

Appendix 3 for J. Rabøl 2026: Reconsidering the goal area navigation hypothesis with special emphasis on juvenile night-migrating passerines and stellar navigation. – Dansk Orn. Foren. Tidsskr. 120: 15-28.

The distribution and track patterns of vagrant birds with special attention to Yellow-browed Warbler and Pallas's Leaf Warbler

(Med et dansk resumé: Forekomst- og forløbsmønstre for sjældne fugle, især Hvidbrynet Løvsanger og Fuglekongesanger i Vestpalæarktisk)

Abstract Geographical displacements are a way to determine whether the standard progress of a migrant population is based on vector orientation/clock & compass (CC), moving goal area navigation (NAVGA), or navigation directly towards the breeding area or wintering ground. Furthermore, simulated displacements in manipulated magnetic fields or star-planetariums may elucidate whether the inferred navigation is based on magnetic or celestial cues, respectively. A supplementary possibility to such displacements by man could be to investigate displacements carried out by the birds themselves. Many vagrant species are found within well-defined tracks or regions far outside their standard migratory routes. Inspired by a paper by H. B. Rooke, I considered such occurrences as outcomes of simple errors when trying to carry out standard migration. Knowing the standard route, one has the possibility to deduce what kind of error in which system (vector orientation versus navigation), or process (loxodrome, orthodrome or flat 'earth'), or cue (magnetic versus celestial) is involved. However, different probabilities in different regions in recording vagrant species may significantly distort the real patterns. Nevertheless, tendencies can sometimes be so strong that a real pattern shines through. The distribution patterns of Yellow-browed Warbler *Phylloscopus inornatus* and Pallas's Leaf Warbler *Phylloscopus proregulus* in western Europe suggests 1) initial reverse (standard) loxodromic navigation after some time and sometimes shifting too much/too early towards the left into mirror-image navigation (compared to the natural development of a reverse navigatory response). Or 2) reverse (standard) orthodromic navigation. Here, reverse NAVGA produces more southerly routes into Europe than reverse navigation directly towards the wintering area.

Introduction

Fifty years ago, I realized that the value of observations of rare birds was not just a passion for bird twitchers. Living in Denmark, I knew about observations of rare birds in the Nordic countries and in the UK with its many bird observatories and the journal *British Birds* reporting on vagrants on every remote island and wind-swept peninsula (Box 1).

Rabøl (1969) reported distinct patterns in the geographical distributions of autumn records of four species of leaf warblers in the UK. The distributions were not compatible with the contemporary view that the orientation and progress of rarities were the results of wind-drift in disoriented birds

Box 1. In a historic perspective

My interest in the orientation of vagrants started in the sixties when reading *British Birds*, in particular the section Recent Reports. Especially the sub-rarities caught my attention, and I reported on these (named “små-sjældenheder”) in Denmark in the late journal, *Feltornithologen*. The number of sub-rarities such as Red-breasted Flycatcher and Barred Warbler was so high that it was possible to find patterns in their distribution in location and time, and for me patterns were in focus, not the records at such. Kenneth Williamson was a great inspirator, and I learned about concepts like “overshooting” in spring exemplified by e.g. Subalpine Warblers arriving to Britain from Africa far north of their Mediterranean breeding grounds. Williamson was much focused on wind drift as the cause of records and distribution of vagrants, but I soon realized that the autumn patterns observed mostly were better explained as simple errors originating under execution of the standard migratory orientation system. I authored a short paper in *British Birds* (Rabøl 1969) with much support from the editor Ferguson-Lees and Tim Sharrock. I analysed the autumn distributions of four vagrant *Phylloscopus* warblers within Britain and claimed that the main factor of influence was reverse migration in a mostly westerly direction (a simple error of an initially about easterly standard direction). I did not speculate much in the orientational system whether it was based in compass orientation or gradient navigation, but I knew Rooke’s (1966) suggestion about reversed migration along a great circle indicating a navigation system. I came close to proposing mirror-image orientation (DeSante 1983), writing that the late autumn occurrences towards southwest within Britain “could be a manifestation of the then southerly standard direction in all four species”. Later and independently of DeSante (1983), Rabøl (1988, fig. 189) used the term complementary orientation covering the same as mirror image orientation.

Back in Denmark I first used the term reverse migration more thorough in Møller & Rabøl (1967) with much focus on the spring migration of Skylarks often reversing their migratory direction late in the morning or midday after an initial progress in about the standard direction. Several causes for reverse migration were considered.

In a mostly ignored paper (Rabøl 1976) the patterns of reverse orientation of vagrants progressing in a compass system contra a navigation system was compared. If the distance to the start position was far away, the outcome of the progress could be very different in the two systems. In the Pallas’s Leaf Warbler, the reverse compass route mostly curved towards the North Pole thus describing very badly. However, reverse orthodromic routes – both 1) towards the wintering area or 2) in a NAVGA context described mostly well, at least for the westernmost breeding populations. For more easterly populations the reverse routes disappeared up in the Arctic Ocean. These reverse orthodromic routes were not calculated but measured with a string on a globe or measured by a ruler on a map with an appropriate polar type of projection.

Disregarding this reasonable fit to great circles, I became sceptic about orthodromes (Rabøl 1978). When planning the present paper, I decided to use loxodromes for calculating the reverse course in a NAVGA system. For a first consideration, loxodromes looked simpler than orthodromes and why use a great circle for calculating orthodromes between two goal areas perhaps only 240 km apart? The orthodrome will only be insignificantly shorter. However, the supposed “simplicity” of the loxodrome rests on weak ground: The loxodromic compass course calculated is the same all the way through, whereas an orthodrome shifts direction continuously. However, both formulas are complicated to about the same extent, and in all probability all too difficult for use by a bird. Therefore, irrespective of system, some kind of a tinkered navigation system probably occurs.

Without any good reason I expected a tinkered loxodrome (close to simple coordinate navigation on a two-dimensional horizontal surface) to be simpler than a tinkered orthodrome (forgetting the proposal of a compass-based substitute of the latter by Alerstam & Petersson (1987). By hindsight I wonder, but anyway, loxodromes necessitated the inclusion of mirror image navigation after some time for a fit of the track into western Europe which was an at least potentially positive step for a nuanced understanding of the system. In fact, there is nothing new in Figs 8-9 not already proposed by Rabøl (1976). However, it is demonstrated more convincingly now, and the NAVGA approach presented here appears to include a larger range of the breeding areas of the two species as the possible origin of vagrants to western Europe. Most importantly, the bad fit of reverse migration in a loxodromic system indicates that neither standard NAVGA nor navigation directly towards the wintering area is carried out as loxodromic navigation. Orthodromic navigation – i.e. its tinkered substitute (Alerstam & Petersson 1987) – seems to be the winner of the game (at least in Yellow-browed and Pallas’s Leaf Warblers). However, Alerstam & Petersson is about maintaining not establishing the course, and the latter is still “the dark side of the Moon.”

(Williamson 1955, 1959): Arctic Warblers *Phylloscopus borealis* had, compared with Greenish Warblers *Phylloscopus trochiloides*, a much more northerly distribution in UK, and the same was obvious for another pair: Yellow-browed Warbler *Phylloscopus inornatus* compared with Pallas’s Leaf Warbler *Phylloscopus proregulus*. These patterns looked like the result of westerly reverse¹ orientation in all four species – corresponding well to expectations of an initial easterly standard direction from the breeding areas, later bending southeast and finally more or less south.

Reading Rooke (1966) was much of an inspiration: Rooke observed that the backward track of Pallas’s Leaf Warblers into Europe in autumn roughly followed a great circle passing through the western part of the breeding area continuing further into the wintering area. A great circle course (an orthodrome) is the shortest distance between two points on the surface of a spherical Earth. Therefore, there was reason to believe that the standard route of the warblers was programmed as energy-saving great circle navigation towards the wintering ground, and the birds that reached Europe were the unlucky victims of reverse navigation in a great circle system.

¹ Probably, the initial standard course from the westerly breeding areas of all four species is approximately eastward. Therefore, the designation “reverse” was not unreasonable.

This was a great insight (or skewed imagination) for a young man. However, many people still believe that the cause of vagrancy is disorientation in connection with passive drift by the wind. Or something called ‘dispersal’, which cannot be perceived as a cause but at best as a description. Disorientation could be considered as a random choice of heading from one migratory step to the next: any direction between 1° and 360° is selected with the same probability, i.e., 1/360. Disorientation should not be confused with misorientation where the bird takes (more or less) the same course from one step to the next but the (mean) direction is different from the standard direction. Simple logic and gross overviews convinced me that most Siberian migrants bound for wintering in Southeast Asia displaying disorientation will never come close to Europe even if steady east or northeast winds are prevailing in every step by the bird.

Background

The first question should be whether the state of vagrants (timing, distribution pattern, abundance) has changed since Rabøl (1969, 1976, 1978, 1988). In general, the number of recorded vagrants has increased enormously partly due to many more skilled observers and much better tools for species identification, including knowledge of the characteristic calls of, e.g., the *Phylloscopus* species. However, as witnessed by, e.g., the increase of the Spanish records of Yellow-browed Warblers (see below), many more vagrants (in some species) are now in circulation. On the other hand, the clear impression is that some other species – such as Rustic Bunting *Emberiza rustica*, Yellow-breasted Bunting *Emberiza aureola*, and also Pallas’s Leaf Warbler (though to a smaller degree) – have been scarce in northwestern Europe during the last 15-20 years compared with the ‘boom’ in the eighties and nineties – the Yellow-breasted Bunting due to a marked decline in the population (Heim *et al.* 2024).

Furthermore, the only possible way to explain the relatively few Irish and Scottish² records of Pallas’s Leaf Warbler is an active WSW-course diving into the Nordic Countries as indicated by Thorup (1998) in funnel-experiments (see below). Now, extending a WSW-course backwards towards ENE leads way back through part of the breeding area to reach part of the wintering ground as if reverse great circle navigation were involved.³ However, this is no proof of reverse great circle navigation in the track towards Europe. It could be an initial reverse progress (towards WNW) changing into mirror-image WSW in the western part of Russia. A steady westward progress as hypothesized by Rabøl (1969) would explain a lot, but we need ‘something’ in the long run bending

² Dymond *et al.* (1989) reviewed the record of rare birds in Britain and Ireland in the period 1958-1985. Here, a total of 341 Pallas’s Leaf Warblers and 2648 Yellow-browed Warblers were recorded. The distributional patterns of the two species look very similar though the latter species is more widespread and northerly. However, Ireland deviated significantly; only single birds of the former species were recorded.

³ As we will see below, it could be impossible to distinguish between reverse and mirror-image orientation/navigation. However, in the case of the Barred Warbler, mirror-image orientation/navigation (towards SW-SSW) could be dismissed. The standard direction from the breeding areas in Europe is approximately SSE bending more due S towards eastern Africa. Nevertheless, an initial reverse NNW is close to the actual progress towards NW, as revealed by the comparatively many records in the Shetlands, Faroes and Iceland).

the course more south-westerly or even further. This ‘something’ could be mirror image migration perhaps elicited by the confrontation with the Atlantic Ocean and the Baltic Sea.

An important, mostly dismissed old contribution

Rabøl (1976) stated that the autumn standard route of migrants could be intrinsically programmed as one-direction (compass) orientation or bi(multi)coordinate navigation. Furthermore, the orientation following a geographical displacement is the key to understanding which of these two systems works (e.g., Rabøl 1969, 1994, 1998). Considering vagrants, their vagrancy should often be considered as simple errors arising when trying to carry out standard orientation. Supposedly, much vagrancy should be considered as reverse tracks appearing as attempts to carry out standard migration. Mirror-image orientation – as an alternative to reverse orientation – never occurred to Rabøl (1976). However, see below. Rabøl (1976) realized that if the breeding area and standard migratory route of the vagrants are far from the region considered – as in the case of Siberian *Phylloscopus* species recorded in Europe – standard routes programmed as one-direction or coordinate navigation may lead to different tracks (progress directions and/or regions passed) in distant Europe. However, as in the case of Barred Warblers *Curruca nisoria*, the distance to the breeding areas could be so short that it would not be possible to distinguish between reverse orientation (NNW) in a vector-orientation system or in a navigation system. Rabøl (1976) also speculated whether differences between orthodromic and loxodromic navigation could be demonstrated, or whether reverse navigation was different if directed towards the wintering area or a moving goal area (NAVGA). He claimed no difference, but in general, this is wrong.

Rabøl (1976) considered especially the pattern of occurrence of Pallas’s Leaf Warbler in Europe in autumns 1968 and 1974. In several figures, I illustrated simulated reversed tracks of Pallas’s Leaf Warblers from the westernmost breeding area around Novosibirsk: reverse tracks originating in a) great circles/orthodromic navigation, b) loxodromic navigation or c) one-direction/compass orientation were presented. The latter mostly spiralled towards the North Pole. Also, b) was too northerly entering western Europe in contrast to the few records in Scotland and an expected SW-WSW course. Orthodromic navigation would sometimes explain well the observed pattern, if the wintering area was high up in China – and if the standard route was more curved (E bending ESE, SE, SSE and even S) compared with the great circle route. However, it only described well for the westernmost breeding populations, and it seems difficult to ascribe all European records from that small part of the total breeding population.

In the 1976 paper, I believed in the process of (reverse) great circle navigation. When writing the 1969 paper, I was not aware of this possible process and therefore proposed a simple W-directed reverse orientation/migration. Later, e.g., in Rabøl (1978), I could not believe in complicated great circle navigation and concluded that following a great circle would not in itself be proof of progress programmed as great circle/orthodromic navigation; it could be a chain of shifting loxodromic courses. However, after rereading Rabøl (1976) and considering also mirror-image courses (see

below), my present feeling is that (reverse) orthodromic navigation – among others – should be considered a serious possibility.

Rabøl (1976) was much aware of the southward shift in the progress of the Siberian vagrants when approaching and passing through (north)western Europe. However, I never proposed what De Sante (1983) later termed mirror-image migration/orientation. Independently of De Sante's concept, fig. 189 in Rabøl (1988) used the term “complementary” orientation/migration meaning just the same as mirror-image migration/orientation. “Complementary” orientation often appears similar to “orientation at right angles” (Rabøl 1988). I was often aware of “orientation at right angles” and (1988) observed that (bimodal) orientation at right angles often occurred in cage/funnel experiments early and late in the migratory season (Emlen *et al.* 1976, fig. 7 in Rabøl 2014), or when the detection of an important orientational cue was difficult (Wiltschko *et al.* 1993).

Funnel experiments

Thorup (1998) found that Yellow-browed Warblers and Pallas's Leaf Warblers trapped in autumn and funnel-tested on Christiansø in the Baltic Sea were bimodal WSW/(ENE)⁴, i.e., on about the same track as found in a plot of European records indicating that the distribution pattern of bird observatories and skilled observers are not – necessarily – the only reason for a WSW progress.

One may wonder why it is not routine at the bird observatories to funnel-test vagrants when they are captured. However, it is not that feasible. Rare birds are not common, and one needs to be well prepared with cages, funnels and appropriate food, together with an outside place far from light during the night for testing the birds. A moonless starry night sky is not always present, and the normal situation is the presence of only a single, captive bird – which often shows no migratory restlessness in the funnel. So, it is a long, tough process. I often – in connection with my other projects – funnel-tested the orientation of a rare bird accidentally captured. A prominent case was the first Swedish autumn record of a Yellow-breasted Bunting trapped at Ottenby in August 1968 showing a significant SE-orientation suggesting standard/compensatory orientation. Anyway, one cannot rely on single birds; replicate samples are needed to generalize results.

Reverse and mirror image orientation

In the context of bird migration, reverse vector orientation means orientation in the standard direction + 180°. If the standard direction is SSE (157.5°), reverse orientation will be NNW (337.5°). If navigation, reverse orientation arises when the bird makes 180° errors in the

⁴ 257°/(77°) – 0.564 (N = 17; four birds in secondary ENE-peak, P < 0.01) for the two species combined. Perhaps, the two species should not have been combined – and Thorup never did that. The orientation of the Yellow-browed Warbler was bimodal W (5)/ENE-E (3) whereas in Pallas's Leaf Warbler, the bimodality was much less pronounced, WSW (8)/NE (1). Most birds were tested more than once and considering the means of individual birds, these were much the same: 271.6°/(91.6°) (N = 6) in the Yellow-browed Warbler, and 249.5°/(69.5°) (N = 4) in the Pallas's Leaf Warbler.

coordinates, or a final 180° error in the compass component of the navigational process (considering navigation in the traditional way as a two-step process, e.g., Able 2001).

The naming “mirror image orientation/migration” dates back to De Sante (1983) and originated as an explanation of eastern American migrants – also Siberian vagrants – appearing in western California during autumn. Mirror-image orientation is defined (Newton 2008) as choosing the correct bearing with respect to N/S and the wrong one with respect to E/W. From the perspective of western California, consider an erected mirror with the long axis N/S in (a) the Rockies or in (b) the Strait of Bering. a) Looking into the mirror towards W, a SE-oriented migration will proceed SW. b) Looking into the mirror towards E, the Siberian birds migrating SW will appear to move in SE if direction.

According to De Sante (1983) and Newton (2008), mirror-image migration is a kind of misorientation, which is said to be an “ability to follow a consistent direction, but not the correct one”. Obviously, the correct one is the standard direction. Therefore, both mirror-image and reverse orientation are by definition misorientations. But of course, misorientation can be in any direction. When a Rufous-tailed Robin *Larvivora sibilans* turned up on Christiansø (55° N/15° E) in the Baltic Sea on 14 October 2012, it certainly did not arrive because of reverse or mirror image navigation/orientation. On the other hand, it should not be considered as a bird just straggling around (displaying disorientation). There would not have been enough time for that. If starting from a breeding area in eastern Inner Mongolia (50° N/120° E), a steady loxodromic course of 274.48° (in reference to geographical N) would bring it straight to the island. The loxodromic distance is 7112 km. If the airspeed of the bird was 30 km/h and if moving eight hours per night = 240 km, the bird would have been on its wings for at least $7112/240 = 30$ steps/days. If migrating every second night, the journey would have lasted two months. The unfortunate bird thus (possibly) started its misorientation at normal kick-off time in the middle of August!

Newton (2008) considered the tracks of e.g., Arctic Warbler and Greenish Warbler into western Europe in autumn as mirror-image migration. Normally, their progress would be designated reverse migration, but the outcomes of the two concepts obviously overlap when the initial standard direction is about east. Finally, in the department for curiosities should be noted, that the mirror-image migration of Siberian vagrants such as Dusky Warblers *Phylloscopus fuscatus* into California, when considered on spherical Earth, proceeds along a reverse great circle route.

Before proceeding, we must consider the array of possible errors emerging when a migrant bird tries to carry out standard orientation/navigation.

Fig. 1 shows an example. The scenario is a sample of birds trapped during autumn migration and tested in funnels at night. The standard direction is ESE, and if one finds a unimodal sample mean vector of – say – 120° – 0.72 (N = 8, P < 0.05), or 99° – 0.53 (N = 14, P < 0.05), it appears as stochastic outcomes around a mean of ESE (112.5°). However, several other kinds of orientation may arise: reverse-, mirror-image-, and right-angle orientation. In a ‘naked’ funnel experiment, we have no possibilities to determine whether the birds (goal area) navigate or use compass orientation.

To do that, we need real or simulated geographical displacements, and one possibility would be to look at birds displacing themselves, such as vagrants from Siberia to Europe.

Fig. 2 exemplifies in a flat plane how reverse- and mirror-image progress may develop in a Siberian vagrant depending on whether compass/vector orientation or goal area navigation is carried out. Two kinds of reverse (and mirror-image) navigation may be imagined. The simplest navigational

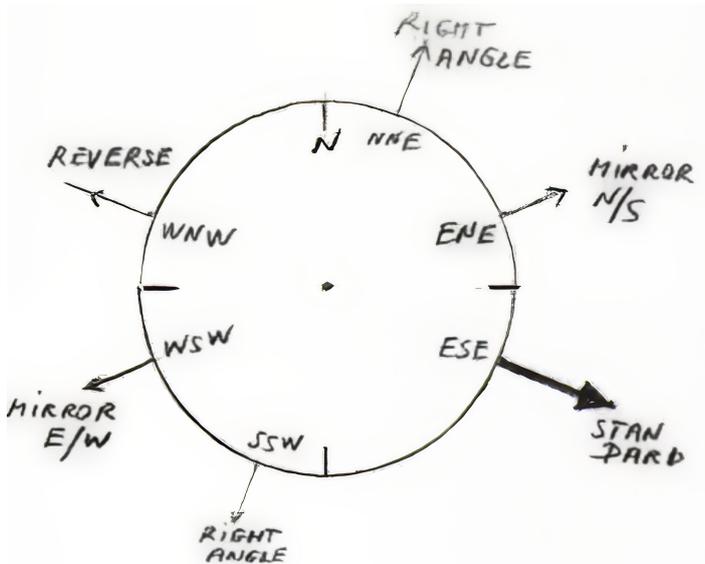


Fig. 1. The standard direction for a bird orienting or navigating towards ESE in autumn. If only standard orientation all variation will be around the mean ESE. However, normally there will be several other maxima of orientation which all may be considered as systematic errors. The most prominent are reverse orientation towards WNW; two versions of mirror image orientation, N/S and E/W, towards WSW and ENE, respectively; right angle orientation (as a compass reaction) towards SSW or NNE could also be significant.

Normaltrækretningen er ØSØ om efteråret, og som udgangspunkt vil vi alene se en vis spredning omkring denne retning. Men der kan være flere andre orienterings-maksima: Et i VNV (omvendt træk); spejlvendt N/S- og Ø/V orientering/træk mod henholdsvis ØNØ og VSV; vinkelret træk/ orientering mod NNØ eller SSV. For en sibirisk trækfugl, der dukker op i Europa, kan omvendt eller spejlvendt Ø/V træk være forklaringen.

output will yield the same pattern (but with smaller variation) as reverse compass orientation. Considered as vectors the outcome of five standard four-steps are E 960 km, ESE 960 km, SE 960 km, SSE 960 km, and S 960 km.⁵

These may be translated to coordinates. The start position is (0.0). The next (960. 0), then (1847.04, -367.36), (2525.76, -1046.08), (2893.12, -1933.12), and (2893.12, -2893.12). If the first coordinate is reversed the following coordinates arise (0.0), (-960.0), (-1847.04, 367.36), ... (-2893.12, 2893.12), and these will be the endpoints of the reverse vectors W 960 km, WNW 960 km, NW 960

⁵ Four-steps mean four steps of 240 km each, corresponding to eight hours of migration with an airspeed of 30 km/hour.

km, NNW 960 km, and N 960 km. I.e., there will be no difference in the reverse tracks of vector orientation and goal area navigation – considered in a flat/planar. I expected that differences would be found on a sphere, but in the two simulations I carried out, the reverse and mirror-image tracks became identical – or at least very much the same – in the navigational and compass systems.

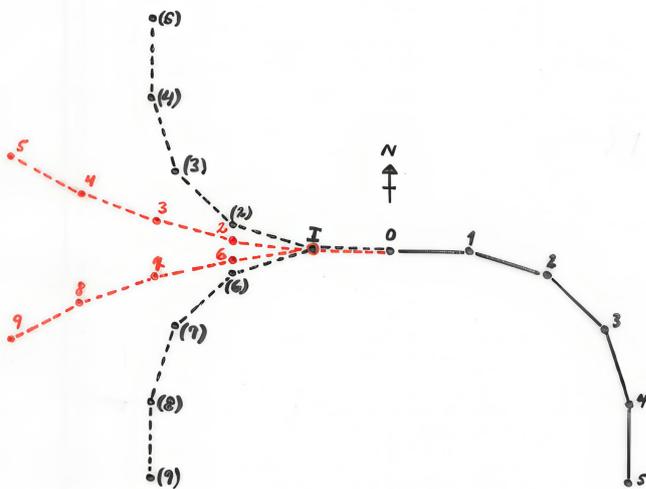


Fig. 2. Calculations of reverse and mirror image progress in a plane. The standard progress is in the five four-steps sections from 0 to 5. The compass direction of the five four-steps is E, ESE, SE, SSE and S, and the reverse compass track in a vector orientation system is shown as 0, I, (2), (3), (4), (5). The compass directions are W, WNW, NW, NNW and N. The mirror image vector orientation track is 0, I, (6), (7), (8) and (9). If the goal area moves reverse or mirrors the navigational tracks will follow the vector orientation tracks. If the goal area moves in the standard track and the birds make a 180° error in the compass component of the navigational process the reverse track will be 0, I, 2 red, 3 red, 4 red and 5 red. The birds start in 0 and navigate towards 1, but make a 180° directional mistake and ends up in I. From here it navigates towards 2 but again makes a 180° mistake and ends up in 2 red. The direction from I to 2 red is 277.46° . From 2 red it navigates towards 3 and again makes a 180° mistake and ends up in 3 red. The direction from 2 red towards 3 red is 284.78° , and so on. The reverse distance covered by a step is the usual one, 240 km. corresponding to 8 hours of migration with 30 km/h. per step. On the figure each step shown is for simplicity in the calculation 4 steps combined, i.e. 960 km. If the birds perform mirror image navigation, they proceed on track 0, I, 6 red, 7 red, 8 red and 9 red. One should notice, the reverse and mirror image tracks are symmetrical around an E/W-line. Of course, on a spherical surface like the Earth the tracks will be somewhat skewed, but the rough picture appears the same.

Beregnete forløb af omvendte og spejlvendte træk kurser for en sibirisk trækfugl, hvis normaltræk forløber som først fire træktrin fra 0 mod Ø, 90° (samlet længde 4 gange 240 = 960 km), så fire træktrin til mod ØSØ, så SØ, så SSØ og til sidst S. De to sorte yder-kurver viser omvendt vektor orientering (øverst) eller spejlvendt Ø/V vektor orientering (nederst). Lignende forløb fremkommer hvis fuglene navigerer mod et målområde, der kører omvendt eller spejlvendt i forhold til normal forløbet. De to røde midterkurver viser de tilsvarende målområde navigations udfald (øverst omvendt navigation), hvis målområdet kører i normalforløbet, men hvor fuglene så foretager en omvendt eller spejlvendt fejl, når de lægger kursen ind.

Now, this was only one of two possible reverse (or mirror-image) goal area navigation scenarios. The other one is exemplified/calculated in the text of Fig. 2. Here the reverse (mirror-image) birds are not following the goal area which behaves in the normal way going east and later bending southeast and south. The birds navigate towards the actual goal area but then make a 180° or mirror-image error, removing themselves further and further away from the goal area. Transferred to a sphere, one would calculate the reverse (or mirror-image) loxodromic direction between the position of the 'bird' and the actual goal area. This reverse direction was converted to a vector with a length of 480 km (corresponding to two migratory step lengths). Now we calculated the new position (in longitudes and latitudes), and then the reverse direction from this position to the position of the next goal area, and so on. The calculation of the loxodrome follows Rabøl (1988).⁶ Yellow-browed Warbler and Pallas's Leaf Warbler are vagrants supposed to start from their westernmost breeding areas, progressing first east, later southeast, and finally close to south to avoid inhospitable areas such as mountains and deserts. Boxes 2 and 3 provide further details.

Box 2. Goal area positions (every second position) simulating the standard track of Yellow-browed Warblers starting in 65.5° N/60° E and ending in 28° N/117° E. Total length about 6075 km (the orthodrome from first to last position is 5689 km). #0 65.5° N/60° E; #1 65° N/70° E; #2 64° N/80° E; #3 63° N/90° E; #4 60.5° N/100° E; #5 57.5° N/110° E; #6 53.4° N/111° E; #7 49.2° N/112° E; #8 45.1° N/113° E; #9 40.9° N/114° E; #10 36.6° N/115° E; #11 32.3° N/116° E; #12 28° N/117° E. Simulation of stepwise reverse and mirror-image loxodromic navigation is treated in the text and Figs 3, 4, 5. Reverse stepwise goal-area navigation in an orthodromic system starting in #0 passes WSW through northern Finland, bending more SW through middle Norway and Scotland – i.e. it looks like a perfect match. For more easterly start-positions the reverse track passes higher up and more W-directed and disappears SW-WSW in the neighborhood of the Faroe Islands and Iceland. Reverse orthodromic navigation from #0 in every step directed towards the wintering ground, #12 leads to a curved progress first WNW toward the Kanin Peninsula in Russia then more W toward North Cape in Norway, then bending WSW and later SW east of Iceland.

Hvidbrynet Løvsanger. Hvert andet målområde-position angivet fra yngleområdet i #0 65,5° N/60° Ø til vinterkvarteret i #12 28° N/117° Ø. I teksten og på Figs 3-5 er behandlet simuleringer af trinvis omvendte og spejlvendte loxodrom-navigeringer. Navigerer fuglene i stedet omvendt i et orthodromisk system fra det formodet vestligste yngleområde i #65,5° N/60° Ø afhænger kursen af 1) om de navigerer trinvis mod målområder på normaltrækruten, eller b) om de navigerer direkte mod det fjerne vinterkvarter (#12). 1) giver VSV-træk gennem Finland og SV-træk gennem det mellemste Norge og Skotland. 2) kører W gennem det nordlige Norge og ender med en SV-VSV-kurs i nærheden af Færøerne/Island. De to forløb matcher således nogle af de kendte mønstre.

⁶ An example should be given. The northwesternmost Yellow-browed Warblers depart at 65.5° N/60° E and initiate an attempt of standard goal-area navigation towards 65° N/70° E. The distance in longitude is 111.111 km times cos 65.25° times 10 = 465.18 km, and in latitude 0.5° = 111.111 times 0.5 = 55.6 km. Considering this in flat/planar and using Pythagoras, the total length is 468.49 km close to 480 km (two steps of 240 km each). The loxodromic direction from 65.5° N/60° E towards 65° N/70° E is 96.81° but the 'bird' makes a 180° error and migrates towards 276.81°. The double step-length is 480 km and the loxodrome ends up at 66.01° N/49.81° E. From here, the 'bird' again attempts standard migration towards next goal area in 64° N/80° E, but again makes a 180° error and performs reverse navigation with a vector of 278.96° - 480 km, ending up at 66.68° N/39.25° E. The next reverse position is 67.41° N/28.20° E, and so on.

Box 3. Goal area positions (every third position shown) of Pallas's Leaf Warbler from the start W of Novosibirsk (#0) to the winter ground (#7) in 22° N/110° E. #0 55° N/80° E; #1 55° N/90° E; #2 52° N/100° E; #3 46° N/101.3° E; #4 40° N/103.33° E; #5 34° N/105.33° E; #6 28° N/107.33° E; #7 22° N/110° E. Stepwise reverse and mirror-image loxodromic navigation is treated in the text and Figs 3, 4 & 5. Reverse stepwise navigation in an orthodromic system leads to a smooth (south of) west progress moving just south of Denmark on a WSW-course. Birds starting on a reverse track following orthodromic navigation directed all the time toward the wintering ground in 22° N/110° E are first directed about NW, then smoothly approaching W culminating at about 72° N/12.3° E, then moving about WSW at 70° N/13.4° W where the simulation was stopped. I also considered starting in 55° N/90° E and reverse orthodromic navigation all the time toward 22° N/110° E. The start direction is NW decreasing to W on about 78° N/7° W. From here the course bends WSW. In conclusion, reverse orthodromic navigation toward the wintering area produced courses far too northerly.

Fuglekongesanger. Hvert tredje målområde-position angivet fra yngleområdet V for Novosibirsk i #0 55° N/80° Ø til vinterkvarteret i #7 22° N/110° Ø. I teksten og på Figs 3-5 er behandlet simuleringer af trinvis omvendte og spejlvendte loxodrom-navigeringer. Navigerer fuglene i stedet omvendt og trinvist i et orthodromisk system fra det formodede vestligste yngleområde i #0 55° N/80° Ø, så trækker de først V og går senere mod VSV lige syd om Danmark. Det ser meget rimeligt ud. Hvis de i stedet orthodrom-navigerer hele tiden direkte mod vinterkvarteret i 22° N/110° Ø forløber det omvendte trækforløb først NV, så V op til 72° N/12,3° Ø, hvorefter mere WSW ved 70° N/13,4° V, hvor simuleringen blev stoppet. Så det ligner overhovedet ikke, hvad Fuglekongesangerne gør i den virkelige verden.

Figs 3 and 4 show the reverse and mirror image routes following stepwise loxodromic goal area navigation⁷ from the populations of Yellow-browed Warbler and Pallas's Leaf Warbler nearest to Europe. Fig. 5 shows what to expect following the breeding areas of the nearest populations expanding further in westerly directions.

There are reasons to believe that Yellow-browed Warblers are presently expanding westwards, perhaps already breeding in easternmost Finland (see below). This means an increased number of vagrants moving west through the northern parts of Sweden and Norway continuing out over the Atlantic and many reaching the Faroes and Iceland. The recent increase of Yellow-browed Warblers to the North Sea coasts and into Spain and even further southwest (The Azores and Cabo Verde) are indicative of dominant mirror-image migration, perhaps after some initial phase of reverse migration. Perhaps also the sight of the Baltic Sea/Atlantic Ocean/North Sea triggers some southwest, south or even southeast (compensatory) migration.

⁷ If using stepwise orthodromic navigation or reverse orthodromic navigation directed towards the wintering area, the tracks will pass through middle or northern Finland bending southwest across the North Sea or the Atlantic Ocean, respectively (Fig. 6).

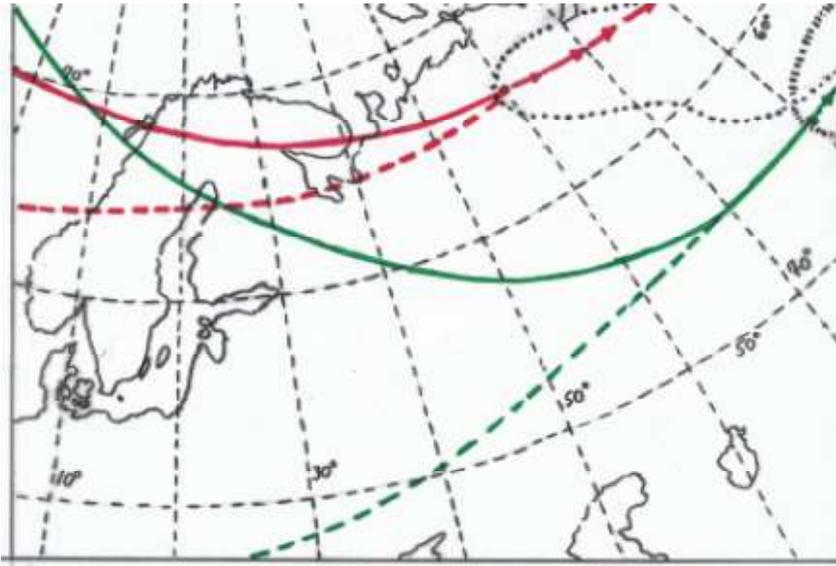


Fig. 3. Westernmost breeding areas for Yellow-browed Warbler (black dotted) and Pallas's Leaf Warbler (black hatched). The red dot is on position 65.5° N/ 60° E. The fully drawn red line denotes the reverse loxodromic track, and the hatched red line the mirror image loxodromic track of 'Yellow-browed Warblers' starting in this position navigating towards a moving goal area which finally stops in 28° N/ 117° E (Tab. 1). The green dot is on position 55° N/ 80° E, and the fully drawn and hatched green lines are the loxodromic reverse and mirror image tracks, respectively of 'Pallas's Leaf Warblers' starting in this position and navigating towards a moving goal area finally ending in 22° N/ 110° E (Tab. 2). For more easterly start positions the 'gap' between the reverse and mirror image tracks opens further up, and the mirror image track of the 'Yellow-browed Warbler' within a certain range appears reasonable as the system behind a penetration into Europe.

De vestligste yngleområder for Hvidbrynet Løvsanger (sort prikket) og Fuglekongesanger (sort kort-streget). Hvidbrynet Løvsanger (rød) yngler frem til $65,5^{\circ}$ N/ 60° E og Fuglekongesanger (grøn) til 55° N/ 80° E (se Tabs 1 & 2). Ruterne viser omvendt og spejlvendt loxodrom-baseret træk i et målområde navigations system, hvor målområdet kører igennem normaltrækruten på normal vis (se Fig. 2, de to mellemste ruter), men hvor fuglen i fastlæggelsen af trækretningen foretager 180° fejl i både N/S og Ø/V (omvendt orientering), eller 'kun' en Ø/V fejl (spejlvendt orientering). De bevæger sig således længere og længere væk i forhold til målområdet. Spejlvendt træk af Hvidbrynet Løvsanger ser ikke helt galt ud og for lidt mere østlige ynglebestande forskyder ruten sig mere syd på og går gennem Danmark. Endnu østligere går det dog 'galt' og ruten går gennem Mellemeuropa.

Anyway, we should always attempt to describe a process in the simplest possible way, since anything can be explained by introducing more complexity/degrees of freedom (but perhaps in an erroneous way compared with what actually happens). However, perhaps the tracks of vagrants into Europe are mixtures of initial reverse migration later turning into mirror-image migration finally bending more southerly. Recall that in an initial west-directed track you cannot distinguish between the two concepts if the standard route proceeds east.

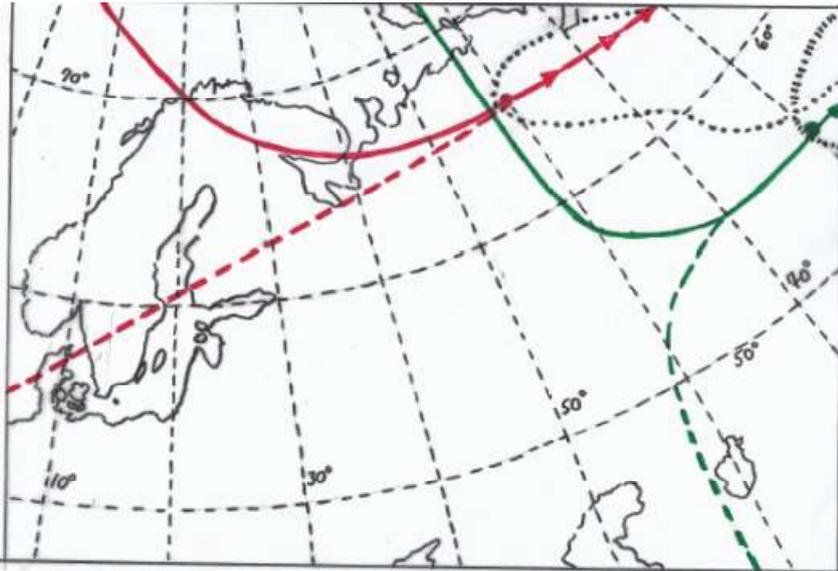


Fig. 4. Same principle as Fig. 3, but the lines originate in a different way. The orientation system is: a) reverse (fully drawn) or mirror image (hatched) vector orientation or b) goal area navigation. There seems to be no difference between the two outputs but see the text. The loxodromic outputs (not shown) in the Yellow-browed Warblers lay within the two red routes shown. In b) the goal area is not moving E towards SSE in the standard route, but the progress is westerly, reverse or E/W mirror image. The reverse tracks seek the North-pole, and also the mirror image track of 'Pallas's Leaf Warblers' develops aberrant, whereas the mirror image route of the 'Yellow-browed Warbler' looks promising. Moving further east the 'gaps' between reverse and mirror image open further up and describe lesser, as in Fig. 3.

Meget af det samme som Fig. 3, og det man ser svarer til de to yderste ruter på Fig. 2. Det kan være baseret i a) vektor orientering eller b) navigation mod et vandrende målområde. I modsætning til hvad er vist på Fig. 3, vandrer målområdet galt. Hvis målområdet var planlagt til at være i position 2 på Fig. 2, er det i stedet i position (2) omvendt navigation eller (6) spejlvendt navigation. I et plan (som på Fig. 2) forløber a) og b) ens; det gør de også på en sfære som Jorden i hvert fald i starten, men specielt når 'fuglen' i en spiral nærmer sig Nordpolen, må der komme forskelle ind.

Summing up, sometimes mirror-image orientation describes well and can – as stated in Rabøl (1976) – also be seen as reverse great circle navigation. The problem for me (as the prime proponent of the goal area navigation hypothesis) is that reverse loxodromic navigation describes badly: if navigating towards a moving goal area, the system should – almost axiomatically – be loxodromic (if the process of loxodromic navigation is simpler than orthodromic navigation).⁸ Therefore, if goal area navigation is the system behind the execution of the standard route, we should expect a loxodromic system in the reverse- or mirror-image tracks, too, but perhaps with

⁸ For short distances, there will be no differences between loxodromes and orthodromes. The formulas for loxodromes and orthodromes both seem inaccessible for birds, so one probably must abandon any expectations, as it is impossible to imagine and be sure of the kind of tinkering going on in the birds' minds.

non-linear influences in the east/west- and north/south-directed coordinates. In the calculations outlined in Fig. 2, I supposed linearity with distance.⁹

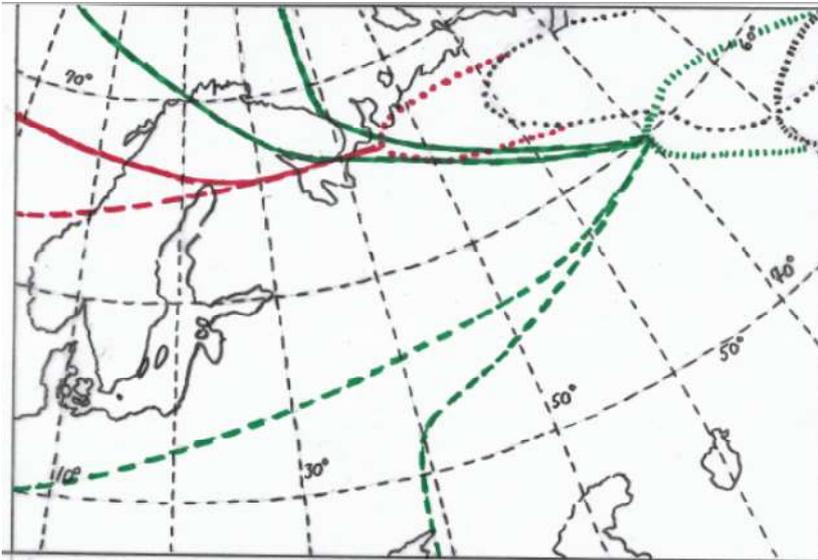


Fig. 5. This figure investigates effects of range-expansions towards 'west' in the two species. Imagine Yellow-browed Warbler expanded to 67° N/ 45° E, and Pallas's Leaf Warbler to 60° N/ 70° E. We smoothed the first, new goal area positions (Tabs 1 & 2) a little. In the Yellow-browed Warbler only the tracks corresponding to Fig. 4 are pictured. The two loxodromic tracks will be squeezed in between. It looks like a narrow W-directed 'beam' entering Europe. Perhaps, some real pattern is caught but certainly we need something more to explain the expansion towards SW in real life. In the Pallas's Leaf Warbler all four outputs are shown. The two outermost correspond to Fig. 4 and the innermost to Fig. 3. The mirror image loxodromic track looks rather reasonable.

Effekten af en udvidelse af yngleområderne mod vest (Hvidbrynet Løvsanger nu, og Fuglekongesanger i firserne/halvfemserne). Fuglene kommer tættere på Europa, og 'Hvidbrynet Løvsanger' kommer ind meget koncentreret, næsten i en 'stråle'. Det passer godt med erfaringerne fra de senere år – i nogle aspekter, for arten bliver talrigere overalt i Europa.

If far between two positions in an east/west-alignment – e.g., a position in Siberia and another position in NW-Europe – a reverse orthodromic course/progress would lead to an initial northwest

⁹ Considering reverse orthodromic steps, these may bend from for example WNW over W towards WSW over SW to even SSW on long distances. Reverse loxodrome steps will always develop gradually within the same quadrant, shifting for example from WNW over NW to NNW. Appreciating that those calculations of ortho- and loxodromes on a sphere must be beyond the capacities of a bird, I investigated the output of a simpler flat/planar simulation based on Box 2 and degrees transformed to kilometres, correcting longitudes for latitude dependence. The reverse goal area tracks curved steadily upwards from 65.5° N/ 60° E and after seven steps of 480 km each ended above northern Iceland at position 71° N/ 15° W (following transformations back from km to degrees). The course closely resembled the reverse loxodromic stepwise output shown in Fig. 3. Anyway, assuming that planar estimations are simpler and possible for the birds, we end up with something close to a loxodromic approach.

orientation curving into an about southwest course mimicking the shift from an initial reverse course into a mirror-image orientation in a loxodromic system. Following Occam's Razor, the orthodromic scenario is perhaps simpler and should be preferred if describing to the same extent. Figs 6 to 9 with Box 4 are attempts to describe the progress of Yellow-browed Warbler and Pallas's Leaf Warbler migration into Europe and further on as orthodromic navigation in terms of 1) reverse navigation towards the wintering ground or 2) reverse NAVGA. In general, both describe rather well (not so well for Pallas's Leaf Warbler) at least for the westernmost breeding populations.

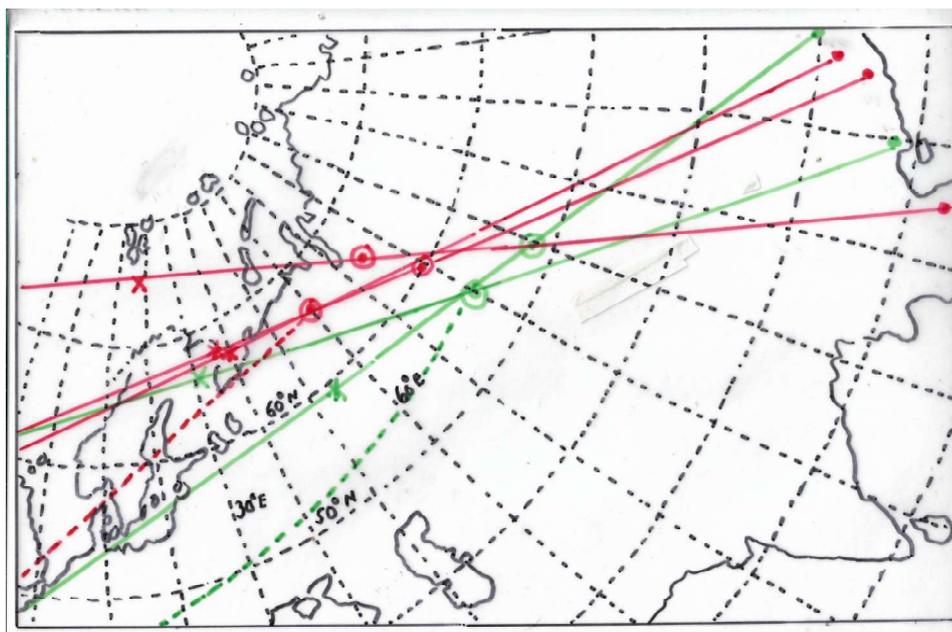


Fig. 6. Orthodromic tracks of three populations of Yellow-browed Warblers (red) and 2 populations of Pallas's Leaf Warblers (green). The birds start in the breeding area (white circles with dots in middle) and navigate all the time towards the supposed wintering ground (dots). The coherent standard/reverse tracks are shown. Due to type of projection the orthodromes follow close to straight lines. If more easterly breeding populations are considered the reverse courses move up more northerly and describe less well compared with field data. The crosses denote the maximum latitude in the reverse tracks (Fig. 7, Box 3). The two hatched routes show the reverse courses from the westernmost breeding areas in a stepwise orthodromic NAVGA system comparable to the reverse loxodromes in Figs 3-5. The two courses were not calculated (see earlier) but measured on a) the present figure, and b) on a globe and on the base of Box 2 and Box 3. In the Yellow-browed Warbler no differences arose but in the Pallas's Leaf Warbler the b)-course passed more northerly through Kent in the UK. Probably, b) is the most correct one.

De sammenhængende normal/omvendte orthodromer mellem yngleområde og vinterkvarter for tre bestande af Hvidbrynet Løvsanger (rød) og to bestande af Fuglekongesanger (grøn). De fuldt optrukne (næsten) lige rette linjer viser tilbage til navigation mod vinterkvarteret i hvert et træktrin. De stiplede linjer viser trinvis navigation/omvendt navigation mod et vandrede målområde (NAVGA). De stiplede kurser er målt på tegningen eller på en globus – med nogen usikkerhed som følge. Den stiplede grønne Fuglekongesanger linje skal formentlig forskydes noget mod N. Målområderne fra Box 2 og 3 har været i brug.

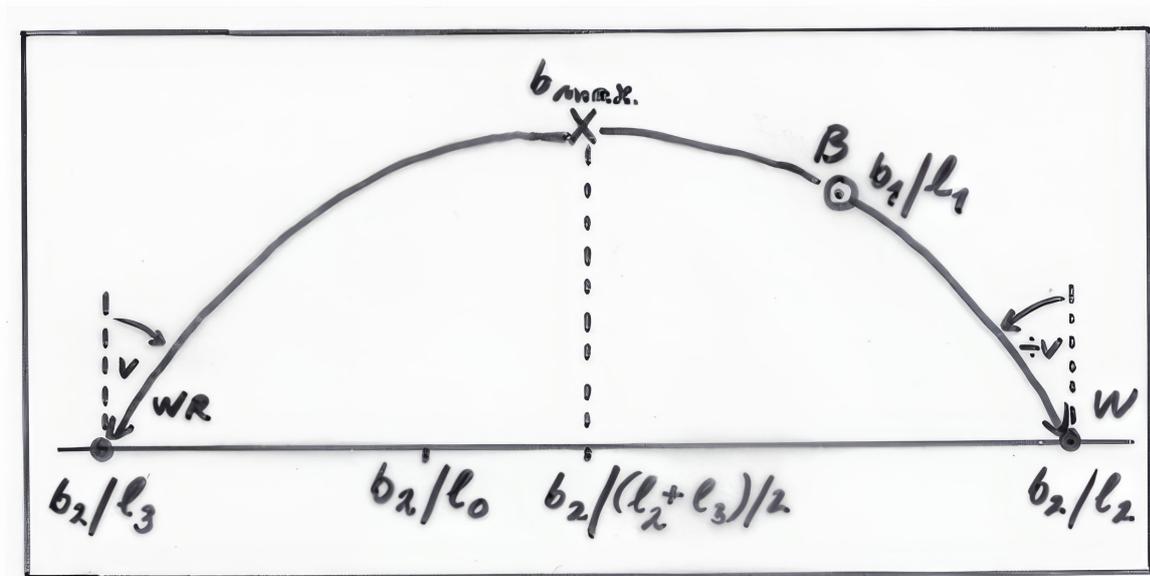


Fig. 7. Orthodrome (curved) between breeding area (B, b_1/l_1), wintering ground (W, b_2/l_2) and reverse wintering ground (WR, b_2/l_3). b and l denote latitude and longitude, respectively. l_0 is the Greenwich median. l_3 is negative if expressed as an easterly longitude. The orthodrome between B and W is calculated. Next, l_3 in WR is found through iteration (the angles v and $-v$ should be complementary). b -max. (crosses on Fig. 6) is then found as shown.

Orthodromen mellem et yngleområde (B), det formodede vinterkvarter (W) og det omvendte vinterkvarter (WR). Bundlinjen viser breddegraden b_2 . l_3 bestemmes ved at gætte på tallet indtil vinklen $+v$ bliver komplementær til den beregnede vinkel $-v$. Heraf fremgår b -max. (krydsene på Fig. 6) med tilsvarende længdegrad $(l_2 + l_3)/2$.

Boxes 2 and 3 describe the presumed migratory routes of Yellow-browed Warbler and Pallas's Leaf Warbler from their most westerly breeding grounds at 65.5° N/ 60° E and 55° N/ 80° E, respectively. The migratory routes for both species are assumed to start towards the east, later southeast and finally close to south to avoid inhospitable areas such as mountains and deserts. Stepwise orthodromic reverse migration from these positions were simulated; furthermore, from other positions such as 60° N/ 70° E and 55° N/ 90° E, respectively. Also, repetitive great circle navigation towards the final wintering area after each step was considered. However, my approach failed because of accumulated systematic errors producing too northerly reverse tracks. I was not successful in correcting by calculus and therefore changed to use a globe and a string cutting the globe into two equal hemispheres. However, reasonable tracks into northwestern Europe were almost lacking. An exception would be an orthodromic track from a wintering area in SW China, through the westernmost breeding area of the Yellow-browed Warbler passing northernmost Norway on a westerly course bending towards southwest passing east of Iceland. Such a reverse track may explain arrival to northern Norway, the Faroes and Iceland. A reverse orthodromic SW-WSW course through southern Finland and middle Sweden passes the westernmost breeding areas of both species but extends further east into the middle or northern part of China too far north of the actual wintering areas of the two species.

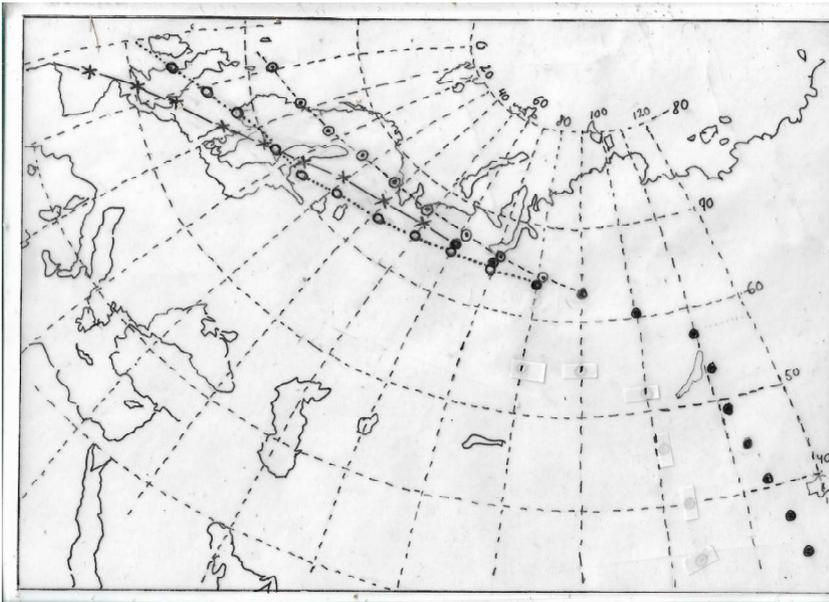


Fig. 8. Reverse orthodromic NAVGA in Yellow-browed Warbler. The black dots follow the positions from 65.5° N/ 60° E towards 28° N/ 117° E (but stop in 32.3° N/ 116° E) given in Box 2. The distance between the dots (exemplifying goal areas) is about 480 km mimicking two steps of each 240 km (airspeed of 30 km/h in 8 hours). Three different start-positions of reverse progress are considered: 65.5° N/ 60° E (crosses), 64° N/ 80° E (open dots) and 63° N/ 90° E (dotted dots). Calculations for a start position in 63° N/ 90° E follow: The birds navigate towards 60.5° N/ 100° E. The direction is 113.37° , but the birds make a mistake and reverse towards 293.37° moving 480 km in this direction ending up (allowing distances of longitudes as casinos latitude influenced) on the position of 64.71° N/ 81° E. The position of the following goal area is 57.5° N/ 110° E and the orthodromic direction from 64.61° N/ 81° E is 103.92° . Again, the birds make a reverse mistake moving 480 km towards 283.92° after 480 km ending up in 65.75° N/ 70.99° E, and so on, next time towards 53.4° N/ 111° E. The reverse progress hits maximum latitude about 50° E then taking a more and more southwesterly course (dotted dots). In conclusion, considered in total the reverse routes describe the progress of Yellow-browed Warbler into Northern and Western Europe very well. Of course, the long step-length (480 km) and the mixture between plain and orthodromic navigation distort the correct reverse progress but the distortions are supposed to be minor compared with the true spherical development.

Omvendt orthodrom/storcirkel-træk af Hvidbrynet Løvsanger i et NAVGA-system. Fuglene (tre bestande) starter fra yngleområderne i 65.5° N/ 60° Ø, 64° N/ 80° Ø og 63° N/ 90° Ø med endemål i vinterkvarteret i 28° N/ 117° Ø (Box 2). Fuglene starter med at orthodrom-navigere mod nærmeste, mere østlige mål ca. 480 km væk. De bestemmer retningen korrekt, men foretager så en 180° fejl og trækker 480 km i den omvendte, ca. vestlige retning. Her raster de et par dage inden de genoptager navigationen mod et mål, der nu er kommet ca. 480 km længere frem i normal-trækruten mod vinterkvarteret. Igen bestemmer de målretningen korrekt men foretager så en 180° fejl og trækker omvendt. Processen gentages indtil vinterkvarteret er det sidste mål. De tre indfaldsveje mod og gennem Europa ligner meget godt de virkelige indfaldsveje af arten, hvorfor man må kunne fæstne nogen lid til mekanismen/systemet som værende det beskrevet. Men det er ikke noget bevis, men en indikation. Der kan være en anden og mere korrekt forklaring.

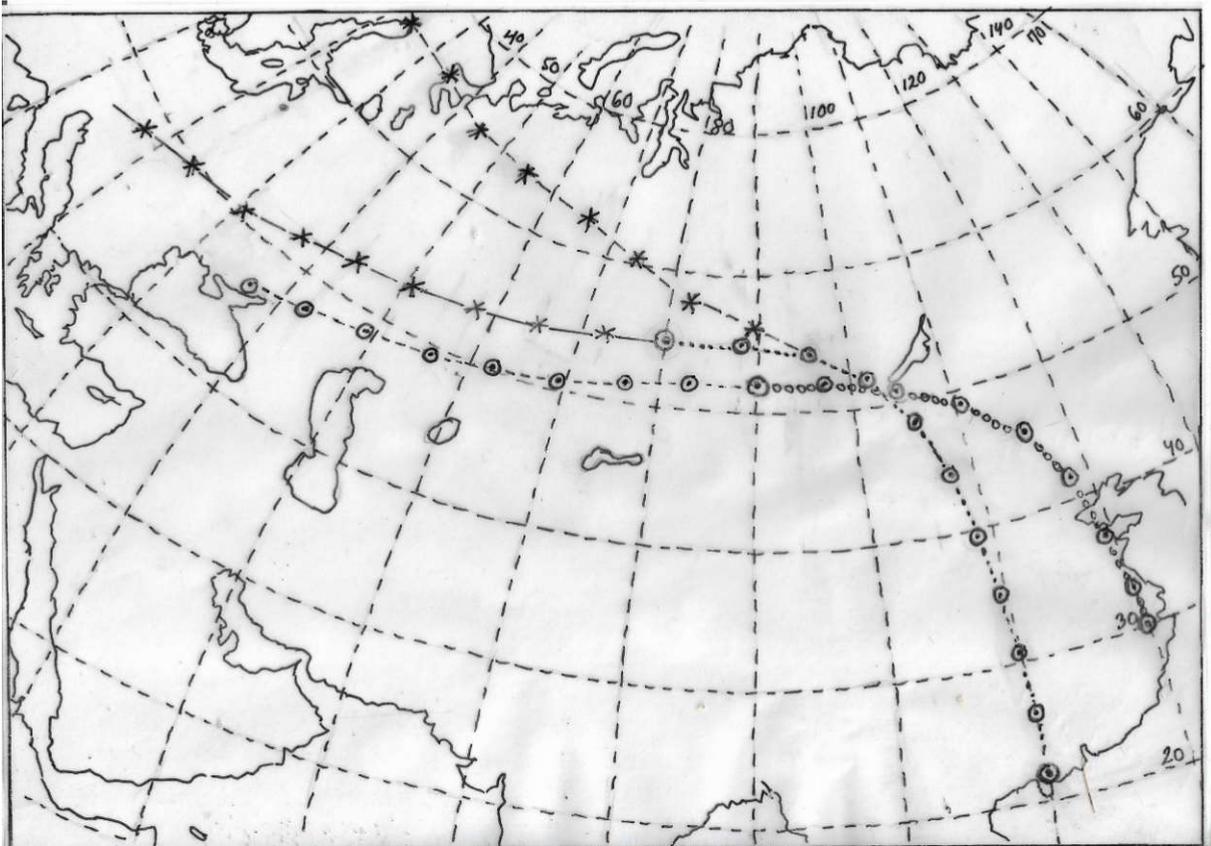


Fig. 9. Reverse orthodromic NAVGA in Pallas's Leaf Warbler. Same treatment as in the Yellow-browed Warbler (Fig.8). The three standard tracks are from 55° N/ 80° E towards 22° N/ 110° E, 54° N/ 96° E towards 22° N/ 110° E, and 52° N/ 90° E towards 30° N/ 120° E. The route of the first two progresses but not the step-lengths (480 km contra 720 km) follow Box 3.

Omvendt storcirkel/ortodrom-træk af Fuglekongesanger i et NAVGA-system. Samme behandling som Hvidbrynet Løvsanger i Fig. 8 De tre normal-træk forløb er fra 55° N/ 80° Ø mod 22° N/ 110° Ø, fra 54° N/ 96° Ø mod 22° N/ 110° Ø, og fra 52° N/ 90° Ø mod 30° N/ 120° Ø. Ruteforløbet af de to første men ikke step-længden (480 km) er den samme som i Box 3.

Box 4. Positions of three populations of Yellow-browed Warbler (YBW) and two populations of Pallas's Leaf Warbler (PLW) cf. Fig. 6 (and 7). The first position refers to the breeding area, the next to a possible/reasonable wintering ground, and the last position to the calculated position with the max. latitude of a reverse great circle course between the breeding and wintering positions (Fig. 7). YBW1 65.5° N/ 60° E, 28° N/ 117° E, 67° N/ 40.15° E. YBW2 65° N/ 75° E, 12° N/ 105° E, 75.7° N/ 18° E. YBW3 60° N/ 80° E, 25° N/ 115° E, 67.5° N/ 36° E. PLW1 55° N/ 80° E, 22° N/ 110° E, 65.5° N/ 30.85° E. PLW2 52° N/ 90° E, 30° N/ 120° E, 59° N/ 55° E.

YBW og PLW refererer til henholdsvis Hvidbrynet Løvsanger og Fuglekongesanger. I det der henvises til Figs 6 & 7, er den første position yngleområdet, den næste det formodede vinterkvarter, og den sidste position refererer til det punkt på den omvendte storcirkelkurs mellem yngleområde og vinterkvarter, hvor breddegraden når sin nordligste værdi (Fig. 7).

Apropos Gilroy & Lees (2003)

In an important paper on vagrancy, Gilroy & Lees (2003) expressed their scepticism towards the tendency to use reverse orientation as a standard explanation. I agree that reverse migration does not explain all cases of vagrancy. There are several exceptions, as also realized in the present paper. Gilroy & Lees considered much reverse orientation to be a pseudo-phenomenon because of “the pattern of observer coverage” which is about WSW from well-covered Finland over Scandinavia to UK. However, they seem to mix the terms mirror image and reverse orientation/migration, and they designate everything “navigation” also when they mean one-direction/compass orientation. Furthermore, the term “long-range dispersal” is used as a kind of explanation on the same level as, e.g., reverse migration. However, “long-range dispersal” is not an operational term but a concept on a different, descriptive level.

Gilroy & Lees (2003) write: “The occurrence patterns of some vagrants reaching Britain can be explained using the idea of long-range dispersal. We suggest that some comparatively regular vagrants reaching Britain are, in fact, performing migration to presently undiscovered wintering grounds in Western Europe or West Africa”. Later: “autumn vagrants act as agents of dispersal by colonizing new wintering areas.” But dispersal is not a causal mechanism/reaction nor an explanation. It is a description of a pattern on the populational level. Anyway, Gilroy & Lees captured something by considering adults who spent at least one previous winter in western Europe/West Africa. However, adults in all probability only constitute a tiny fraction of the total of vagrant Yellow-browed Warblers in autumn. So, the great majority of the vagrants could not be navigating towards a wintering area in the southwest they never visited before.

For a first and initial consideration, I was positive about the “pseudo-vagrancy” hypothesis of Gilroy & Lees (2003) as an explanation of the increased number of, e.g., Yellow-browed Warblers during autumn in Europe. These birds could be normal migrants on their way to unknown wintering areas in the Mediterranean or North Africa. Certainly, we should consider such a scenario. Bird migration is multi-faceted; seldom does one single hypothesis explain (almost) everything.

However, “reverse orientation”, “long-range dispersal” and “pseudo-vagrancy” are not mutually exclusive. In fact, they are concepts at different levels; the first is an operational concept, the two latter purely descriptive. When Gilroy & Lees (2003) consider vagrants as possibly normal migrants on their way towards an – for us – unknown wintering area, it appears to be a reasonable and straightforward possibility and explanation. Sorry, it is not! Probably, Gilroy & Lees share the traditional attitude that juveniles only perform vector-orientation (CC) whereas adults navigate towards positions earlier experienced such as an area where they spent the winter for the first time. However, this navigational process and progress cannot be transferred genetically to their offspring. If you believe in vector orientation as the one and only intrinsic program, only CC is transferred, and almost all vagrants – including Yellow-browed Warblers – are juveniles. So, it is out of context considering such birds being on their way towards an (for us) unknown wintering area. It is also unknown for the juveniles. Furthermore, it may be the outcome of reverse or mirror-image goal area navigation. However, if CC birds with a SW-WSW mis-orientation in their yearly lifecycle survive

better than birds equipped with an east bending SSE standard program, their offspring have an advantage. However, such a scenario is not supported by observations. Too few birds are observed in Europe on return-migration in spring to reproduce the thousands of autumn birds.

However, if Gilroy & Lees – as I – accept goal area navigation as a possible phenomenon, an E/W-mistake could be considered navigation towards an (for us) unknown wintering area. Considering an example with Yellow-browed Warblers as a model: the birds start in 65.5° N/60° E first moving east, later south towards a wintering area at 28° N/117° E. If making a mirror-image mistake, the (erroneous) wintering area is at 28° N/3° E, i.e., somewhere in Algeria. Certainly, in order to match the observed pattern in northwestern Europe, the birds may proceed more west (WNW) at the start before bending towards SSW ending up in Morocco. However, this is cosmetics. Compared with the standard progress, such an approach may still be designated reverse and/or mirror image orientation/migration.

Apropos Dufour *et al.* (2023)

The paper by Dufour *et al.* (2023) provides an overview of the thousands of recent records of Yellow-browed Warblers in Europe. According to their abstract “we review the conceptual framework and empirical challenges of distinguishing regular migration from vagrancy in small obligate migratory passerines and explain how this can inform our understanding of migration evolution”. The first and formal problem is that the definition of vagrancy – at least in long-distance migrants such as Yellow-browed Warblers – appears outdated: “a phenomenon called vagrancy and defined as the occurrence of individual birds outside their regular breeding grounds, non-breeding areas and migratory flyways”. Dufour *et al.* must appreciate that regular migratory flyways also include reverse tracks, mirror-image tracks, and perhaps also reverse changing into mirror-image tracks.

Therefore, the authors miss that – at least under basic conditions – there is no urgent need for any selective advantage for reverse or mirror migration/vagrancy to manifest itself/being preserved in the population: they always will be there and come out with minor/medium probabilities. Both should be considered as unavoidable ‘errors’ coupled to a certain standard direction (or goal area direction; see below) positively selected for. The point is that all reverse- or mirror-oriented birds may die without influencing the selective forces on the standard direction: every autumn they are back on the scene and probably in varying numbers/ratios because of varying environmental conditions. Therefore, Dufour *et al.* (2023) make a mistake when maintaining “Vagrancy is an individual-level phenomenon, it is not part of the normal behaviour of the species ...“. In my opinion, it is also – and more importantly – a population-level phenomenon, where reverse/mirror migration constitutes a major part of what is called vagrancy.

Anyway, the authors understand that increasing numbers of eastern ‘vagrants’ in Europe in recent autumns could be because of 1) breeding range expansion towards west and/or 2) increasing amount of reverse/mirror migration. Probably, there is a positive causal coupling between 1) and 2).

An obvious missing point in the Dufour *et al.* (2023) contribution is that they almost totally omit talking about the orientational/navigational system behind vagrancy. Implicitly, (juvenile) migrants are considered orienting in a vector orientation/clock-and-compass system. Only once is reverse great circle navigation mentioned as a possibility, referring to Thorup (1998), who in turn refers to Rabøl (1976). As obvious from the present contribution, outcomes of reverse and mirror-image orientation depend much on whether vector orientation or navigation is the process behind the vagrancy. This is not understood – nor appreciated – by Dufour *et al.* (2023).

The relatively few Yellow-browed Warblers recorded in Europe during spring do not support the hypothesis of an important wintering area in SW Europe/NW Africa. Of course, individual birds may survive during winter in this region up to southern Scandinavia – just like Common Firecrests *Regulus ignicapilla* and Chiffchaffs *Phylloscopus collybita* regularly do. But there is still no need to talk about an important wintering area. Anyway, such a wintering area may well be on its way.

Recent developments

Consulting the Finnish website Tarsiger.com and Shetland and Fair Isle “Latest sightings” and others revealed that since about 2013, an enormous increase of Yellow-browed Warblers in Europe has been observed. Northern Norway reports on more than 150 birds in a locality in a single day; the same was reported in a locality on the English east coast, and very many birds per day were found on Fair Isle. The Faroes and Iceland reported on close to 100 birds per autumn despite remoteness and very few observers. Spain ‘exploded’ in Yellow-browed Warblers in the autumn of 2014. Formerly, Yellow-browed Warblers and in particular Pallas’s Leaf Warblers were rare birds during autumn and winter (mostly) in the Iberian Peninsula and Las Canarias (De Juana 2008), but now 140 birds were recorded in a single year with peak numbers in NE-Spain and eastern Canarias during the normal autumn season of October and early November (Tarsiger.com referring to Cousido *et al.* 2017). Clearly, something shifted in the state of the Yellow-browed Warblers, and the most obvious explanations are an extension of the breeding area towards the West and perhaps also an increased amount of reverse and in particular (later on) mirror-image migration.

Up to 2017, well-watched Fair Isle, Shetland, produced ‘only’ 40 Pallas’s Leaf Warblers (according to the official bird list), including a single very unusual day record of 10 birds. However, the species was not recorded on Fair Isle since 2005 (according to “Latest sightings” from Fair Isle Bird Observatory).

Probably, Pallas’s Leaf Warblers decreased in Europe since about 2004. At least, on Christiansø in the Baltic Sea the number of ringed birds decreased very clearly: total number 1976 through 2017 was 92, with peaks 1979-82 (18), 1987-91 (20), and 1994-97 (34) (M. Lausten pers. comm.). Mean per year since 1998 was 0.75, and no years had more than two. Before 1979, only single birds were ringed (1970, 1977). So, it looks like a broad peak of European occurrences in the 1980s and 1990s. 2003 was probably the last high number year (85) in Sweden (Strid 2004).

Strid (2004) reported a total of 1090 Pallas's Leaf Warblers in Sweden until and including 2003, compared with 816 Yellow-browed Warblers. Sweden appears to be the only European country with most Pallas's. Denmark comes rather close with 283 Pallas's Leaf Warblers and 422 Yellow-browed Warblers until and including 2003 (A.B. Kristensen pers. comm. in De Juana 2008). Since then, the number of Yellow-browed Warblers has increased and Pallas's Leaf Warblers decreased, so now the ratio is probably 1:5 (or maybe 1:10). Since then, a new checklist of the birds of Denmark has been published (Christensen *et al.* 2022) confirming my estimation well: From 1950-1999 the number of *inornatus* and *proregulus* recorded in Denmark were about 370 and 230, respectively (*proregulus*-ratio = 0.38), whereas the corresponding numbers from 2000-2019 were about 1370 and 210 (*proregulus*-ratio = 0.13).

According to M. Lausten (in litt.) the number of banded leaf warblers of the four species Yellow-browed (I), Pallas's (P), Dusky Warbler (F) and Radde's Warbler *Phylloscopus schwarzi* (S) for autumns 1976 through 2018 on Christiansø were I: 73 ($73/(73+92+14+11) = 0.384$); P: 92 (0.484); F: 14 (0.074) and S: 11 (0.058). Compared with British, Norwegian and Finnish numbers (but not Swedish; see above) the number/ratio of Yellow-browed Warblers on Christiansø is astonishing low. As the four species probably have about the same probability for being trapped in a net, banded birds better than observed birds supposedly give the best proportional numbers. Probably, the 'few' Yellow-browed Warblers on Christiansø is a clear signal that the great majority entering Europe come in north of the island.

According to the official bird list for Helgoland from 1840 to 1996 there were 312 Yellow-browed (83%) and 64 Pallas's (17%). Since then, the ratio may have been skewed even more towards dominance of the Yellow-browed Warbler. At Blåvand, westernmost Denmark, the banded numbers 1984-2013 were 74 Yellow-browed (78%) and 21 Pallas's (22%) (Bent Jakobsen pers. com). Up to 2018, the Faroes (Silas Olofson pers. comm.) recorded four Pallas's (under 1% of the recorded Yellow-browed), and Iceland 0 Pallas's contra hundreds of Yellow-browed (official Icelandic bird list).

Tarsiger.com on the Yellow-browed Warbler

Consulting the Finnish website Tarsiger.com, the developments in Yellow-browed Warbler during the last eight years before 2020 were as follows:

Cabo Verde: Two records; March 2013 and January 2019.

Madeira: Five records 2014 through 2018 (including 6 birds 27 February 2017 on Madeira and nearby Porto Santo); 2 birds in November and 2 in December. Madeira thus still shows the same late autumn/winter scenario as described by De Juana (2008).

Azores: Between 2017 through 2019 3-4 birds on Corvo 23-26 October 2019. Single birds on Sao Miguel 2 November 2018, 9 December 2017 (perhaps the same bird 9 April 2018), and 3 January 2019. Before 2017, the Azores only had a single record.

Morocco: A few birds before 2012, but between 16 October and 6 November 2012 through 2014, 7 records of 10 birds.

Malta: About 40 birds recorded until 26 October 2013.

Cyprus: 25 October. 2018 1 bird (20th record for Cyprus).

Norway: Selected high numbers. 7 through 22 September 2013 478 birds in Norway. In Lofoten Islands on Værøy (about 67.5° N) at least 70 on 21 September 2013 and 160 on 22 September 2013; corresponding figures on Røst, 44 and 80. Even more northerly on Husøy close to Tromsø 60 birds were recorded 22 September 2013.

Finland: In the autumns 2012 through 2017 between 337 and 1028 per year (mean 602). During each summer some birds were recorded indicative of an approaching breeding area.

UK: 21 September 2016 at least 54 birds on Fair Isle and astonishing 127 at Flamborough Head on the east coast. 26 September 2013 at least 450 birds in Shetland and the east coast. An important supplementary note from Nanjizalbirds.wordpress.com 2020/12/31 “Yellow-browed Warbler, 2020“ (no author): Nanjizal is a coastal site in south-westernmost Cornwall close to Land’s End. Up to 2013, 38 Yellow-browed Warblers were ringed in autumn. The total up to 2020 is 269, 107 of which were ringed in 2016 (considered to be the highest annual total for any site in Great Britain), and 40 in 2020. Two British banded birds were recovered at Nanjizal: 1) One from Gibraltar Point, Lincolnshire 536 km towards NE (3 Oct./10 Oct. 2015), and 2) one from St. Abbs Head in Borders, Southeasternmost Scotland 694 km towards NNE (9 Oct./30 Oct. 2017), i.e. indicating a Southwestern migration through Britain. These figures indicate a very significant mirror image or a reverse orthodromic migration towards about SW within Great Britain.

Canary Islands: A single bird ringed on Helgoland 28 September 2013 was found on Lanzarote 10 January 2014 mirroring a reverse great circle course passing through Canary Islands, the (at least formerly) nearest breeding area in Ural, Russia at 65.5° N/60° E and the wintering ground in southern China.

Spain: In autumn 2014, 145 Yellow-browed Warblers were recorded in Spain (Cousido *et al.* 2017). Most birds on Lanzarote/Fuerteventura during September through December; second-most in NE-Spain. 145 is more than three times the former autumn total. Records in Spain and Portugal until 2005 can be found in De Juana (2008).

It looks like an increase in the number of breeding birds/offspring and/or an expansion of the breeding area westwards into Russia and perhaps even reaching Finland. For the naïve eye and on another explanatory plane it also looks like a development of a new wintering ground in western Europe/NW-Africa – and perhaps even farther S of Sahara (a few stragglers have reached Cabo Verde and Senegal). However, although the number of spring records in Europe is increasing, spring birds (also of Pallas’s Leaf Warbler) are (still) under one percent of the many autumn birds. Some people – like De Juana (2008) – believe that most autumn birds from Europe return to Asia

already the same autumn. I believe the vast majority end in the Atlantic Ocean. Spain/NW-Africa may well be too small and too northerly/cold as a wintering area for the two small Siberian warblers. For a large and warm wintering area, they must go south of the Sahara, down to latitude 10° or 15° N. The great circle distance from 65.5° N/ 60° E to 10° N/ 5° W is 7855 km, about the same as the great circle distance 7809 km from 65.5° N/ 60° E to southern China (28° N/ 117° E; Box 2). Moving further eastwards in the breeding area, the distances to NW-Africa and tropical Africa in particular grow longer and longer, and it looks like a bad business going west. However, for Yellow-browed Warblers expanded to the middle part of Finland (63° N/ 27° E), the great circle distance to tropical Africa (10° N/ 5° W) is only 5932 km, and to Morocco (33° N/ 5° W) only 4009 km. If saving energy means much, Morocco – but also tropical Africa – are candidates as new wintering-areas for westward expanding Yellow-browed Warblers. Even Brazil could be a remote possibility.

Conclusion

A wise man once said “Seek simplicity and distrust it” (Whitehead 1919). The simplest explanation for the vagrancy of eastern *Phyllocopus* warblers into Europe is westerly reverse-compass orientation from the breeding areas (Rabøl 1969). This explanation is reasonable: 1) the initial standard direction is approximately east, and 2) compass orientation is generally considered simpler than gradient/coordinate navigation.

However, I consider goal area navigation (the birds migrating towards consecutively moving goals along the flyway like pearls on a string = NAVGA; Rabøl (2022) as the fundamental system, at least in long-distance passerine migrants. It is typically perceived as multi-stepped NAVGA, but sometimes, as in the case of Greenlandic Wheatears *Oenanthe oenanthe leucorhoa* it manifests as single-step navigation directly from the breeding ground across the Atlantic towards the wintering area in western Africa (Thorup *et al.* 2006).

The next question is whether the navigational process occurs on a flat ground or a sphere. The latter involves working in terms of loxodromes or orthodromes. It is important to remember that navigation requires periodic updates. A Wheatear in Greenland may determine the orthodromic course towards Dakar before departure but must re-determine its position relative to the goal and adjust the course several times while crossing the Atlantic. If navigating towards a moving goal area (NAVGA), there is no need to use the complex formulas of loxodromes or orthodromes, instead approximate substitutes can be used as if Earth’s surface was a flat ground. I attempted this in a few simulations, and the outcome – reverse/mirror image tracks – appeared as approximate loxodromes.

The question is which type of mis-orientation (reverse, mirror image, right angle) is most significant? Generally, I consider reverse orientation the most important. I considered Siberian vagrants with an E/W mirroring. Possibly, Middle Eastern vagrants (wintering in eastern Africa) such as Pied Wheatear *Oenanthe pleschanka*, Isabelline Wheatear *Oenanthe isabellina*, Desert Wheatear *Oenanthe deserti*, Asian Desert Warbler *Curruca nana*, Common Nightingale *Luscinia*

megarhynchos (both *golzii* and *africana*), Isabelline/Red-tailed Shrike *Lanius isabellinus/phoenicuroides*, but not White-throated Robin *Irania gutturalis* (which is a very scarce but 'regular' overshooter into northern Europe in spring) as scarce actors in a slow autumn progress towards NW-NNW possibly exhibiting a north/south mirror image error (or perhaps, alternatively, a right angle response; Fig. 1).

Almost finally, which cue-system (magnetic, celestial, olfactory, visual) do I consider most likely behind the orientation of vagrancy? I tend to favour the celestial.

Finally, recommendations for future investigations: 1) more orientation experiments with vagrants (funnel/GPS), including geographic displacements; 2) more and better simulations of reverse and mirror image orientations, e.g., the step-length used should be much shorter.

Resumé

Forekomst- og forløbsmønstre for sjældne fugle, især Hvidbrynet Løvsanger og Fuglekongesanger i Vestpalæarktis

Normalt opfattes observationer af sjældne fugle som et krydderi på tilværelsen, men nogle sjældne fugle kan også bruges til andet. Som de fleste vil vide, er der mønstre i deres forekomstråder, og et mønster kræver en forklaring, i hvert fald hos sådan en som mig.

Nogle mønstre er lette at forklare. En art som Pallas' Græshoppesanger *Locustella certhiola* observeres ganske ofte på Fair Isle (Shetlandsøerne) og på Utsira (ud for Stavanger i Vestnorge); her er der en del fuglekikkere til at få øje på den kryptiske fugl, og den har svært ved at gemme sig på de træ- og buskfattige øer. Men begge øer ligger også i et godt strøg for arten, der fra Sibirien på omvendt træk kommer nordligt ind i Nordvesteuropa. Arten er således ikke set i selve Danmark men på Færøerne (M.W. Kristensen pers. comm.).

Som det fremgår af overskriften, er dette især historien om de to sibirske arter, Hvidbrynet Løvsanger og Fuglekongesanger. De er/har været 'talrige' i Europa på det man må opfatte som fejlslagent træk. De burde jo være på vej fra Sibirien først østpå, senere mod SØ og S (SSV) til Sydøstasien. Hvorfor flyver de i tusindvis af kilometer galt?

En rimelig forklaring kunne være, at fuglene i stedet for at vise normal-træk foretager omvendt eller spejlvendt træk, der er eksemplificeret i Fig. 2. Vi kan så gå ind og se på, om det fejlslagne træk passer bedst med omvendt eller spejlvendt, og om det med størst sandsynlighed forekommer i regi af vektor-orientering eller målområde-navigation (Fig. 3 og 4). Hvis vi er meget heldige, kan vi måske også finde indicier på, om det er stjernehimlen eller Jordens magnetfelt, der leverer information til orienteringen/navigationen.

Fuglekongesangeren kommer meget langt østfra – og det er ubegribeligt, at den kommer til Vesteuropa i så store mængder, som den gør (eller vel især gjorde for få år siden) – med mindre, at

der er et meget langt V-rettet trækforløb. De vestligste bestande ved Novosibirsk på ca. 55° N/ 80° Ø har måske et Ø-rettet normaltræk over ca. 30 længdegrader (svarende til ca. 2000 km, dvs. 30 gange 111 km gange $\cos 55^\circ$), inden de drejer mod SØ og senere over til måske SSV. Men ekspanderer de rent faktisk mod vest, er der tale om 80 længdegrader (5000 km) inden 0° -længden nås i Sydengland, hvor arten tidligere var regelmæssig i modsætning til hvad den er/var i N-England, Skotland og Irland. Det V-rettede træk (omvendt/spejlvendt) er måske selvforstærkende, fordi forskellen mellem den aktuelle position og standard-positionen vokser og vokser (Fig. 2). Jeg bliver mere og mere klar over, at kun V-rettet fejlorientering kan producere alle de 'sibirerere'. Det vil så også sige, at måske skal vi ikke gøre os for store forhåbninger om at forstå normaltrækkets programmering ud fra forekomst-mønstrene i sjældenhederne.

Måske var Fuglekongesangeren også en overgang i 1980'erne og '90'erne tættere på Europa, end den er nu (Fig. 5), og det ville andet lige give flere observationer i Europa. Det fører os over i Hvidbrynet Løvsanger, som formelig er eksploderet i antal i Europa siden 2013. Det kan næsten kun forklares ved, at arten er rykket $10-20^\circ$ længdegrader vestpå som ynglefugl – langt vest for Uralbjergene, på $40^\circ/50^\circ$ østlig længdegrad (Fig. 5).

Hvidbrynet Løvsanger er på enkeltlokaliteter i Nordnorge og Østengland set i antal op til 150 pr. dag, og på mange andre steder i og ved Atlanterhavet/Nordsøen i antal på 50 pr. dag eller mere. Arten er også blevet meget mere almindelig på Færøerne og Island med op til 100 fugle pr. efterår til trods for meget få observatører. Spanien (med Kanarieøerne) registrerede 140 fugle i efteråret 2014, mod tidligere en samlet total på 1/3 heraf. Den er nu også set på Azorerne og Kap Verdeøerne, og er muligvis ved at etablere et sekundært overvintringsområde i Sydvesteuropa/Nordvestafrika.

De Hvidbrynedede Løvsangere er blevet meget mere almindelige langs den jyske vestkyst (og på Helgoland), medens antallet på Christiansø ikke er steget, givetvis fordi de fleste Hvidbrynedede Løvsangere går nord om øen på omvendt træk, der enten allerede er eller snart vil afbøje til spejlvendt træk følgende princippet i fig. 197 i Rabøl (1988). Bemærk at det ikke giver mening at kalde et rent vestgående fejltræk for omvendt eller spejlvendt træk. Man kan ikke i denne situation skelne mellem de to. Det er både og.

Hvis jeg skal drage en forsigtig konklusion, så kan det være, at begge de to arters forekomstmønstre og trækforløb forklares bedst som omvendt og spejlvendt orientering i et navigationssystem. Omvendt og spejlvendt kompas/vektor orientering giver som generel regel for stejle N- og S-gående forløb (se Fig. 3, 4 og 5). Det giver derfor mening at opfatte normaltrækket som styret af et navigationssystem, og formentlig et målområde-navigationssystem. Men det er ikke nemt det her, og jeg skal beklage de mange løse ender. Vi bliver klogere – her som i øvrigt – når vi kan GPS-spore sjældenhederne. Det nærmeste, vi indtil videre er med eksakte målinger, er Kasper Thorups (1998) tragtforsøg med de to arter fanget på Christiansø et efterår, hvor de mod sædvane viste 'store' tal samtidigt. Fuglekongesangerne var VSV- og 'de Hvidbrynedede Løvsangere V-orienterede, men kun få fugle blev testet. Fuglekongesangerne var måske slået over i spejlvendt træk – eller

måske var det en gang fantastisk, usandsynligt, omvendt storcirkeltræk direkte væk fra vinterkvarteret i Sydkina. De sidste beregninger/simuleringer (Fig. 8 og 9) kunne tyde på det.

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