Reconsidering the goal area navigation hypothesis with special emphasis on juvenile night-migrating passerines and stellar navigation

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(*Med et dansk resumé: Comeback for og præcisering af målområde-navigations betydning for nattrækkende småfugle*)

Abstract Goal area navigation (NAVGA) refers to navigation towards a goal, that, over the course of the year, shifts along the migratory route, sometimes remaining stationary for extended periods, particularly during the breeding and wintering seasons. Historically, inherited NAVGA has been regarded as genetically unprogrammable. The interpretation of most experimental results has also tended to discredit such a system as governing the migratory progress of naive juvenile birds during their first autumn migration. However, the alternative, an inherited clock & compass/vector navigation system (CC), is increasingly considered inadequate. This necessitates a re-evaluation of NAVGA, especially given that the movement patterns of the "starry sky" in most of the few planetariums used for experiments were unnatural and, therefore, perhaps unsuitable for eliciting a NAVGA response. Here I demonstrate that east-west (E/W)-navigation as well as north-south (N/S)-navigation, can be genetically programmed with reference to the stellar sky. Furthermore, NAVGA simulations of migratory progress in night-migrating passerine birds show a reasonable correspondence with actual data, whereas CC simulations do not. Additionally, the tracks of vagrant birds are better described by simple (reverse, mirror-imaged) errors in a standard NAVGA system than by errors in a simple CC system. Taken together, these findings suggest that goal area navigation warrants renewed consideration as a plausible mechanism underlying the migration of night-migrating passerines.

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Introduction

The very first autumn migration by juvenile night-migrating passerine birds must proceed without following their parents or other adult conspecifics. This raises the question of whether these birds follow:

a) a vector navigation/clock-and-compass system laid down in the genes, and whether this is based on a compass direction in combination with a sense of the distance, or

b) a goal navigation system of one kind or another; a goal consisting of some kind of perception of celestial-based geographical latitude and longitude or magnetic variables such as inclination and intensity?

To distinguish between a) and b), the most straightforward approach would be to study how the birds orient themselves after a geographical displacement. If the birds do not compensate for the displacement, i.e., the orientation is the same before and after the displacement, option a) is supported. If the birds show compensatory orientation (e.g., shifting from SSE to SW after a displacement towards the east), this suggests navigation towards a goal along the migratory route, or ultimately towards the wintering area.

What is the evidence for a) and b)? In particular, the unchanged orientation in juvenile birds and the compensatory orientation in adult birds in the displacement of thousands of Common Starlings *Sturnus vulgaris* in autumn from the Netherlands to Switzerland (Perdeck 1958) was widely accepted and generalised as the norm. Most juveniles did not compensate for the displacement, indicating that an inherited compass system was in control. Most adults compensated for the displacement, indicating learned navigation towards the wintering area. However, in experiments, with other species such as Rabøl (1998) and Thorup & Rabøl (2007), juveniles mostly did compensate for displacements, indicative of a navigation system.

For many years, it was considered impossible for migratory birds to possess an inherited mechanism for navigation. Navigation was assumed to be something birds had to learn (Rabøl 2023). In this essay, I will present three kinds of evidence that warrant a re-appraisal of this view. This is presented in a rather concise form and elaborated in five online appendices.

However, conceptual considerations alone are insufficient. We need experiments that can distinguish between outcomes of clock & compass/vector orientation (CC) and navigation towards a progressively forward-moving goal area (NAVGA):

1) In particular, E/W celestial navigation (involving a time-sense) seemed impossible to be genetically fixed. However, E/W celestial navigation may be broken down into several components, which, considered individually, appear feasible.

2) Simulations offer another way to investigate the scope of a navigational model tested against a CC model. Henning Noer developed a model *(pers. comm.)* based on contour ellipsoids, enabling comparisons of the area of ellipsoids based on NAVGA or CC. Using reasonable assumptions, the NAVGA model generally provided better fit (Fig. 1).

3) If most vagrancy is considered as simple errors occurring when carrying out the standard migratory program, we have a tool for understanding what drives standard orientation, i.e. CC, NAVGA or direct navigation towards the wintering area. Such errors could involve reverse or mirror-image orientation, which, depending on the system (CC or NAVGA), manifest differently, and thus may indicate which system is most likely involved: NAVGA-based systems predominate.

4) Just as the stellar sky, the Earth's magnetic field seems an obvious candidate for providing cues for both CC and navigation. As the isoclines of magnetic inclination and intensity run almost parallel E/W across much of Europe and Africa (both offering potential opportunities for N/S-navigation), magnetic declination (the angular difference between gN and mN) could potentially serve as an approximate E/W parameter. A magnetic system is also consistently available, whereas the stars cannot be used during daylight or under cloudy skies.

Sections 1) through 5) are my main contributions and they are presented and discussed below, with further elaboration in the appendices available online.

The five main topics

Celestial based navigation in migratory birds, with special attention to longitudinal E/W-navigation (see the online Appendix 1 for a detailed outline)

In general, people do not consider celestial-based E/W-navigation a realistic possibility due to the necessary involvement of biological clocks, which must be extremely accurate and stable over several months. One is tempted to believe that this is beyond the capabilities of a biological clock. However, as discussed below, the traditional clock-based

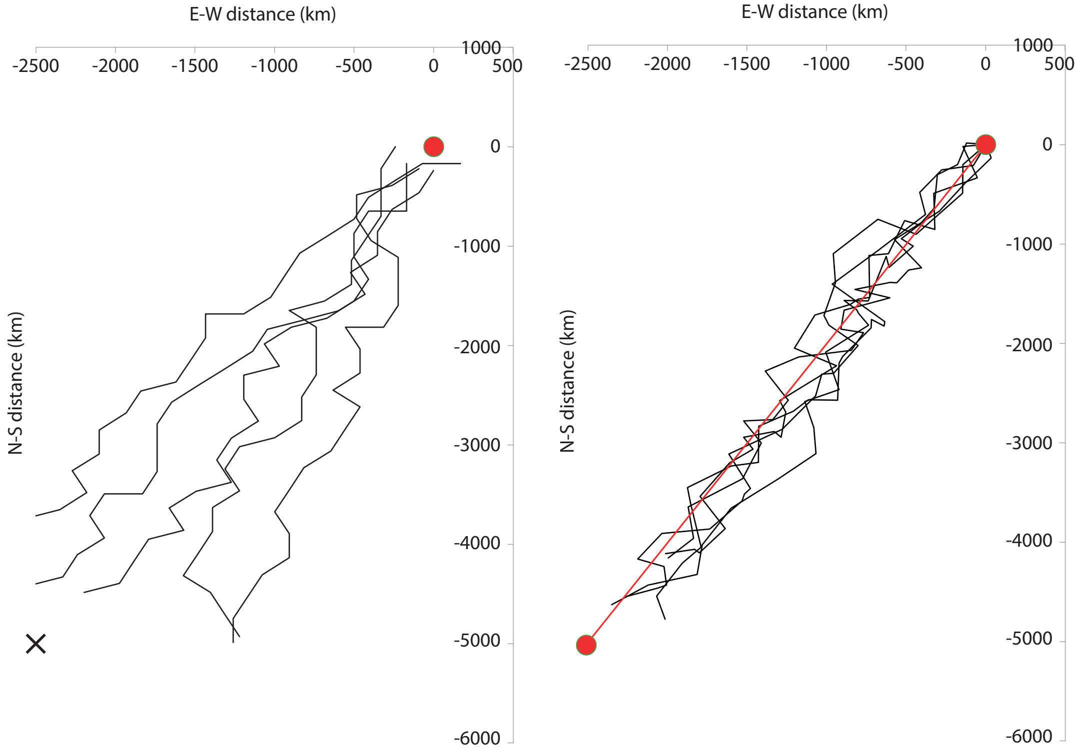

Fig. 1. Tracks of five simulated birds after 25 steps in a CC-system (left) and a NAVGA system (right). When variation is layered, the five CC-birds spread "parabolic" and the five NAVGA birds more narrowly and parallel-sided (in spite of highest step-variation) with much better chance of reaching the wintering site. See figs 1 & 2 in Rabøl (2023) for more information.
Sammenligning af trækforløbene af fem simulerede CC-fugle og fem NAVGA-fugle efter 25 trækdistancer på hver 224 km og en ideel konstant retning på 207°. Efter indlagt variation spreder CC-fuglene sig "parabolsk", medens NAVGA-fuglene spreder sig mere snævert og "parallel-sidet" så de har langt større chance for at ramme vinterkvarteret.

scenario may be overly rigid, and celestial-based E/W-navigation could in fact be simpler than normally assumed.

First, a historical note: Wallraff (2013) observed that homing pigeons use olfactory signals for navigation when returning to their loft after a displacement. Olfactory deprived pigeons failed to orient homeward upon release and rarely succeeded in returning. Therefore – Wallraff concluded – we are past the point of questioning the existence and importance of olfactory-based navigation. The question now is how pigeons respond to olfactory signals; how they navigate, and Wallraff proposed a plausible model.

Using "displacements" of juvenile night migrating passerines under a planetarium "stellar sky", Rabøl (1998) found significant evidence of both latitudinal and longitudinal stellar navigation. Thorup & Rabøl (2007) supported these findings. Therefore – following Wallraff's logic (although he may not recognize the analogy) – one should take the next step and propose models for how stellar-based navigation might function.

Two different models[1] for stellar navigation are proposed, both incorporating a N/S-coordinate based on the altitude of the rotation centre of the starry sky, located near Polaris (as a measure of latitude). However, the E/W-coordinates are different in the two models.

In Model I, longitude is determined by a highly stable and precise intrinsic clock – as described by e.g. Rabøl (1980).

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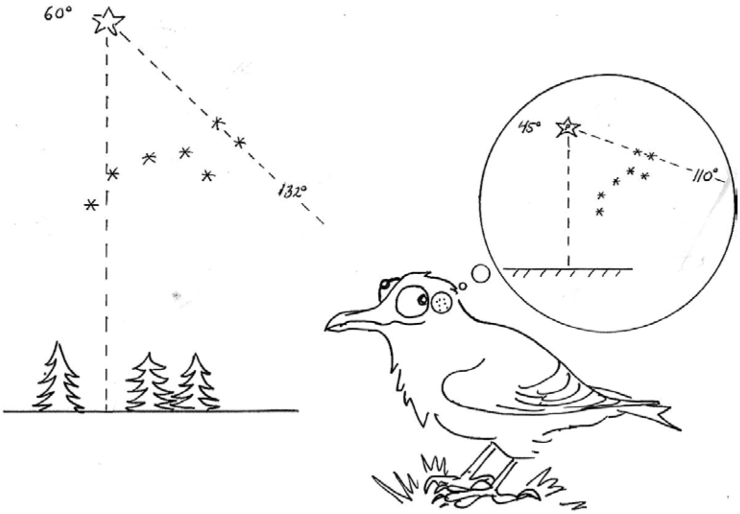
[1] A third possible E/W-coordinate is the magnetic declination (Appendix 1 in Rabøl 2023).



Stellar NAVGA navigation, Model I. The bird compares the present outdoor pattern of the Big Dipper and Polaris with the goal area pattern of the Big Dipper and Polaris in its mind.
Konstrueret eksempel på stjerne-navigation følgende model I. Fuglen sammenligner aktuel position af Nordstjernen og Karlsvognen med målområdets position i sin hukomelse. Se Appendiks 1 for forklaring.

In Model II, longitude is determined through a combination of several relatively simple processes, which, considered individually, appear to be within the bird's cognitive and sensory capabilities. Therefore, the extension of Wallraff's pigeon/olfaction scenario and reasoning seems acceptable.

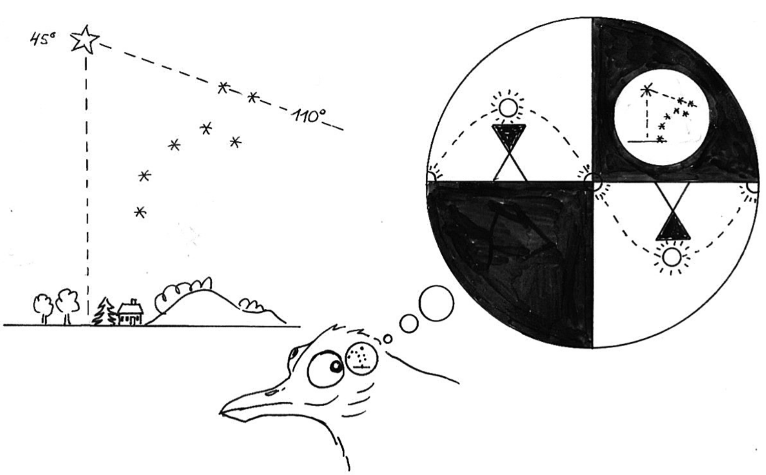
In fact, the migratory progress of a naïve juvenile migrant could be as simple as stopping upon reaching the coordinates of the wintering area. If the starting latitude is, say, 60° N (i.e., Polaris 60° above horizontal), and the latitude of the wintering area is 10° N, then the bird must move 50° towards S and then adjust to the right or left until the correct longitude is reached. The latter could be genetically encoded as 30° west of the starting longitude. At midnight, the time on the stellar watch (Figs 1 & 2 in Appendix 1) is, for example, 135°, which is imprinted. If the wintering latitude is reached after, say, 56 days and nights, this corresponds to a local midnight time of 135° + 30° - 56° = 109° (in fact, slightly more (0.8°), because the rotational speed is not exactly 1°/day but 360°/365.2422 = 0.98478°/day). Local midnight is 12 hours after local noon, when the sun altitude culminates. This is feasible, provided the bird is equipped with a mechanism akin to a sextant. Now everything depends on the uncertainties of a) counting days and nights, b) determining time/angle on the ″stellar watch″ (e.g. the angle of the ″bib″ of the Plough/Big Dipper extended to Polaris), c) identifying the time of local noon in the current position, and d) extrapolating local noon 12 hours ahead to local midnight, and e) measuring Polaris's altitude above the horizon (latitude). It should be noted that all errors along the migratory track are negatively feed-backed with reference to the final goal, the wintering area.

Simulation of vector orientation and goal-area navigation in night-migrating passerine birds (see the online Appendix 2 for a detailed outline)

This contribution was authored together with Henning Noer, who unfortunately passed away in autumn 2018, leaving our collaborative work unfinished. Henning was the mathematician and programmer who brought several of my conceptual ideas to life, so what remains was largely preliminary, yet still valuable as inspiration for other researchers in the field. The use of contour ellipsoids was a central focus, and H. Noer's method for calculating these was not accessible to me, as I am not a trained mathematician (see the chapter "Further considerations" and the section *"Contour ellipsoids"* in Appendix 2). However, as further explained in Batschelet (1978; see Appendix 2), I found a workable approach using Hotelling's test procedure, which in my best judgement proved adequate. See section "Contour ellipsoids" in Appendix 2.

Two populations of long-distance migrants were considered:

1) A population of European Pied Flycatchers *Ficedula hypoleuca* from Drentje in the Netherlands (Ouwehand *et al.* 2016) and



Stellar navigation, Model II. The bird uses a sort of hourglass to estimate local time/E-W position compared with time in actual goal area. See Appendix 1 for further explanation.
Stjerne-baseret navigation, Model II. Fuglene bruger en slags timeglas til at estimere den lokale Ø-V-position sammenlignet med tiden i målområdet. Se Appendiks 1 for yderligere forklaring.

2) a population of Red-backed Shrikes *Lanius collurio* from Gribskov, Denmark (Pedersen *et al.* 2020). Henning was not involved in the latter species. In both studies the birds were equipped with and tracked using of geolocators.

In case 1) above, we considered birds migrating from the Netherlands to southern France, then to north-western Spain/northern Portugal, followed by an offshore route along the West African coast to approximately Cabo Blanco in Mauretania. From there, the course changed roughly SSE to Sierra Leone, and finally eastwards to the Ivory Coast.

Different scenarios of vector-orientation and goal-area navigation were explored. We simulated the outcome of migratory programs based on vector orientation/clock-and-compass (CC) and navigation towards a moving goal area (NAVGA) and found that vector orientation was insufficient, even with partial compensation for wind drift. Full compensation within a vector orientation system is considered impossible.[2]

Both NAVGA simulations (including the one with no compensation for wind-drift in the step considered) described to a reasonable degree, i.e., the area of the calculated contour ellipsoid was acceptable small. This suggests that goal-area navigation deserves serious consideration.

In broad terms, we estimated the 70% contour ellipse of the wintering area of the Dutch Pied Flycatcher population. The estimated area was 117 000 km^2, with the long and short semi-axes of the 70% ellipsoid measuring 530 km and 70 km, respectively.

In case 2) above, the Red-backed Shrike, the focus was on the four stop-over sites/wintering areas the Balkans, Sudan, Namibia/Botswana and Kenya. The estimated 70% contour ellipsoids of the areas of these were 980 177 km^2, 1 369 844 km^2, 563 036 km^2, and 781 710 km^2, respectively. The Namibia/Botswana area was the smallest, indicating that a vector orientation program is inadequate for southward movement from Sudan. Clearly, the area of Africa shrinks when moving south, but the shrikes were only recorded in the western half of southern Africa. If migrating in a CC-system, about half of the recoveries – corrected for other influences – should have been found in the eastern half of southern Africa.

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[2] Linscott *et al.* (2022) report close to full compensation for wind drift on a long-distance flight across the Pacific Ocean from Chile to the Mexican Gulf in Hudsonian Godwits *Limosa haemastica*. Full compensation was inferred by the close to great circle course as NAVGA and not CC migration. Probably, the birds navigated towards goal areas on the standard route on the north coast of the Mexican Gulf on their way back towards the high latitude breeding area. However, as the track was close to due N it is difficult to distinguish orthodromes, loxodromes (following navigation or CC in a sphere), or flat/plain CC. Already Alerstam (1982) noticed that shorebirds migrating between northern Siberia and staging grounds in Western Europe/wintering areas in Africa sometimes followed great circles, and in other instances constant compass courses.

In conclusion, in the absence of wind, CC could provide an adequate explanation, but winds of shifting directions and strengths would frequently disrupt the outcome. Wind-drift is the primary reason for the failure of a CC-system, and for the selective success of either NAVGA or direct navigation towards the final goal.

The distribution- and track patterns of vagrant birds (see the online Appendix 3 for a detailed outline)

Records of ″vagrant″ birds may not be randomly distributed, but will often follow distinct tracks, suggesting specific errors in the execution of their standard orientation/navigation program.

At least as an initial observation – focusing on Siberian passerine vagrants – westerly reverse migration seems to be essential. Additionally, in the case of the Yellow-browed Warbler *Phylloscopus inornata*, westward expansion of the breeding area into or close to Finland seems to be significant (Rabøl 1969, 1976, 1978; Appendix 3).

Disorientation over land combined with wind drift clearly cannot account for birds ending up thousands of kilometres outside their normal range.[3] The only plausible explanation is errors during execution of the standard migratory program, i.e., one or more forms of misorientation, perhaps amplified when species undergo range expansions.

A key observation is that reverse and mirror-image migration in a CC system for Siberian vagrants typically results in tracks curving steeply towards the N or the S, respectively, leading the birds away from southern Scandinavia and the British Isles. These patterns do not match observed record patterns. In contrast, loxodromic reverse combined with mirror-image tracks in a NAVGA system reasonably describes the observed patterns. However, reverse orthodromic tracks alone, whether in a NAVGA-system or directed towards the wintering grounds, provide an even better and conceptually simpler fit, and should therefore be conceived as the most likely mechanism.

Siberian vagrants such as Yellow-browed Warblers and Pallas's Leaf Warblers *Phylloscopus proregulus* seemingly start on an approximately westerly track (see Dufour *et al.*/2022), which extend over long distances, e.g. 2000 km, during which it is difficult to distinguish between reverse and mirror-image vector orientation or navigation. A plausible development (as already hypothesised in fig. 197 in Rabøl 1988) is an initial north-of-west reverse course, which later shifts into a mirror-image course south-of-west. Such a transition may be necessary to bring Pallas' Leaf Warblers on a south-of-west course SE of Scotland/Ireland, where relatively few birds are recorded.

When considering reverse and mirror-image goal area navigation, two scenarios emerge (Fig. 2 in Appendix 3):

1) The goal area moves normally as in the standard progress, but the birds move in reverse or mirror-image directions away from the moving goal area, and

2) The goal area from the very beginning moves reverse or mirror-image and the birds just navigate towards the wrongly reverse/mirror-imaged moving goal area.

Scenario 1) is termed reverse/mirror-image navigation. Scenario 2) is navigation towards a goal-area moving reverse or mirror-image. In a flat/planar navigation system, scenario 2) produces the same patterns as reverse/mirror-image vector orientation. In a spheric navigation system the outcome is close to the corresponding reverse/mirror-image vector orientation system. Comparing the two scenarios, 1) provides the best fit to observed data.

In summary, Siberian warblers observed in autumn in Europe and further towards the SW should be regarded as true migrants rather than mere vagrants, as assumed by Dufour et al. (2022). They operate within a migratory system, albeit one in which something went wrong during the execution of the standard program.

The three central questions are:

1) Is the standard program based on compass orientation (CC), navigation towards a moving goal area (NAVGA), or direct navigation towards the wintering area?
2. If navigation is involved, is the system based in a flat/planar or a spherical (loxodrome or orthodrome) framework?
3. Is the error based on reverse or mirror-image orientation?

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[3] On the contrary, passive drift by the wind – perhaps even an active downwind component – seems to be a good explanation for American vagrants appearing in Europe after crossing the Atlantic Ocean.

First, CC performs poorly when the standard route extents far to the east. When the origin is closer, e.g. west of 30° E, as in the case of Red-breasted Flycatcher *Ficedula parva* and Barred Warbler *Curruca nisoria* (Rabøl 1976), it is not possible to distinguish between reverse CC and reverse navigation.

In general, one should begin by considering the simplest navigation system. Flat/planar navigation is the most basic, followed by loxodromic and orthodromic navigation (Alerstam & Pettersson 1991[4]). Flat/planar and loxodromic reverse/mirror-image navigation describe rather similarly and generally poorly, as they require a two-step shift in order to match actual data: first reverse then mirror-image progression (Figs 3-5 in Appendix 3). Surprisingly, orthodromic navigation provides the best fit (Figs 6, 7 & 8 in Appendix 3) in both reverse navigation directly towards the wintering area or reverse NAVGA. Rabøl (1976) had already reached this conclusion, although it was considered perhaps too complex and therefore unlikely (Rabøl 1978, 1988).

Magnetic navigation in migrant passerine birds and other animals (see the online Appendix 4 for a detailed outline)

As previously stated (e.g., Rabøl 2014, 2022), most claims of magnetic orientation/navigation are supported more by belief than by empirical evidence. Rabøl (2014, Appendix 2) lists many studies featuring questionable interpretations in favour of magnetic navigation. These, along with some new cases, are presented in Appendix 4.

The many claims about magnetic navigation are heavily influenced by 1) the broad American usage of the term "navigation" and 2) the general tendency to interpret even minimally apparent magnetic influence as evidence of navigation, including in the British sense, where "navigation" refers specifically to coordinate/gradient navigation. In American English, "navigation" may also refer to compass or one-direction orientation. By adopting this broader definition, many researchers unintentionally convey the misleading impression that true coordinate/gradient navigation is involved.

A recent example could be Dreyer *et al.* (2025), who clearly demonstrated the use of the stellar sky for compass orientation in the Bogong moth *Agrotis infusa*, yet provided no compelling evidence for a magnetic navigation system, despite extensive discussion of "navigation". European authors should be aware of the precise meaning of "navigation" and avoid mislabelling compass orientation as navigation, especially when it is clearly not coordinate-based.

Clearly, it is up to proponents of magnetic navigation in birds to demonstrate the existence of such a system through appropriately designed displacement experiments either in artificial magnetic fields or within natural geomagnetic configurations, and in contexts where celestial and olfactory cues are effectively excluded.

It is possible that birds, prior to autumn migration, imprint on certain magnetic parameters at their departure site (Wynn *et al*. 2022), later using these cues for navigation in the final stages of the spring migration, much like imprinted olfactory signals, Polaris altitude (as a proxy for latitude) and visual landmarks. However, in my view, magnetic navigation is unlikely to play an important role in any other phase of a NAVGA system.

For further considerations, see the online Appendix 5, where the present state of NAVGA and the importance of funnel experiments also in the future are discussed. Furthermore, a presentation of an in my mind too simple attempt to describe and explain migratory orientation in simple CC terms (McLaren *et al*. 2022) are presented together with comments on the impact of R. & W. Wiltschko within the field. When entering the scene of bird and animal orientation and navigation, their focus on magnetic orientation and navigation took the lead as witnessed when comparing the surveys of Emlen (1975) and Holland (2014). Unfortunately, their leadership was not followed by openminded attitude towards olfactory and stellar navigation in homing pigeons and migrant birds. and their meaning about inherited navigational skills in migrant birds remained on an outdated 'Perdeckian' position.

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[4] Alerstam & Pettersson (1991) showed that setting out on an about easterly or westerly compass course a migrant bird – using a time-compensated solar compass but not considering the sun's actual longitude shifts in course of the step – would move on a track close to a great circle/orthodrome. Their system will work well for e.g. a shorebird on very high latitudes with sun on the sky all the time and for one single long step or several steps only separated by short resting times in between. However, very probably, it may not work well for say a Yellow-browed Warbler on reverse migration in Sep./Oct. with a pronounced L/D-shift migrating during a starry night and with several nights on the average between the steps.

Discussion

Loxodromic, orthodromic and flat/planar navigation in a NAVGA context

This paper introduces NAVGA as a novel acronym, although the underlying concept has been developed in several of my earlier publications (Rabøl 1969, 1970, 1972). It has consistently provided the most compelling explanation for compensatory orientation following real or simulated displacements. However, responses resembling NAVGA have also been observed and are likely involved in certain cases. As early as Rabøl (1970, p. 36), I recognised the limitations of NAVGA inspired by the long-distance single-step migrations of Sedge Warblers *Acrocephalus schoenobaenus* and Blackpoll Warblers *Setophaga striata*: "The migration program of these birds might not necessarily be conceived as a continuous sequence of goal areas. It could involve direct navigation towards the wintering area or towards a few traditional waypoints along the route". Furthermore, in Rabøl (1994, fig. 1), I realized that what appears to be compensatory orientation towards a goal area in funnel-tested displacement experiments could in fact represent:

1) CC combined with navigation back towards the site of origin (cf. W. Wiltschko's re-navigation hypothesis; Rabøl 2023),
2) CC combined with a reversed compass based magnetic vector towards the site of origin, or
3) cross-axis compass orientation.

Navigation on Earth does not occur on a flat, two-dimensional planar, but on the surface of a sphere. Consequently, it necessitates calculations and courses that follow either loxodromes or orthodromes (Fig. 2), i.e., flat/planar navigation cannot reliably lead to the intended goal. Loxodromes are considered simpler, requiring only an initial calculation of the direction to the goal. In contrast, orthodromic navigation demands repeated calculations of directions after each step, as the course continuously changes. Thus, following Occam's razor, loxodromic navigation may be preferable in NAVGA scenarios involve many short steps, whereas orthodromic navigation is more suitable for long, single-step migrations to distant goals.

However, several of the assumptions outlined above are flawed. These inaccuracies led to my initial reverse/mirror-image NAVGA simulations, which ultimately provided valuable supplementary insights.

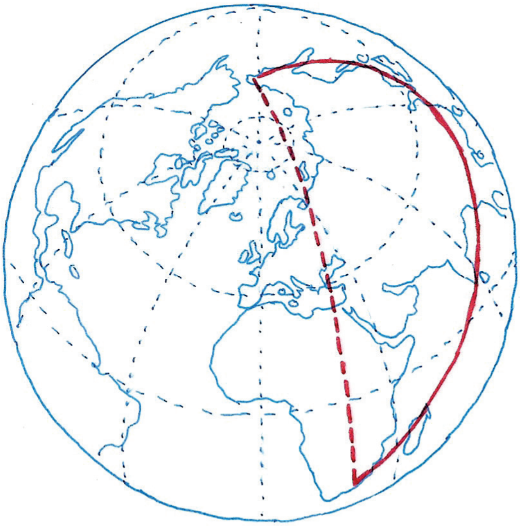

Fig. 2. Example of a substantial difference between the orthodromic and the loxodromic routes. Willow Warblers Phylloscopus trochilus breed across a vast range extending from Europe to easternmost Siberia. During the non-breeding season, they migrate to sub-Saharan Africa. This example presents two hypothetical migratory paths from 67°N, 170°W to 24°S, 28°E. The orthodrome (hatched line) is 15 061 km and with initial and terminal bearings of 336° (NNW) and 198° (S–SSW), respectively. In contrast, the loxodrome (solid line) covers a longer distance of 17 369 km maintaining a constant bearing of 234° (SW–WSW). Obviously, following the great circle/orthodrome would be more fuel efficient.

For en Løvsanger, der yngler tæt ved Beringsstrædet og overvintrer i tropisk Afrika, er der stor forskel på forløbet af orthodromen (storcirklen) og loxodromen (konstant kompasretning i forhold til geografisk N). Orthodromen starter mod NNW, tangerer Nordpolen og dykker herefter mod S-SSV. Loxodromen – der er 2308 km længere – holder en konstant kompaskurs mod SW-WSW.

In reality, all three forms of navigation – loxodromic, orthodromic, and flat/planar – require repeated recalculations. A bird's flight is invariably influenced by wind drift, landscape cues and error correction.

The determination of both loxodromic and orthodromic paths involves complex formulae, which are almost certainly beyond the cognitive capabilities of a bird. Instead, birds must rely on simple approximations, which should evolve only when necessary. Therefore, the perceived simplicity of loxodromic navigation compared to orthodromic is illusory. Moreover, loxodromes are disadvantageous in other respects, as they require more time, distance, and energy to complete a migration.

The assumption that flat/planar navigation is unusable on a spherical Earth is also easily challenged. In practical navigation, imprecise estimates are corrected in subsequent steps. For example, when migrating within a grid system of longitudes and latitudes, a bird might – without long-term issues – treat the distance between adjacent longitudes as equal to that between adjacent latitudes, even though the actual longitudinal distance is 111.111 km multiplied by the cosine of the latitude. At higher latitudes, individual navigational steps become less precise, yet the bird still reaches its final destination, albeit with some delay. The advantage of such a navigation system lies in its simplicity and accessibility for avian use, compared to the complex equations required for loxodromic and orthodromic navigation.

In conclusion: a wader fledged in Taimyr, Siberia, and destined for wintering grounds in Mauretania, West Africa with a stop-over in the Wadden Sea, would most plausible undertake two orthodromic flights across land and ocean; a Northern Wheatear *Oenanthe oenanthe* migrating from West Greenland to Senegal should also follow a comparable orthodromic route across the Atlantic Ocean.

In contrast, a Pied Flycatcher fledged in Finland is likely to employ a NAVGA-based system, migrating first SW to Spain or Portugal, then bending SSW over the Atlantic, aiming for land north of Dakar, before turning SSE to Sierra Leone, and finally proceeding eastward to the Ivory Coast for wintering. In this case, the navigational system is best described as flat/planar. In hindsight, there is no inherent necessity for orthodromic or loxodromic navigation.

The same principle applies to a Yellow-browed Warbler originating slightly east of the northern Ural region in Russia (65.5° N/60° E), migrating to southern China (22° N/117° E). While a flat/planar navigation system was initially expected to suffice, the actual explanation appears more complex. During standard migratory progress, predictable errors may arise—most notably reverse progress and two forms of mirror-image progress. These error patterns were investigated and yielded surprising results, as detailed in Appendix 3. Examining these errors offers insight into the underlying mechanisms of the navigational system. Both loxodromic and flat/planar reverse navigation produced migratory tracks bending north-westward towards the North Pole, which poorly reflect observed patterns in Western Europe. Combinations of reverse followed by mirror-image navigation sometimes provided reasonable approximations, but reverse orthodromic navigation offered the best fit for the observed migration from Siberia into Western Europe (see figures in Appendix 3). This raises a compelling question: why would orthodromic navigation be employed in a NAVGA system characterized by many short-distance steps?

In Rabøl (1969), I proposed a simple westward-directed explanation for the distributional pattern of the two Siberian *Phylloscopus* warblers in the UK. However, the observed migratory progress of at least the Yellow-browed Warbler bends south of west (or even more southerly) upon reaching the Atlantic as evidenced by the high numbers trapped in outermost Cornwall (Appendix 3).

An important point is that what appears to be orthodromic navigation may – as remarked by Alerstam & Pettersson (1991) – be uncompensated solar compass orientation. Juvenile birds initiate their east-west autumn migration at high latitudes using a fixed compass direction relative to the sun, maintaining this direction without compensating for the sun's movements over several days.

This hypothesis is testable. For instance, juvenile Red Knots *Calidris canutus* from northern Ellesmere Island, bound for the Netherlands (Kok *et al*. 2020) may be displaced to Alaska. The orthodromic direction from Ellesmere is a slightly north of east, while from Alaska it is approximately NNE. If the Knots rely solely on compass orientation, their direction from Alaska should mirror that from Ellesmere. Kok *et al*. (2020) did not conduct such a displacement, but an adult Knot in their study migrated about SE from Ellesmere suggesting loxodromic navigation, or perhaps SE compass orientation. However, this may be a later adaptation to maximise land-crossing.

A similar displacement experiment to Alaska could involve juvenile Wheatears from West Greenland bound for Senegal. The great circle direction from West Greenland to Senegal is SSE, while from Alaska it is NE.

Appendix 3 outlines the historical development of my thinking, beginning with a focus on loxodromes and little consideration of flat/planar navigation in a spherical context. Over time, both orthodromic and flat/planar navigation were incorporated into the framework, with orthodromic navigation emerging as a most plausible mechanism.

New evidence supporting NAVGA and direct navigation towards the wintering area

It is to be hoped that the hypothesis of a moving goal area – *NAVGA* – will be reconsidered for serious scientific scrutiny, rather than being dismissed out of hand. Encouragingly, recent evidence lends support to this concept. Carneiro *et al*. (2023) provide relevant data, although the inferred navigation in juvenile birds appears more directly oriented towards the wintering area than strictly NAVGA-based. Their study compares the autumn migratory progress of juvenile and adult Icelandic Whimbrels *Numenius phaeopus islandicus* wintering in West Africa. The introductory remarks merit citation: "Migratory behaviour in young individuals is likely developed by using a complex suite of resources, from molecular information to social learning. Comparing the migration of adults and juveniles provides insights into the possible contribution of those developmental factors to the ontogeny of migration. We show that, like adults, juvenile Icelandic Whimbrels […] fly non-stop to West Africa, but depart on average later, follow less straight paths, and stop more after reaching land, resulting in slower travel speeds. We argue how the variation in departure dates, the geographical location of Iceland, and the annual migration routine of this population make it a good model to study the ontogeny of migration". These words echo the cautious statement by Thorup *et al*. (2020) cited in Appendix 5 under "The role of R. & W. Wiltschko": "Young Cuckoos respond similarly to long-distance displacements as adult Cuckoos".

Fig. 1 in Carneiro *et al*. illustrates strikingly similar autumn tracks for both juvenile and adult Whimbrels migrating from Iceland to West Africa. The ellipsoid pattern in both groups suggests direct navigation towards the wintering area, as a special case of NAVGA (cf. Rabøl 2023). Carneiro *et al*. (2023) did not consider the time ripe for such an interpretation.

Anyway, the generalization by Perdeck (1958), that initial CC in the juveniles in some way transforms into navigation in the adults, does not hold across all migrant bird species.

Earlier, Gschweng *et al*. (2008) documented a similar pattern in GPS-tracked juvenile and adult Eleonora's Falcons *Falco eleonorae* migrating from Sardinia to northern Madagascar. Juveniles migrated independently of adults, and both groups followed ellipsoid paths suggestive of direct navigation towards the wintering area. Remarkably, this interpretation did not occur to the authors, who were firmly anchored in their CC-based expectations. To their credit, the migration may have begun as CC-guided, but from around the equator it certainly transitioned into true navigation.

NAVGA reconsidered

When I first proposed what is now termed NAVGA (Rabøl 1969, 1970), it was conceived as an alternative to constant navigation directed towards the wintering area. At the time, any observed compensation following displacement was interpreted as navigational. My current view is more nuanced: what appears to be compensatory navigation in free-flying birds may indeed be navigational, but it could also reflect directional responses to previous or ongoing wind drift or be an after-effect of prolonged aberrant movement along a coastline. However, compensatory orientation recorded in funnel experiments, and especially in simulated celestial or magnetic fields, is difficult to interpret as anything other than navigational.

NAVGA may be latent throughout the migratory journey, only becoming active in the later stages as navigation towards the wintering area. Researchers such as Holland (2014), McLaren *et al*. (2022), and Karwinkel *et al*. (2024), who traditionally support an innate CC-based system, are increasingly acknowledging the necessity of navigation in juvenile birds during the final approach. The conceptual gap between my perspective and that of mainstream researchers is clearly narrowing.

The need for a new paradigm

As previously noted, the hypothesis of the moving goal area (now termed NAVGA) was introduced by Rabøl (1969) and subsequently revisited in several publications (Rabøl e.g., 1978, 1980, 1985, 1994, 2023). Emlen (1975), in his important review, acknowledged the hypothesis. However, on the European front, H.G. Walraff as well as R. & W. Wiltschko remained sceptical and soon strongly opposed the concept – particularly due to its coupling with stellar navigation (cf. Rabøl 1980), which they mistrusted.

The Wiltschkos consistently championed their magnetic cue system, expressing scepticism towards the primary role of celestial cues in migratory birds and olfactory cues in pigeons. Their conceptualisation of navigation was shaped by their emphasis on the outward transport route of pigeons in relation to

Preparation for night-experiments with eight magnetic coil-fields. Photo: Peter Lyngs.
Opstilling til orienteringsforsøg med kunstige magnetfelter på Christiansø i efteråret 2006. Se Rabøl (2022).

the magnetic field. Wallraff, meanwhile, focused on homing pigeons, where stellar navigation is irrelevant and olfactory navigation is central

A comparison between the reviews of migratory orientation/navigation by Emlen (1975) and Holland (2014) reveals a stark contrast. At the time of Emlen's review, the Wiltschkos were only beginning to develop their magnetic orientation framework, and celestial navigation remained the dominant paradigm. By contrast, Holland's (2014) review reflects a near-total dominance of magnetism, with celestial navigation relegated to obscurity. Notably, F. Sauer (1957), a pioneer in planetarium experiments, is not mentioned – nor am I, except for my contribution to Thorup & Rabøl (2007).

That study demonstrated that compensatory orientation – particularly in juvenile birds – is the typical response to real or simulated displacements. Holland did not sufficiently acknowledge this, especially in relation to stellar navigation, which had become a "forbidden concept". The third actor on the stellar navigation scene, Emlen (1967a, 1967b, 1975) is mentioned by Holland for his results interpreted as the outcome of a CC-system. No clear examples of navigation were identified. However, Emlen's planetarium displayed a ″stellar sky″ that rotated abruptly 3.75° every 15 minutes, i.e., it was stationary almost all the time. A setup perhaps unsuitable for demonstrating stellar navigation, much like the stationary ″stellar sky″ in the widely cited paper of Mouritsen & Larsen (2001). Consequently, their findings too cannot be considered as a proof of CC.

Rabøl (2014) mentions many studies with questionable interpretations favouring magnetic navigation. While Holland (2014) could not have known my 2014 contribution, his review lacks the critical scrutiny one might expect. Since then, additional papers with questionable claims on magnetic navigation have emerged, such as Illieva *et al*. (2023) on *Acrocephalus* warblers.

Karwinkel *et al*. (2024) offer a long-awaited, cautious critique of the dominant role of magnetic orientation and navigation in birds. Their work represents a significant shift, authored by six researchers not overly constrained by prior magnetic biases. I am no longer alone in this perspective. However, it appears that Karwinkel *et al.* are unaware of my contributions – at least, key works such as Rabøl (2014, 2022, 2023) are not cited, even though one of the co-authors is Danish.

Karwinkel *et al.* (2024) focus on the broader issue of contradictory results that plague the magnetic navigation literature. These inconsistencies cannot in the long run be explained as just caused by different bird species, methodological variation, stochastic outcomes, competing cues, or opportunism (the latter absent from their discussion).

It is clear that a reassessment of the role of magnetism in bird navigation – and indeed in compass orientation – is urgently needed. Rabøl (2022), in carefully controlled experiments, was unable to confirm the inclination compass hypothesis (first proposed by Wiltschko & Wiltschko 1972), and no evidence of a functioning magnetic compass was found. This lack of repeatability was already noted by Emlen (1975), and later inspired Mouritsen & Hore (2012) to describe it as the "chronic disease" of the field.

As emphasized in Rabøl (2022), a new era must follow the Wiltschko's, who were consistently selective and directed in their efforts to establish a strong magnetic and CC-based framework. What is needed now are simulated magnetic displacement experiments that demonstrate compensatory responses indicative of a magnetic navigational system. Additionally, new displacement experiments should be conducted under a planetarium sky rotating with the natural speed of the starry sky also in the test phase.

Acknowledgements

This contribution is the final part of a trilogy including Rabøl (2022, 2023), which may be considered my legacy on bird migration and orientation and the successor of my book *Fuglenes træk og orientering* (Rabøl 1988). I am my friends and colleagues Hans Meltofte and Jon Fjeldså deeply indebted for their trust and confidence in me in spite of my often "challenging" style. They did a great job in improving the manuscripts, and these papers had not been possible to publish in any other research journal than DOFT. For reasons I never quite understood, I always was a controversial person, starting with my focus on the phenomenon of "headwind migration" (Rabøl 1964, 1967), which was followed by my introduction of the concept of "goal area navigation" (Rabøl 1969). An anonymous reviewer provided useful suggestions for improvements, David Boertmann kindly improved my English, and so did David B. Collinge. Finally, a last salute to my late soul mate, Henning Noer. Unfortunately, his untimely death put an end to our fruitful collaboration.

Resumé

Comeback for og præcisering af målområde-navigationsbetydning for nattrækkende småfugle

I det følgende tænkes især på en nat- og langt-trækkende spurvefugl. Før træk-start har den juvenile fugl – for at kunne finde tilbage til start-området = yngle-området næste forår – indprentet sig synet af omgivelserne, de stedlige duft-gradienter, magnetfeltet med parametrene intensitet, inklination og misvisning, solhøjden midt på dagen, samt højden af Nordstjernen over horisonten, og stjernernes mod-urs rundgang om Nordstjernen, der som viserne i et ur kan oplyse trækfuglen om klokken på dagen/natten, datoen og Ø/V-positionen/længdegraden.

Trækfuglen har nu forankret yngleområdet, så den har noget at navigere tilbage til næste forår. Men den har også gjort sig fortrolig med stjernerne, Solen og magnetfeltet, der i princippet alle tre danner et verdensomspændende koordinatnet, der kan bruges til navigation.

Fuglen starter sit efterårstræk fx den 20. august ud fra anvisninger nedlagt i dens gener, der går i samspil med input fra omgivelserne. Starter den nu bare i en retning mod – skal vi sige – SV, der så efter 15 træktrin på hver 240 km (8 timer hver anden nat med en flyvetid på 30 km/timen) = 3600 km, hvorefter den skifter retning til SSØ og så stopper trækket efter 10 træktrin til = 2400 km. I alt har den så fløjet 6000 km på 50 døgn, og datoen er 8. (eller 9.) oktober. Den stopper så, fordi den ifølge sit genetisk fixerede trækprogram har nået sit vinterkvarter, hvor den nu skal tilbringe 'vinteren' de næste syv måneder før den midt i april starter hjemrejsen mod det område, hvorfra den startede sidste år. Et sådant træksystem kaldes CC (= Clock & Compass).

A. C. Perdeck publicerede i 1958 en skelsættende artikel om Stære fra Østeuropa ringmærket på efterårstræk i Holland på vej mod VSV til overvintring i England. Perdeck flyttede i tusindvis af ringmærkede Stære til Schweiz, slap dem der, og noterede, hvor de senere blev genfundet. De fleste af de juvenile Stære blev fundet mod VSV i Frankrig/Nordspanien, mens de fleste voksne Stære trak NV til England, til det vinterkvarter, som de allerede mindst en gang tidligere havde besøgt. Fortolkningen af forsøget var klar: de juvenile fugle kompasorienterede mod VSV, efter anvisninger nedlagt i deres gener. De voksne Stære navigerede mod det vinterkvarter, som de var blevet præget på i mindst en tidligere vinter.

Dette forsøg med sin rimelige konklusion, blev nu generaliseret som model for alle trækfuglearter. Det var ikke rimeligt.

Senere forsøg af især undertegnede viste, at juvenile nattrækkende spurvefugle mestendels kompenserede for forflytninger enten disse nu var virkelige eller simulerede med fugle tragttestede under den naturlige stjernehimmel eller i planetarier med andre 'stjernehimle' svarende til andre samtidige positioner på Jorden. Disse kompensationer var ikke rettet mod vinterkvarteret men mod at såkaldt vandrende målområde på sin vej i trækruten mod vinterkvarteret.

I mine forsøg med mange kortdistance-forflytninger og en del mellem- og langdistance-forflytninger er der en generel tendens til kompensation for forflytningen, der peger tilbage på et medfødt navigationsprogram kaldet NAVGA (NAVigation towards a moving Goal Area). Her bevæger et målområde sig kontinuerligt i løbet af træksæsonen langs

Many years of experiments with juvenile night migrating passerines suggest that the birds use a programme of consecutive goal areas along the migratory route like pearls on a string, the so called NAVGA navigation system. Garden Warbler Sylvia borin, photo: John Larsen.
Mange års eksperimenter med juvenile nattrækkende småfugle indikerer, at fuglene følger et program af fortløbende målområder langs trækruten som perler på en snor, det såkaldte NAVGA-system. Havesanger.

trækruten som perler på en snor, hvor fuglen altså skal være på en bestemt position på et bestemt tidspunkt på året (se Fig. 1).

Især for nonstop-trækkerne, men i princippet for alle Ø/V-trækkende fugle er nu tilbage er at finde ud af om navigationen sker loxodromisk eller orthodromisk. En loxodrom holder en konstant kompaskurs fra start til slut, men en sådan er meget ofte især for store Ø/V-lige forskelle mellem start og mål betydeligt længere og dermed mere energikrævende end ved orthodromen. En sådan forløber den korteste vej mellem start og mål (Fig. 2), dvs. langs en storcirkel. Vadefugleforskerne har flere gode eksempler på orthodrom-forløb.

Det store spørgsmål er endvidere, hvilke eksterne systemer der styrer specielt efterårstrækket hos de juvenile fugle: Er det Solen og stjernehimlen, eller Jordens magnetfelt? Der er lavet alt for få forflytningsforsøg, virkelige eller simulerede i et stjerne-planetarium eller i kunstige magnetfelter. Stjernehimmelforsøg viser som oftest kompensationer for forflytninger på kortere distancer fra måske 400 km og op til nogle tusind kilometer, men resultatet af langdistance-forflytningerne er ikke altid lette at tolke. Mestendels er et NAVGA-baseret træk dog en rimelig fortolkning. Juvenile fugle testet om efteråret viser ikke navigatorisk kompensation i ændrede magnetfelter, og magnetisk navigation er sandsynligvis et meget overvurderet fænomen også hos andre dyr end fugle.

NAVGA har i over 50 år stået til rådighed som et forslag til, hvordan man kan fortolke specielt de mellem- og langdistance-trækkende spurvefugles medfødte trækprogram. Men de allerfleste forskere har forkastet muligheden, dels på grund af for meget Perdeck-generalisering, dels fordi systemet forekom for kompliceret til at kunne programmeres ind i generne på en trækfugl. I de sidste 10-15 år er man dog begyndt at tale højt om, at et CC-system ikke slår til alene som det medfødte trækgram; der må være navigation indblandet. For nu at bringe NAVGA helt i perspektiv: Jeg tror det ligger latent hos alle trækfuglearter, men det kan i større eller mindre grad 'overrules' af andre systemer/processer. Specielt kompensationerne under en planetarie-stjernehimmel er dog ikke lige til at bortforklare som noget andet end NAVGA-relaterede.

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Appendix 1: https://pub.dof.dk/link/2026/1.appendix1
Appendix 2: https://pub.dof.dk/link/2026/1.appendix2
Appendix 3: https://pub.dof.dk/link/2026/1.appendix3
Appendix 4: https://pub.dof.dk/link/2026/1.appendix4
Appendix 5: https://pub.dof.dk/link/2026/1.appendix5

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