Appendix 5 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.

Further considerations

In the mirror of reflection

This contribution is about the reconsidering of NAVGA (navigation towards a progressively forward moving goal area), a system proposed more than fifty years ago (Rabøl 1969, 1970) but not even mentioned in the review of avian migration by Newton (2024).

NAVGA should only be considered one kind of alternative to a clock & compass/vector navigation system (CC) in migrant birds. NAVGA is found particularly in long-distance migratory passerines primarily crossing land but sometimes also smaller or medium distances of sea.

Another navigation system – perhaps sometimes developed from a NAVGA system – may be a direct one-step navigation from the breeding ground towards the wintering area involving huge sea crossings such as in Greenlandic Northern Wheatears *Oenanthe o. leucorrhoa* (Thorup *et al.* 2006b). Many Arctic shorebirds probably belong to this category including the most extreme, the Bar-tailed Godwit *Limosa lapponica baueri* flying nonstop from Alaska to New Zealand and Eastern Australia in up to 11 days (Battley *et al.* 2012).

Finally, a modification where the migration starts as CC and then in course of the progress develops into genetically based navigation towards the wintering area may also be found. A possible example could be Eleonora's Falcons *Falco eleonorae* migrating from Sardinia through Africa to the northern part of Madagascar (Gschweng *et al.* 2008).

When I back in 1969 and 1970 introduced what later was named NAVGA, it was because the compensatory orientation following a man-made geographical displacement was not normally directed towards the wintering ground but towards a closer position some way down the migratory route. Now, in a CC system birds displaced by the wind may show a counter-reaction towards the wind resembling a navigational based compensatory orientation. Here true navigation is not necessarily involved. However, birds showing compensation as just outlined following geographical displacement by man, and particularly in case of simulated displacements (e.g., changing the rotationally phase and/or the altitude of the rotational point of the ”stellar sky” in a planetarium) is considered proof of a NAVGA system. Thorup & Rabøl (2007, extended by Rabøl 2023), in a meta-analysis of all funnel/cage-experiments found that this is the normal response, and Rabøl (1998) provided the core experiment: the grand mean vector of the sample mean directions of 16 ”displacements” under a planetary ”stellar sky” was 197° – 0.154 in reference to geographical N and -11° – 0.755 ($P < 0.01$) in reference to a goal in Eastern France (SW of the trapping site of the autumn migrants on Christiansø in the Baltic Sea).

Is there any evidence that also the magnetic field may be involved in a NAVGA system? The very short answer is no! More details below.

Rabøl (2014) added an artificial magnetic coil field, up- and downgrading the magnetic inclination and intensity to 76.5°/70 μT and 53°/27 μT, respectively (the normal field on Christiansø, Denmark is 70°/48 μT) thus simulating geographical displacements towards about N and S, respectively. Three groups of juvenile Africa-migrants (including a control group) were tested in autumn comprising seven samples each. The birds were tested under a starry sky. The expected orientations were highly concentrated S-SSW, concentrated SSW-SW and more scattered W-N for N-”displacements”, controls and S-”displacements”, respectively. In short, the expectations were not met. The N-groups showed medium concentrated SSE-S, the controls clearer SSE-S, apart from a single sample with NW/(SE) and the S-group clear SSE-orientation. Conclusion: no indication of any magnetic inclination/intensity in a NAVGA system.

Chernetsov *et al.* (2017) autumn-tested birds trapped in Rybachy, Kaliningrad (magnetic declination +5.5°) and ”displaced” to Dundee, Scotland (magnetic declination -3°). A single group of adult Common Reed Warblers *Acrocephalus scirpaceus* showed a significant shift from WSW towards ESE matching the NAVGA expectations. However, juvenile Reed Warblers were disoriented (see Rabøl 2023). Later, Chernetsov *et al.* (2020) tested adult Garden Warblers *Sylvia borin* and adult and juvenile European Robins *Erithacus rubecula* under the same conditions, with no significant change in (about standard) directions. To conclude, there was at least in juveniles no indication of a NAVGA system based on magnetic declination.

Rabøl (2023) added a fairly weak horizontal magnetic field to the magnetic field of the Earth on Christiansø (towards NNE (20°) or NNW (-20°)), and in this way changed the combined declination to +15° or -9° (the declination of Christiansø is +3°). These two declinations correspond to positions in the Ural Mountains and somewhere between The Faroe Islands and Iceland. The resultant inclination is 49°, and the resultant intensity 1.24 times the natural on Christiansø = 59.5 μT (perhaps this un-natural composition matters; we do not know). The birds were tested under a starry sky in autumn 2016. First, a group of Africa-migrants (Common Redstarts *Phoenicurus phoenicurus*, Garden Warblers and European Pied Flycatchers *Ficedula hypoleuca* were considered. Unfortunately, the controls were disoriented (345°/165° – 0.275, N = 11). The E- and W-”displaced” experimentals were also disoriented, i.e., insignificantly oriented in the about NW and NE expected, but nevertheless showed the expected W- and E-deflected orientation (295° – 0.341 (N = 16) and 43° – 0.242 (N = 16), respectively). Later, a group of European Robins were tested, and if only unimodal sample mean directions were considered, the grand mean vector, 225° – 0.698 (N = 5) was close to significance ($0.05 < P < 0.10$). The E-”displacements” showed 258° – 0.104 (N = 16), whereas the W-“displacements” oriented significant in the ”wrong” direction 252° – 0.543 ($P < 0.05$, N = 13). In conclusion, there was no tendency to NAVGA compensations based in the magnetic declination.

Simulation of some simple CC systems: navigation not considered

McLaren *et al.* (2022) analysed the progress of migration for several animals; in a similar way as done by me but more theoretically and elaborately, focusing explicitly on CC and ignoring NAVGA (including CC with wind) as alternatives. The migratory progression in seven species (six birds and one butterfly) was simulated in five different systems: 1) geographic loxodromes, 2) magnetic loxodromes, 3) magneto-clinic progress in sense of Kiepenheuer (1984), 4) sunset-compass orientation without time compensation, and 5) sunset-compass orientation with time compensation. The orientation (showing parabolic spread) is depicted in reference to a circular wintering area and – as a first approach – it is up to the reader to judge the explanatory power by a simple look at the patterns. Next, several ways of treatment are presented, e.g., leading to a percentage of the birds ending in or passing through the wintering area. No influence of a wind-vector is explicitly considered, but what probably ends up as close to the same, is an overlayered establishment/maintenance directional variation upon a basic intraspecific directional concentration on e.g. 0.99. Thorup & Rabøl (2001) did about the same – but less elaborate/detailed – when considering the autumn progress of Barred Warblers *Curruca nisoria* to East Africa.

McLaren *et al.* (2022) present a very basic CC-approach: it is mostly not possible to distinguish between the ”goodness” of the models (except that the magneto-clinic hypothesis in general describes rather poorly, and the time-compensated sunset-compass orientation model on the average describes best (as mentioned, no NAVGA(-like)-models are presented). McLaren *et al.* also show selected species, where the migratory route is more or less straight or slightly curved, whereas in many other species the route bends dramatically, in some cases more than once, as in case of European Pied Flycatchers from The Netherlands (Ouwehand *et al.* 2016).

My concept of goal area navigation was not recognized by McLaren *et al.* (2022) nor Holland (2014) and as said above, not even mentioned in the review of avian migration by Newton (2024). Furthermore, the compensatory orientation observed is much talked down and not appreciated by Holland (2014).[1,2]

McLaren *et al.* (2022) write that “overall directional errors being reduced over many flight steps, known as the many-wrongs effect”. Is this the same as named by me as the parabolic spread characterizing a CC progress (fig. 1 in Rabøl 2023)? – as also observed in fig. 4 in McLaren *et al.* (2022). Clearly, McLaren *et al.* cannot mean that there is some kind of negative feedback (compensation) involved in a CC-progress? Certainly, there is not. Perhaps they just mean that the error in calculating the mean direction diminishes with number of trials?

In their introduction, McLaren *et al.* (2022) write: “A critical yet unresolved factor for migrating populations is how inexperienced (hereafter naïve) individuals can perform inaugural migrations through unfamiliar habitats in unpredictable conditions. Experienced migrants are thought to

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[1] In my mind, latitudinal navigation does not appear more complicated to program in the genes than a shifting compass direction. Longitudinal navigation perhaps does; see Appendix 1).

[2] The hypothesis of the moving goal area was first mentioned by Rabøl (1969), and later many times (Rabøl e.g. 1978, 1980, 1985, 1994).

perform true navigation." The birds are, in other words, not assumed to be born with a "map" or navigational coordinates, which is something developing after birth through learning/imprinting.

Next, the subject of magnetic orientation/navigation is an area of much opportunism. McLaren *et al.* (2022) consider the magneto-clinic hypothesis of Kiepenheuer (1984) as a serious possibility. Now, it is always possible to find at least parts of curved migratory paths matching this hypothesis. However, the rationale behind the hypothesis is rather weird and there are many examples (e.g., Ouwehand *et al.* 2016) of migratory routes incompatible with a magneto-clinic course. Why have people (e.g., H. Mouritsen and D. Kishkinev) with their appropriate equipment never tested the magneto-clinic hypothesis? Nothing would be easier: test a sample of European Robins from Finland in autumn in overcast/indoor conditions and with inclinations shifting several times/nights alternatively between +60° and +35°. If we assume magneto-clinic orientation, we should predict a mean vector shifting between about 230° and 200° [3]. Perhaps, one need a little patience as both individual and sample concentrations are mostly low when funnel-tested in overcast/indoors conditions. One should be careful selecting a species/population where the known migratory route roughly follows the prediction of a magneto-clinic shift. Otherwise, this may be the reason why your test fails. As far as such a test is not carried out, Kiepenheuer (1984) will be referred to uncritically every time magnetic orientation is considered.

The role of R. & W. Wiltschko

The following might be considered too personal, but it had the important consequences for me that the moving goal area hypothesis never had a role to play and was not even mentioned in the important reviews by Holland (2014) and Newton (2024). In his abstract, Holland promises "Unlike many general texts on migration, which avoid discussion of these issues (i.e. the "conflicting and confusing results") this review will present these conflicting findings and assess the state of the field of true navigation during bird migration." Unfortunately, not always so.

Wiltschko & Wiltschko (1999) brought distorted information about several of my displacements among these the significant compensatory orientation – indicative of navigation – in my planetary experiments (Rabøl 1998). According to the Wiltschko's "Vorstellungen von der Steuerung des Vogelzugs wurden gelegentlich Hypothesen vertreten, die angeborener Navigation zum unbekannten Ziel anhand Sternbildern ausgingen (z.B. Sauer 1957, Rabøl 1972, 1985, 1998). Die in Arbeit I. Abschnitt 4. beschriebenen Versuche zur sternorientierung sowie die hier in Abschnitt 2.1 vorgestellten Versuche sprechen jedoch dafür, dass Sterne erlernt warden und nur zur Kompassorientierung dienen." Very clearly, this a mixture of a (too) strong adherence to the "official" scenario, a misuse of the word "unbekannten" added to none or too superficial reading of the paper. Here the central Fig. 2 shows without reasonable doubt that the interpretation of my planetarium experiments must be NAVGA and not CC: the grand mean vector of the 16

[3] Or perhaps better inclinations +80°, +60°, +35°, and +10° with corresponding expected directions at about 260°, 230°, 200°, and 185°, respectively.

displacements in reference to geographical N was 197° – 0.154, whereas the grand mean vector in reference to a goal area in France was -11° – 0.755 ($P < 0.01$).

Another example also from Wiltschko & Wiltschko (1999) is the orientation of European Robins displaced in autumn from Denmark to La Gomera, Islas Canarias (Rabøl 1981). According to the Wiltschkos, these results "erbrachten unklare, schwer zu interpretierende Ergebnisse." This is simply not true: the juveniles at least partly compensated for the displacement towards W showing ESE-orientation indicative of a navigational process, whereas the adults showed clear S-SSW orientation close to standard, what they should not do according to the prevailing expectation of navigation in adults. Here, a compensatory NE-navigation towards Spain was expected. Anyway, the patterns of juveniles and adults were not unclear but rather beyond the settled imagination of most people within the field.

The same words from the Wiltschkos referred to the orientation of 20 European Pied Flycatchers (10 adult, 10 juvenile), 18 Garden Warblers *Sylvia borin* (10 adult, 8 juvenile) and seven Lesser Whitethroats *Curruca curruca* (all juveniles) displaced in autumn from Denmark to Naivasha, Kenya (-1° N/36° E, -23° magnetic inclination; Rabøl 1993) and tested from 13 September through 10 December 1987. Here the results are more complex and open for different interpretations. Anyway, the wording of the Wiltschkos is misleading. The amount of westerly orientation was striking, indicating that the birds were aware of an easterly displacement counteracted by some kind of navigation. A general awareness (indicative of navigation) of a southerly displacement was not observed in the Garden Warblers but northerly orientation constituted a significant secondary peak in the flycatchers, and the prominent peak in the Lesser Whitethroats.

In more details, significant amounts of (initial) northerly compensatory orientation – indicative of NAVGA – were observed in the juvenile compared with the adult European Pied Flycatchers. On the contrary, the late autumn W-WNW orientation was prominent in the adult flycatchers – suggestive of navigation towards the wintering area in the Ivory Coast. Contrary to the CC-expectation, the juvenile flycatchers showed no SE-orientation in late autumn whereas the adults – again contrary to a CC-expectation – showed a significant secondary amount of SE-orientation (whole autumn). In the Garden Warblers, there was no difference between adult and juvenile birds, and an overall SSW-SW-orientation was obvious. If CC, there should have been much SSE-orientation in late September and October, and perhaps there was the presumed "pressure" of westerly compensation taken into consideration. All seven Lesser Whitethroats were juveniles, and most orientation was compensatory northerly indicative of navigation. If CC, the orientation should have been SSE.

Summing up, including the European Robins translocated to the Canary Islands, indications of navigation were found in several cases – and more in juveniles than in adults (same tendency as in Thorup & Rabøl 2007). The occasional lack of compensation (navigation) in adult birds clearly surprised Wiltschko & Wiltschko (1999). Another important point, as already stressed by Rabøl (2023), is that a re-navigation system as proposed by W. Wiltschko (1973), if extended beyond a single step, would develop into a CC-system with a parabolic spread in the long run. Probably, the Wiltschkos all the time since 1973 considered an extended re-navigation system appropriate for explaining compensatory orientation in juvenile birds. Finally, as argued by Rabøl (2023), it is difficult to see how a learned navigation system could develop from an inherited CC-system.

Because of misinformation, silence about papers demonstrating indications of stellar navigation and too much and uncritically adherence to the importance of magnetic cues, several people such as McLaren *et al.* (2022), Holland (2014) and Newton (2024) seemingly do not know the hypothesis of goal area navigation as the system behind compensatory orientation. Or perhaps they just consider it as outdated just as the sun-arc navigation hypothesis of Matthews (1968) and Pennycuick (1960). I admit that I was too reluctant to insist on mentioning the goal area navigation hypothesis explicitly as a co-author in more recent papers (e.g., Thorup *et al.* 2010, 2011). However, the term goal area navigation was mentioned in Thorup & Rabøl (2001, 2007), which are broadly referred to. Perhaps, people believe that mentioning the concept would reduce the likelihood of acceptance of a submitted manuscript. Even Thorup *et al.* (2020) apparently tries to avoid using the controversial term.

It is time to realize that any consistent compensatory orientation following a displacement – if not obviously influenced by a disturbing taxis – is navigational, whatever weak the tendency may be. You cannot avoid navigation by naming it CC + something compensatory.

Are funnel experiments on the way out?

When Emlen & Emlen (1966) published the funnel-method, the field of passerine bird migration and orientation changed significantly. I was among the first (1967) to follow Emlen (1967a, 1967b) testing birds in funnels, followed up by the Blåvand/Ottenby displacement experiments in the autumn of 1968 (Rabøl 1969). In Germany, W. Wiltschko (1968) already was on his way with the radial-perched Frankfurt-cage. This type of orientation cage was occasionally in use up into the nineties (Weindler *et al.* 1996, 1997) and perhaps also later.[4] Then the Germans shifted using funnels, where the interpretation of the foot scrape pattern was more straightforward than the movement pattern on radial perches in the Frankfurt cage.

The alternatives to cage-testing are 1) analysing recovery-patterns of banded birds (such as Perdeck 1958, 1967), 2) tracking released birds by eye (during daytime with pigeons, or during night with a light-stick glued to the tail (Ottosson *et al.* 1990, Mouritsen 1998), 3) radio-tracking by means of car and/or airplane (introduced many years ago, Cochran 1972, Thorup *et al.* 2007), 4) geo-locators (Ouwehand *et al.* 2016, Pedersen *et al.* 2020), or 5) satellite-tracking first of larger birds such as raptors (e.g. Thorup *et al.* 2003, 2006a) and gulls (Wikelski *et al.* 2015) and presently down to the size of a Common Cuckoo *Cuculus canorus* (Thorup *et al.* 2020). However, funnel-testing – presumably for a long time into the future – is still the only way to study direct manipulations of the

[4] When I visited the Wiltschkos in Frankfurt in 2001 they used funnels for recording the orientation of European Robins in an exercise carried out with their students: Robins are well oriented in both kinds of cages. Beck & Wiltschko (1983) report that European Pied Flycatchers are well oriented in funnels but not in Frankfurt cages.

magnetic field or the starry sky. Therefore, funnel experiments will still contribute to our understanding of what is going on out there in this bewildering natural world.

In the rather near future

Probably, the war in Ukraine for a long time ended the possibilities of scientists from Western Europe to work in Russia with displacements over large E/W-gradients (e.g., Thorup *et al.* 2020). This is a great drawback for the study and understanding of the orientational/navigational system of migratory birds. The promising work of Thorup *et al.* with GPS-tracked Common Cuckoos will stop because of political rather than technical problems.

If the weight of transmitters must be limited to be no more than 5% of the weight of the bird, we are still some way from GPS tracking Red-backed Shrikes *Lanius collurio* and a long way from tracking Northern Wheatears – for investigating the influence of E/W shifts – e.g., displaced from Alaska to Greenland, and from Greenland to Alaska.

Working with geo-locators, Pedersen *et al.* (2020) never realized that they were in position to extend their investigation, i.e., transferring geolocator equipped fledgling shrikes into well-marked painted outdoor aviaries, feeding them well and releasing them after departure of their parents. Probably, the juvenile birds would then stay in the neighbourhood for some days and nights and imprint on the aviary and nearest surroundings before departure (a process already started in the aviary) and return next year for a possible recapture revealing their movement in the past year. Without such a procedure, the fledglings will disperse away from their natal area, not being available for recapture. The normal picture for most passerines is that only the adults – and in particular the males – return to the very breeding site from previous years (e.g., Ouwehand *et al.* 2016).

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Author's address: Jørgen Rabøl (jrabol@hotmail.com), Søndermølle 16, DK-8789 Endelave, Denmark