdeck (1958).

Compensation for displacement

Until recently it was thought possible to distinguish and demonstrate one-direction orientation and bicoordinate navigation by the reactions following displacement of migrating birds (e.g. Perdeck 1958, and Rabøl 1969a). If the displacement was followed by a directional shift towards the original migratory route or the wintering ground, the presence of bicoordinate navigation was demonstrated.

It was thus in contradiction to the common view that Evans (1968) and Rabøl (1969a, 1970, 1972) found that juvenile chats and warblers on their first autumn migration also compensated for displacement and oriented towards their migratory route. Furthermore, Rabøl (1969a, 1970, 1972) concluded that the juvenile birds navigated towards goal areas on the migratory route. This interpretation was met with pronounced scepticism (e.g. Walraff and Wiltschko, mentioned in Rabøl 1972).

Heredity and navigation

Navigation towards points where the bird has never been before involves hereditarily fixed goal areas. At first sight it seems improbable that a bird should be born with the knowledge that the goal area e.g. on Oct. 15 should be Spain in the vicinity of Barcelona, and on Nov. 10 Timbuctoo on the southern border of the Sahara. Of course, heredity does not work in such a way, but one could imagine a moving goal area consisting of intrinsically programmed shifts in the values of at least two parameters as a function of the season. Such a hereditarily fixed programme may still seem improbable, but should be compared with the most simple programme imaginable: programmed shifts in direction in the course of the season. Most migratory routes are doglegged, and the birds cannot use the same fixed direction during the whole season.

In conclusion, a programme based on bicoordinate navigation towards goal areas is only a little more complex than a programme based on one-direction orientation only — and the advantages of a navigation programme are obvious (accurate compensations for the numerous displacements caused especially by the wind or by errors in the establishment and execution of one-direction orientation in the open system).

Compensation and navigation

As pointed out by Wiltschko, for example (in Rabøl 1972) there is, however, no urgent need for the presence of bicoordinate navigation towards a goal area for the production of an appropriate compensation. The distance and direction of the displacement may be more or less accurately measured by the bird, either by integration of linear and angular accelerations twice (Barlow 1964), or by means of bicoordinate navigation from the new position in relation to the point from which the displacement took place. A compromise between such reverse vector- or bicoordinate navigation towards that point on the one hand and the standard direction (established by means of one-direction orientation) on the other hand might produce an appropriate compensatory reaction.

Wiltschko may of course be right, but if the compensatory reaction of juveniles could be explained without bicoordinate navigation towards goal areas then the same alternative interpretation could be applied to all claimed proofs of bicoordinate navigation towards the migratory route or the wintering ground in adult birds — including the adult Starlings *Sturnus vulgaris* in Perdeck's (1958) famous displacement experiments.

Proofs of navigation

Such considerations make it difficult to prove the presence of bicoordinate navigation in the process of bird migration. Wallraff (1974) — who believes in bicoordinate navigation in experienced birds — tries to do this in a theoretical way, and he finds some evidence in the case of pigeon homing. An entirely different approach may be the analysis of the tracks of vagrant migrants.

As mentioned, for example by Rabøl (1969b) and Sharrock (1974) most of the autumn passerine vagrants to the British Isles occur in certain areas or along certain tracks. These facts are often indicative of reverse orientation, i.e. the birds are moving in a direction approximately opposite to their standard direction. Furthermore, the great majority of such reverse birds are juveniles on their first (and presumably last) autumn migration.

In most cases it is impossible to say whether the reversal of orientation originates in a programme based on one-direction orientation or bi(multi)coordinate navigation. In some species the distance between Northwestern Europe and the breeding ground is, however, so great that the reverse orientation will differ significantly according to which of the two programmes are operating.

PALLAS' LEAF WARBLER IN EUROPE

Pallas's Leaf Warbler *Phylloscopus proregulus* appears to be an appropriate species to investigate. The nearest known breeding area is Novosibirsk in Siberia, and the species is recorded almost annually in Europe from late September to the end of November.

We shall deal in particular with the autumns of 1968 and 1974 which produced the highest number of European records.

The 1968 records

At least 33 birds were recorded (Fig. 1). Apart from the two Danish and Polish birds (Dyck *et. al.* 1970, Wiatr 1970) the records are from two main areas: 1) Southwestern Finland and central Sweden, 13 birds between Sept. 29 and Oct. 19 (Hildén 1968, Broberg 1970). The first three birds arrived on Sept. 29, and the average date is about Oct. 4 - 5 (Hildén does not date all the Finnish records). 2) The British Isles, especially Southeastern and Eastern England, 18 birds between Oct. 18 and Oct. 30 (Smith *et al.* 1969). The average date of all the records is Oct. 21. The British records may be subdivided into four: a) Kent and Sussex, 7 birds between Oct. 18 and Oct. 30, b) Yorkshire, Lincolnshire and Norfolk, 7 birds between Oct. 19 and Oct. 27, c) Scilly and Clear, 3 birds Oct. 21 to Oct. 23, and d) Aberdeenshire, 1 bird Oct. 22. The first bulk of arrivals on Oct. 18 to Oct. 20 clearly falls at the same time in a) and b). In Fig. 1 thesign denotes countries or bird observatories where the species was not recorded (Hildén 1968, Lindholm *et al.* 1972, Holgersen 1969, Vauk

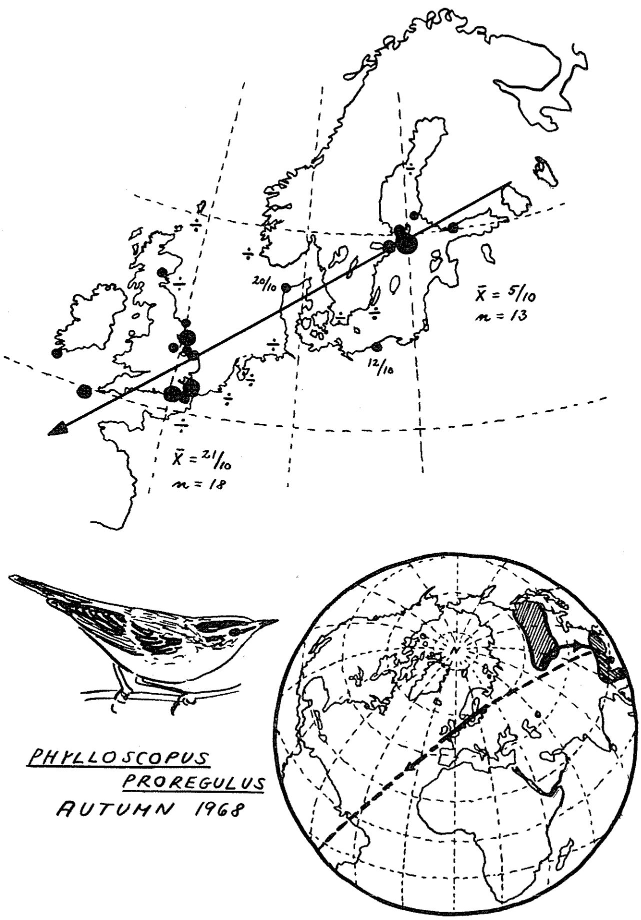

Fig. 1. The upper figure shows the records of Pallas's Leaf Warbler *Phylloscopus proregulus* in Northwestern Europe in the autumn of 1968. The number of records (n) and the average dates of the Finnish-Swedish and the British birds are shown. Ashows a country or a station where the species was not recorded. The pattern in area and time makes a progress towards SW-WSW very likely. In the lower figure are shown the breeding area in Siberia, the presumed migratory route of the most westerly population, and the wintering ground in China-Vietnam. If the SW-WSW track in Europe is extended in both directions as a great circle, this goes close to or through the breeding area, the normal migratory route, and the wintering ground.

Forekomsterne af Fuglekongesanger i Nordvest-Europa i efteråret 1968. Over 30 fugle blev set, og forekomsterne fordeler sig tidsmæssigt langs en linie forløbende mod SV-VSV. På den lille figur over Jorden ses artens yngleområde, trækrute (for den vestlige bestand) og vinterkvarter. De europæiske forekomster synes at forekomme på en storcirkel-kurs væk fra vinterkvarteret (eller mod vinterkvarteret den »gale« vej rundt om Jorden).

1970, Smith *et al.* 1969, Lippens and Wille 1972, and Herder *in litt.*).

The differences in the dates of arrival in Finland (Sweden) and Britain correspond well to known speeds of progress of normal migratory movements of comparable species, e.g. Garden Warbler *Sylvia borin* and Blackcap *Sylvia atricapilla* (Klein *et al.* 1973).

Hence the pattern of the records in area and time strongly suggests a direction of progress towards SW-WSW.

The 1974 records

At least 30 birds were recorded, and three 'waves' may tentatively be distinguished (Fig. 2). The first birds arrived at Lågskär, Finland on Sept. 29 and at Kabli, Estonia on Oct. 2 (Holmström *in lett.*). The two next were in Northumberland, England on Oct. 3 and 4 (Smith *et al.* 1975). Then two birds appeared at St. Færder, Norway on Oct. 5 (Michaelsen and Ree 1975). Five more birds were recorded in England from Durham to Scilly in the following period from Oct. 9 to Oct. 14 (Fig. 2 A).

The next 'wave' was initiated with at least five different birds at St. Færder, Norway on Oct. 15 - 18, and a single bird at Utsira, Norway on Oct. 17. Then five more birds were recorded from Oct. 21 to Oct. 24 at Utsira, in Denmark, and in England (Fig. 2 B).

The last — and much more slowly moving — 'wave' produced two birds at Akeröya, Norway on Oct. 27 and at Mierzeja Wislana, Poland on the same date. Then single birds appeared at Beachy Head, England on Nov. 3 and at Ottenby, Sweden on Nov. 6 (Holmström *in litt.*). Four more birds were finally recorded in Hampshire and Sussex, England and at Rijsterbos, Holland on Nov. 17 to 24 (Smith *et al.* 1975. Tekke *in litt.*) (Fig. 2 C).

It should be mentioned that no Pallas's Leaf Warbler was recorded at Heligoland,

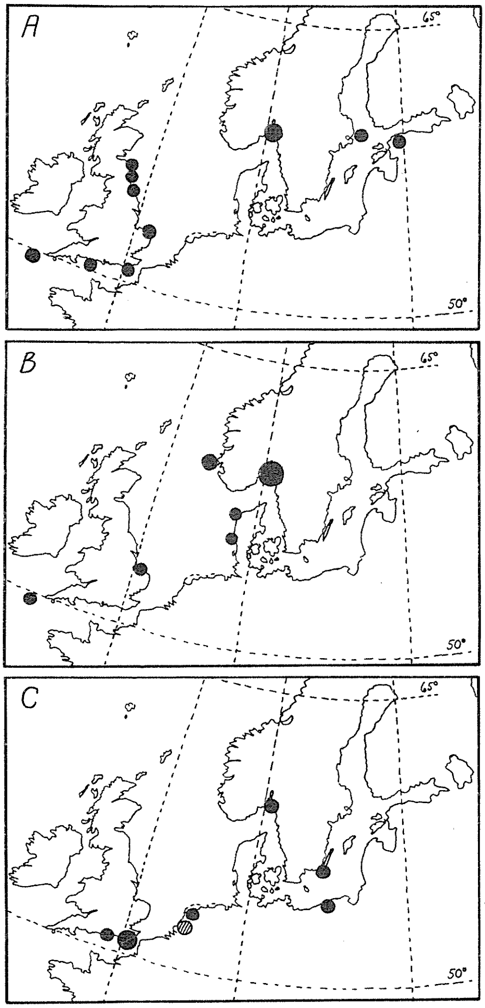

Fig. 2. The 1974 records of Pallas's Leaf Warbler in Northwestern Europe. A shows the first 'wave' between Sept. 29 and Oct. 14. B the second 'wave' between Oct. 15 and Oct. 24, and C the rest of the records between Oct. 27 and Nov. 24 – including the Dutch winter record (hatched circle). *Forekomsterne af Fuglekongesanger i Nordvest-Europa i efteråret 1974. Der blev set ca. 30 fugle. A, B og C viser de tre »ankomst-bølger«. Man bemærker, hvorledes den tidsmæssige adskillelse af de østlige og vestlige forekomster ikke er så udtalt som i 1968.*

Germany in the autumn of 1974 (Vauk 1975). Furthermore, a single bird wintered in Waageningen, Holland from Jan. 20 to March 23 1975 (Tekke *in litt.*).

The 1974 records, too, are clearly distributed along a SW-WSW track, but compared to the 1968-track the 1974-track is situated more to the north – especially over Finland and Scandinavia. The main track is probably north of the Åland archipelago, Finland and passes through Southern Norway. The British records are just a little more displaced to the north compared with the 1968 records.

The 1974 movement proceeded faster than the 1968 movement. The mean date of all the Scandinavian, Finnish, Polish, and Estonian records is Oct. 16 – compared to the British and Dutch mean date of Oct. 25. The distance between the two areas of records however, is also considerably smaller in 1974 than in 1968.

Other autumns

The SW-WSW trend is essentially the same in other autumns though composite material (e.g. Rooke 1966) shows a greater scatter than the records from a single autumn. In some other autumns the species is also recorded in very small numbers in the Southern Baltic region (especially Southern Sweden), at Heligoland, and in Holland, Belgium, and Northern France. Until 1974 the species was recorded very rarely in Norway. There seem to be only four records from Revtangen (Bernhoft-Osa 1964, Michaelsen and Ree 1975). The species is almost unknown in Scotland and Ireland. There seem to be only two Scottish records – the first one was an early Oct. bird from Fair Isle in 1966 (Smith *et al.* 1967). The Irish 1968-record is the sole one.

The autumn of 1975 certainly produced more European records than in any previous autumn. At least 30 individuals were recorded in Britain (Christie *et al.* 1976) – the first bird at Fair Isle on Oct. 10. Most birds were, as usual, recorded in Southeast England. There were also records in Finland (at least 4), Sweden, Norway, and Denmark (1 trapped at Blåvand Oct. 25). Most data are, however, not yet available.

The SW-WSW direction

The question now is whether the SW-WSW orientation is real or just a result of one or several environmental influences. 1) Winds are known to displace and/or canalize migratory movements. A wind shifting from SE in Western Russia and Finland through E in Sweden and Norway towards NE-N in the North Sea may well produce a secondary SW-WSW 'orientation' in a primarily more or less westerly movement. Such wind conditions in fact prevailed at the end of Sept. and in the beginning of Oct. 1974 and may be at least part of the explanation of the actual progress — especially of the shift towards 'NW' compared to 1968 and other years. In the autumn of 1968 the winds in Finland and England were South- and Southeasterly just prior the the main arrivals in both areas. Probably, slight winddrifts occurred towards 'NW' from a main route of progression in a more southerly position. This main route, however, must still have been directed South of W. If wind drift played an important role in the distribution of the records, SE-winds should certainly produce many more records in Scotland. In conclusion, I find it highly unlikely that winddrift is responsible for the SW-WSW directed progress. 2) The distribution of observers and bird observatories in Northern and Western Europe is directed more or less ENE-WSW. Birds approaching from the east should thus acquire a secondary 'orientation' towards WSW. The small scatter of the records — especially in the autumn of 1968, and the almost complete lack of Scottich and Irish records are, however, difficult to understand in the absence of an active orientanation South of W with just a small directional variation around the mean direction. Furthermore, a South of W tendency is by no means present in all eastern vagrants in Northwestern Europe. In the Barred Warbler *Sylvia nisoria* and the Scarlet Rosefinch *Carpodacus erythrinus* a primary reverse orientation North of W is very obvious (Rabøl 1969 c, Sharrock 1974). 3) Rabøl (1969 a) and Sharrock (1974) mention the general tendency of several eastern vagrants towards late arrivals in the Southwestern part of Britain compared with Scotland and Eastern England. The question is whether this reflects a primary «sw-orientation in all cases or whether a secondary SW-'orientation' may (also) be involved. In his model (Fig. 110 C) Sharrock (1974) avoids assuming a progress South of W (= a primary orientation), but considers the primary reverse orientation as being about W. As the northern part of the population is supposed to leave the breeding ground earlier or is nearer to Europe than the southern part, the birds arrive earlier in Northeastern- than in Southwestern Britain. This is an example of secondary SW-'orientation'. An important question is whether the northern populations as a general rule leave earlier? In Denmark the northern races of Willow Warbler *Phylloscopus trochilus* and Yellow Wagtail *Motacilla flava* arrive later in the autumn than the southern races. In the case of the Yellowbrowed Warbler *Phylloscopus inornatus* — but not in Pallas's Leaf Warbler — the northern part of the breeding area is, however, nearer to Europe, and Sharrocks model may well hold partly true for this species. The hypothesis in its simple form, however, cannot be a significant explanation of the pattern of records of Pallas's Leaf Warbler in Northwestern Europe.

Much of the late arrivals of Barred Warbler, for example, in Southwestern Britain may be understood in terms of a directional scatter around a primary reverse mean direction (see Fig. 9 in Rabøl 1975). We have illustrated this point of view in Figs. 3 - 4. The later arrivals in Southwest Britain —

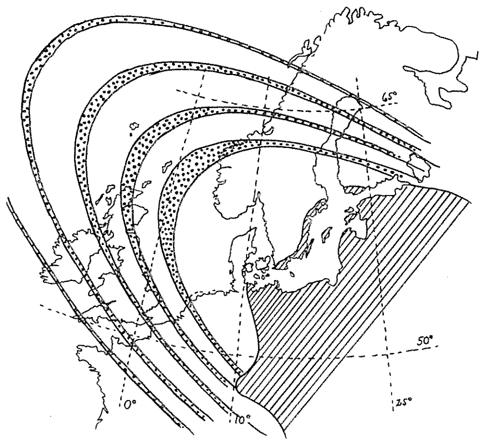

Fig. 3. Reverse migration towards 'NW' of the Barred Warbler *Sylvia nisoria*. The breeding area is hatched and extends further east- and southward. The lines denote isoclines with respect to time of progress, and the thickness of the dotted area in combination with the isoclines is a measure of the number of birds involved. The number of birds involved decreases with distance away from the breeding area. The actual progress of a single bird consists of several or many steps of migratory movements which on average are directed 'NW' — but with a certain variation around this mean direction. So, the largest number of birds and the fastest progress is along a 'NW' track in the middle of the area — with a small number of birds moving slowly on the outermost flanks of the mean track. This model describes very well the early and large number of birds in Scotland compared to the few and late records in Southwestern Britain (see the data presented by Sharrock 1974).

Omvendt træk mod »NV« af Høgesanger. Figuren skal tjene som model for de britiske fund af arten beskrevet af Sharrock (1974) og gengivet i Rabøl (1975). De »omvendte« fugle når tidligst frem til Skotland og i størst mængde, medens der når meget færre — og senere — fugle frem til Sydvest-England.

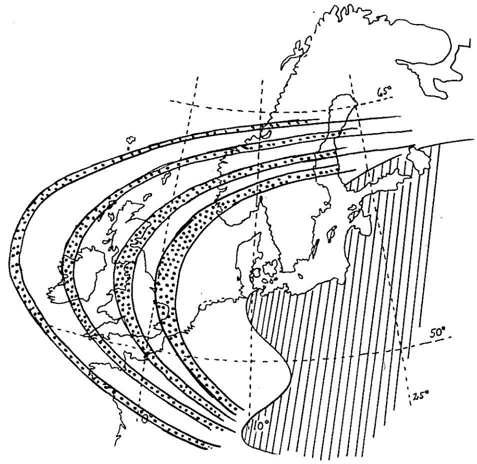

Fig. 4. Reverse migration towards 'W-WNW' of the Redbreasted Flycatcher *Siphia parva.* The model again describes very well the data presented by Sharrock (1974).
Omvendt træk mod »V-VNV« af Lille Fluesnapper. Også denne figur tjener som model for de britiske fund af arten (se Rabøl 1975).

especially in the case of the Barred Warbler — fit well into Sharrocks (1974) figures of the seasonal distribution of the records. If the orientation of Pallas's Leaf Warbler in Northwestern Europe is to be explained in a similar way, we may (as Rabøl 1969 b and Sharrock 1974) postulate a westward orientation. In this case the first arrivals should be on the Eastcoast of England (in Norfolk), with later arrivals in Southeast England and especially in Scotland. The latest records should be in the Southwest. However, the latest bulk of records is in the Southeast, not in the Southwest, and the earliest records are from Northeastern England (Fig. 2) and Fair Isle. Furthermore, the number of records in Scotland should be much higher than is actually the case. The principle of progression as outlined in Figs. 3 - 4, however, may match the actual records if the primary orientation is South of W. We shall return to this point below. 4) The conclusion should be that Pallas's Leaf Warbler shows a primary SW-WSW orientation in Northwestern Europe.

The next question is how this orientation is established?

REVERSE ORIENTATION

I consider the SW-WSW orientation of Pallas's Leaf Warbler in Europe as the result of successive 180° mistakes in the execution of the normal migratory programme.

Furthermore, I shall assume that the stimuli used for one-direction orientation have the same orientation through all Eurasia in relation to geographical or magnetic North, and also that the coordinates of the navigation system are running N-S and E-W. Small deviations from these conditions will not however, disturb the picture. The appropriateness of these expectations can, of course, be doubted (c.f. Walraff 1974).

The migratory route of Pallas's Leaf Warbler

In Figs. 6 - 8 are shown the breeding area and wintering ground of the subspecies of Pallas's Leaf Warbler recorded in Europe. Unfortunately, there seems to be no detailed knowledge of the migratory routes of the different populations of this subspcies.

If these routes follow great circles, the direction from the most westerly breeding area to the most northerly wintering ground (Shanghai) is from about 120° shifting to 140° (N = 0° = 360°). The great circle directions from the same breeding area towards the southern part of the wintering ground (Laos) are from 155° to 160°. It should be mentioned that the shortest way between two points on the surface of the earth is along a great circle, which divides the earth into two hemispheres. The equator and the longitudes are wellknown examples of great circles.

Normally, migratory routes do not follow great circles, but deviate more or less in order to avoid inhospitable areas such as high mountains, deserts and seas. For such reasons the normal migratory route of the most westerly population of Pallas's Leaf Warbler may be slightly curved from E or ESE over SE to SSE or even S (Figs. 6 and 8).

Principles involved in reverse orientation

The principles involved in reverse one-direction orientation and reverse bicoordinate navigation are outlined in Fig. 5. A problem arises in the case of bicoordinate navigation as the surface of the earth is spherical and not plane. Does the bird perceive the earth as a spherical body and make use of great circle bicoordinate navigation towards its goal? Walraff and Graue (1973) have investigated this problem in the case of transatlantic displacements of Homing Pigeons. The initial orientation (the departure directions) of the pigeons and the pattern of

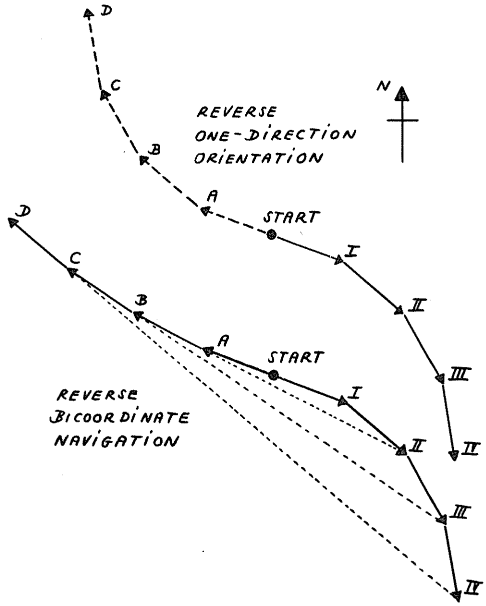

Fig. 5. The principles involved in reverse one-direction orientation and reverse bicoordinate navigation shown by theoretical examples. The normal migratory routes consist in both cases of four 'vectors' of equal length — from START to I (110°) from I to II (130°), from II to III (150°), and from III to IV (170°). Reverse one-direction orientation in each of the four steps produces a progress (START to A (290°), A to B (310°), B to C (330°), and C to D (350°)) which exactly mirrors the normal migratory route. In the case of reverse bicoordinate navigation the coordinates (parameters) are supposed to run N-S and E-W. At START the bird determines its position in relation to the goal area (I), but then makes a 180° mistake in the settlement of the one-direction orientation. The bird moves to A. After some time the 'goal area' has 'moved' to II, and the bird determines its position in A in relation to II. Again a 180° mistake occurs, and so on. The reverse track becomes START to A (290°), A to B (297°), B to C (304°), and C to D (311°).
Princippet i omvendt retnings-orientering og omvendt mål-område-navigation illustreret med eksempler. De to omvendte kurser bliver ikke helt identiske (fordi trækruten fra START til IV er retlinet), og hvis man forestiller sig processen bestående af endnu flere trin og skuepladsen henlagt til jordoverfladen, bliver forskellene endnu større (Fig. 6 - 8).

recoveries in relation to the release site gave no clear indication. On average, however, the directional deviations from the rhumbline course (a rhumbline is the straight line between two geogrphical positions on a mercator projection) towards the home loft were smaller than they were from the great circle route. I have therefore calculated the reverse tracks both for the case of rhumbline (Fig. 6) and great circle bicoordinate navigation (Figs. 7 - 8).

The reverse tracks

It is obvious that the hypotheses based on reverse one-direction orientation and reverse rhumbline navigation (Fig. 6) are not matched by the pattern of records. The reverse great circle navigation hypotheses (Figs. 7 - 8), however, describe the pattern of records in a fairly convincing way, but it is impossible to distinguish between these two latter hypotheses.

Both of the hypotheses in Figs. 7 - 8 make it difficult to understand the almost total lack of Scottish and Irish records. A probable explanation may be much reduced survival of birds involved in the most northerly tracks towards Europe. I have illustrated this possibility in Fig. 9. Comparisons should be made with the Yellowbrowed Warbler, whose breeding area is more northerly and extends much further towards Europe (westwards to the Petchora river). This species is much commoner in Scotland and Ireland than the Pallas's Leaf Warbler (Rabøl 1969 b, Sharrock 1974). The reverse tracks towards the wintering ground of the westerly population of the Yellowbrowed Warbler are directed towards Scotland without much contact with the Arctic Sea and the survival of birds involved in these northerly tracks is presumably much higher than in the case of Pallas's Leaf Warbler.

The answer to the question, whether the tracks of the Pallas's Leaf Warbler in Western Europe can be explained by reverse one-direction orientation or whether bicoordinate great circle navigation has to be assumed, then clearly is that the latter alternative is the more likely one. Especially so, if at least some of the corrections in Figs. 8 - 9 are included in the hypothesis. Several hybrid-models could also be proposed — e.g. reverse one-direction orientation at the beginning of the migratory season followed up by reverse great circle navigation (towards goal areas on the normal migratory route and/or the wintering area) during the later part of the season.

The hard core is that I believe in the presence of reverse great circle navigation as a significant part of the process and thus as an explanation of the geographical situation and direction of the SW-WSW track of Pallas's Leaf Warbler in Europe.

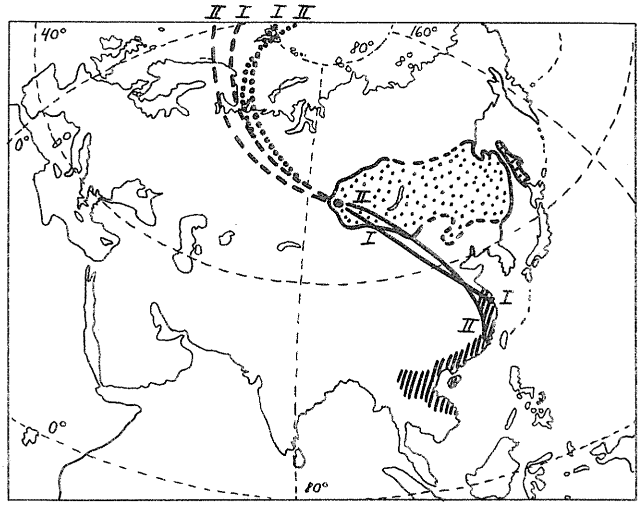

Fig. 6. The breeding area and the wintering ground of the subspecies of Pallas's Leaf Warbler *Phylloscopus proregulus proregulus* recorded in Europe. After Dementiev and Gladkov (1951 - 54). Two possible migratory routes of the most westerly population are shown. I follows a great circle, whereas II is slightly curved in order to avoid inhospitable areas. If these two normal migratory routes are programmed on the basis of one-direction orientation only, and the birds make successive 180° mistakes, the two reverse tracks should roughly follow the two dotted curves. If the birds make use of rhumbline navigation and navigate towards goal areas on the migratory routes, the reverse tracks will roughly follow the two dashed lines. If the rhumbline navigation in I is directly towards the wintering ground the reverse track will be even more northerly than the one shown. None of the reverse tracks shown match with the European records (Figs. 1 - 2). If the reverse tracks of more easterly populations are plotted this discrepancy grows even greater.

Der er vist to mulige trækruter af Fuglekongesangeren fra den vestligste del af yngleområdet mod vinterkvarteret (I og II). Hvis disse normaltrækruter er fastlagt ved hjælp af retnings-orientering, vil omvendt træk resultere i de to kurser vist med prikkede linier. Hvis trækruterne er fastlagt ved plan-navigation mod målområder (II) eller ved plan-navigation direkte mod vinterkvarteret (I), bliver de omvendte kurser som vist med de stiplede linier. Ser vi på de omvendte kurser af mere østlige bestande rammer de endnu tidligere nordpå og op i Ishavet. Disse former for omvendt træk har ingen eller kun meget ringe chance for at manifestere sig ved forekomster i Nordvest-Europa.

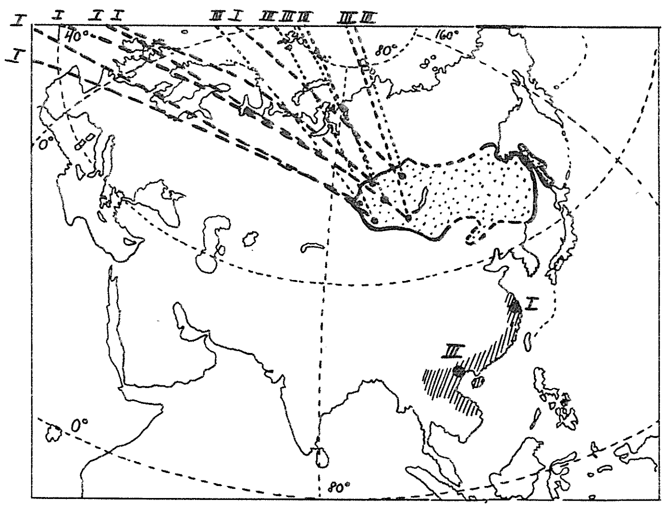

Fig. 7. Reverse tracks along great circles towards different parts of the wintering ground (I and III) from six sites in the western part of the breeding area. The tracks have been drawn supposing reverse bicoordinate navigation on a sphere. The reverse navigation could also be towards goal areas on the great circle course from the breeding area to the wintering ground. This will produce the same reverse tracks. The directions in Northwestern Europe are in very good accordance with the actual SW-WSW progress, but the tracks are on an average situated too northerly to match the actual pattern of records. There should be many more Scottish and Irich records. A possible explanation (Fig. 9) may be reduced survival of the most northerly birds when moving across such inhospitable areas as the Arctic and Atlantic Ocean.

Omvendt storcirkel-navigation mod vinterkvarterene I og III fra seks steder i den vestlige del af Fuglekongesangerens yngleområde. Indfaldsretningen i Nordvest-Europa svarer meget godt til den observerede SV-VSV orientering af de faktiske forekomster.

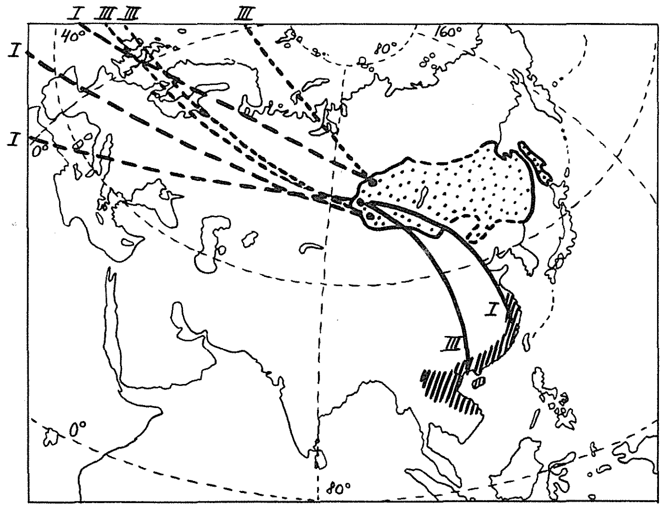

Fig. 8. Reverse bicoordinate navigation along great circles towards goal areas on slightly curved normal migratory routes towards wintering grounds I and III from three sites in the most westerly breeding area. Only routes from one of these sites are shown. A southward shift in the position of the tracks compared to Fig. 7 is obvious, but many tracks should still be directed towards Scotland-Ireland. The track direction in Northwestern Europe becomes slightly more westerly than the track shown in Fig. 7. *Omvendt storcirkel-navigation mod mål-områder på let krummede trækruter. Indfaldsvejene i Europa bliver sydligere end i modellen på den foregående figur.*

It should once again be emphasized that Rooke (1966) was the first to propose the hypothesis of reverse great circle navigation towards the wintering ground as an explanation of the SW-WSW track of Pallas's Leaf Warbler in Europe – and his proposal was a great inspiration to me when I treated the occurrences within Britain of four vagrant *Phylloscopus* warblers (Rabøl 1969 b). At this time I found Rooke's hypothesis unlikely – especially because of the lack of Scottish and Irish records. I therefore proposed a more simple hypothesis of westward vagrancy which I already at that time felt to be too simple, but otherwise a good preliminary starting point.

Orientation experiments

The problem of the primary orientation of Pallas's Leaf Warbler – and other vagrant species – may in principle be investigated by means of orientation experiments.

Unfortunately, there seem to exist very few orientation experiments with vagrant birds – though the funnel method (Emlen and Emlen 1966, Rabøl 1972) is easily applied and should be standard equipment at every bird observatory.

On September 27 1970 the second Danish Pallas's Leaf Warbler was trapped at Christiansø in the Baltic Sea. The bird was placed in a funnel under a starry sky – but displayed no activity at all.

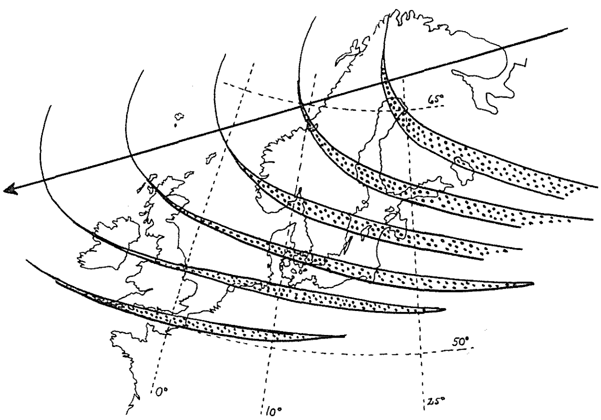

Fig. 9. The reverse great circle mean track towards Europe of Pallas's Leaf Warbler. The isoclines and dotted areas have the same significance as in Figs. 3 - 4. The earliest arriving birds following the mean track are few in number because of much reduced survival as they pass over or nearby the Arctic and Atlantic Oceans. This figure may well explain some of the difficulties arising from Figs. 7 - 8.

Pilen viser den gennemsnitlige indfaldsvej i Nordvest-Europa af den vestlige bestand af Fuglekongesanger. Da dødeligheden er størst mod nord langs de ruter, der fører over og tæt ved Ishavet og Atlanterhavet, passerer hovedmassen af fugle syd for den gennemsnitlige indfaldsvej.

Final remarks

While waiting for the results of such orientation experiments with Pallas's Leaf Warbler and other vagrants, it would be interesting to know whether the very long journey to Europe and the apparent SW-WSW direction may be explained in other ways, e.g. by means of some diverted form of one-direction orientation. Until then, one must acknowledge the probable existence of bicoordinate navigation towards a position where the juvenile Pallas's Leaf Warbler has never been before. (It should be admitted that reverse navigation towards the home site will produce much of the same tracks as the observed ones, but this possibility is not found likely. As far as we know today, migratory birds show no relation to their home during their autumn migration).

In fact, such a view is not far from some remarks of Wallraff (1972 and 1974), who otherwise assumes an *experienced home position* to be essential for all kinds of navigation. Wallraff (1974) says: '—denkbar, dass Zugvögel einem Gebiet zustreben, das in einer bestimmten Lagesbeziehung zu ihrem Herkunftsort steht'. Expressed in another way: Navigation towards a position which is not the home (or another experienced place) may be imagined, if this position is *developed* from the imprinted home position. This is exactly the way I consider a goal area, which in the course of the season 'moves' from the breeding area (home) down the migratory route towards the wintering ground.

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SUMMARY

The track of Pallas's Leaf Warbler in Europe in the autumn cannot be described solely on the basis of reverse one-direction orientation, and a significant part of the process may involve bicoordinate navigation along great circles.

This conclusion is not in accordance with the commonly accepted view that juvenile birds are not able to navigate towards a position where they have never been before.

DANSK RESUME

Fuglekongesangerens *Phylloscopus proregulus* orientering i Europa.

Denne artikel beskæftiger sig med de europæiske forekomster af Fuglekongesanger, men den handler primært om at finde ud af hvilket orienterings-system, der ligger til grund for forekomsterne. Herigennem håber jeg at kunne sige noget generelt om det trækprogram som ungfugle er udstyret med, når de begiver sig ud på deres første efterårstræk.

Dette er nemlig et kontroversielt spørgsmål — eller rettere, det er ved at blive det.

Siden sidst i 1950'erne har man troet på, at gamle fugle fandt vej til deres vinterkvarter ved hjælp af navigation, medens ungfuglene på deres første efterårstræk blot bevægede sig stereotypt afsted i en normaltrækretning, som de fastlagde ved hjælp af retnings-orientering (at navigere betyder at bestemme sin position i forhold til et mål — f.eks. vinterkvarteret, og derefter bevæge sig mod målet. At retnings-orientere betyder at holde en retning eller en kurs i forhold til en eller anden ydre påvirkning. Begge processer forløber under medindflydelse og styring af ydre faktorer såsom f.eks. Solen, stjernerne og jordmagnetismen). Man forestillede sig, at evnen til retnings-orientering (der er den relativt simple proces) var medfødt, medens der i et navigations-forløb indgik indlæring, såsom prægning på vinterkvarterets position. Efter denne opfattelse kan en fugl kun navigere mod et sted, hvor den har været før — og en ung fugl på sit første efterårstræk har jo ikke tidligere været længere fremme ad sin trækrute eller i sit vinterkvarter.

Nyere forflytningsforsøg med unge, nattrækkende småfugle tyder imidlertid på, at de er i stand til at navigere mod såkaldte mål-områder på trækruten. Disse resultater kan dog også (bort)forklares ved hjælp af en kombination af retnings-orientering i normaltrækretningen og navigation tilbage mod forflytningens udgangspunkt.

Det er næsten umuligt at designe forsøg, der tillader en klar skelnen mellem disse to hypoteser.

Heldigvis synes naturen at have designet et brugbart forsøg, hvor aktøren er Fuglekongesangeren.

Fuglekongesangeren yngler ikke nærmere Europa end Novosibirsk i Sibirien, og den overvintrer i Sydkina — Indokina. Hvordan kan det så gå til, at den træffes i Europa om efteråret? Ja — det kan ikke være den rene tilfældige omstrejfen i forbindelse med vinddrift. Dertil er afstanden til Europa alt for stor, og desuden grupperer de europæiske forekomster sig tydeligt i et ret snævert bælte, der løber SV-VSV fra Ålandsøerne mod Sydøst-England. Man må forestille sig, at forekomsterne i Europa er udslag af det, man kalder omvendt træk, hvorved forstås en bevægelse enten modsat normaltrækretningen eller i retningen væk fra det aktuelle mål. Og vi er her ved sagens kerne. Set fra Europa er der nemlig så stor afstand til Fuglekongesangerens normale forekomst-regioner, at en omvendt orientering falder ret så forskelligt ud alt efter hvilket orienterings-system, som fuglene benytter sig af. Hvis de laver omvendt retnings-orientering eller

omvendt plan-navigation, vil de ikke komme Europa meget nærmere end Kola-halvøen (Fig. 6), hvorfra de stakkels fugle så vil forsvinde ud over Ishavet med en kurs lidt til venstre for Nordpolen. (At plan-navigere vil sige at navigere i et system, der opfatter Jorden som en flad mercator-projektion). Hvis fuglene derimod laver omvendt storcirkelnavigation mod mål-områder på trækruten eller mod vinter kvarteret, vil de komme ind i Nordvest-Europa på den faktisk konstaterede SV-VSV kurs (Fig. 7-8). I praksis kommer de noget sydligere ind, end man skulle forvente ud fra modellen, men dette kan forklares ved (Fig. 9), at de nordligste af de omvendte trækkurser passerer tæt forbi eller over Is- og Atlanterhavet med deraf følgende stor dødelighed. (At storcirkelnavigere vil sige at udstikke den kurs, der følger den korteste vej mellem to punkter på en kugle-overflade. Jorden er som bekendt (stort set) kugleformet. Længdegraderne og ækvator (men ikke de andre breddegrader) er eks. på storcirkler. En storcirkel løber hele Jorden rundt, bider sig selv i halen og inddeler Jorden i to halvkugler. På Fig. 1 ses at den nærmeste vej fra Danmark til Kina — langs storcirklen — er mod NØ-ØNØ, og ikke som man umiddelbart skulle tro mod ØSØ-SØ).

Konklusionen er altså, at der er involveret omvendt navigation i den proces der fører Fuglekongesangeren frem til Europa — hvormed man altså (i hvert fald hos denne art) har demonstreret tilstedeværelsen af et navigations-element i den unge fugls trækprogram. Denne navigation finder efter alt at dømme sted mod målområder på trækruten eller mod vinterkvarteret, d.v.s. mod steder, hvor fuglen ikke før har været.

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