Appendix 2 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.

Simulation of vector orientation and goal area navigation in night-migrating passerines

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(*Med et dansk resumé: Simulering af vektororientering og målområdenavigation hos nattrækkende småfugle*)

Abstract Currently, vector-orientation/clock-and-compass orientation (CC) is considered the only genetically fixed orientation system in long-distance migrant passerine birds. However, considering contour ellipsoids of geolocator-tagged birds or virtual 'birds' indicate that such a system is not adequate for 'delivering' the necessary number of surviving juvenile birds to the wintering area. Here we demonstrate how a system based on goal area navigation, i.e., birds navigating towards a progressively forward moving goal area (NAVGA) can work. Populations of European Pied Flycatchers *Ficedula hypoleuca* from the Netherlands and Red-backed Shrikes *Lanius collurio* from Denmark are used as models.

Introduction

The general perception within the field of bird migration, orientation, navigation and homing is that juvenile birds are endowed with a vector orientation/clock & compass system, whereas adult/experienced birds are able to navigate towards imprinted goals (Perdeck 1958, Thorup *et al.* 2007, Box 1).[1] This paradigmatic faith leads to an unrecognized (or in fact a repressed) problem: How does an imprecise inherited system 'transform' into a more precise real-world system?[2] The

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[†] Henning Noer passed away in 2018 and has not had the possibility to approve the manuscript.

[1] The claimed clearcut difference between non-compensating juveniles and compensating adults following a geographical displacement does not exist. The juvenile White-crowned Sparrows *Zonotrichia leucophrys* of Thorup *et al.* (2007) compensated/navigated significantly, though to a smaller extent than the adults (Rabøl 2023; Appendix 3). Additionally, some of the juvenile Common Starlings *Sturnus vulgaris* studied by Perdeck (1958, 1967) compensated, while some of the adults did not (Rabøl 1981).

[2] A related paradox arises when R. Wiltschko (e.g., Wiltschko *et al.* 2008) and R. Muheim (e.g., Sjöberg & Muheim 2016) argue for imprecise magnetic- or sunset-compasses, respectively, calibrating the fundamentally much more precise stellar compass (appendix 4 in Rabøl 2022).

only possible way of understanding is through differential mortality on the population level. However, apparently this leads to an unrealistic 'overkill' of juveniles (e.g., Thorup & Rabøl 2001).

Probably, the mortality is kept at a sufficiently low level, if the juvenile birds start with a rough kind of inherited navigation where natural selection 'sharpens' the variation. This has been the point of view of JR for the past c. 50 years. After years of reluctance K. Thorup and his group[3] – based on satellite-tracking of Common Cuckoos *Cuculus canorus* – cautiously seem to approach this point of view (Vega *et al.* 2016, Thorup *et al.* 2020). However, most people within the field still adhere to the paradigm of vector orientation as the one and only inherited orientation system.

Anyway, we need more experimental research (Rabøl 2023, appendix 4) and realistic simulations of the two 'rival' systems of vector orientation and goal area navigation. This contribution is mostly about the latter, using data from a small population of European Pied Flycatchers *Ficedula hypoleuca* and Red-backed Shrikes *Lanius collurio*.

The present appendix developed over the course of several years but is still premature compared to a true scientific contribution. Anyway, the purpose is to understand what bird migration is about, and if just a few sections or sentences could catalyse positive conceptions in the mind of other scientists, this would be sufficient for me to release a publication.

Box 1. Prelude

Henning Noer (HN) and I first met each other at the lighthouse of Knudshoved, easternmost Funen, Denmark in the spring of 1963. Twenty-three-year-old I was on my favourite stand taking notes on migrating birds. My observations of primarily Skylarks *Alauda arvensis* were published in Rabøl (1964, 1967). HN was only fifteen years old but had already demonstrated great talent. We became friends though for the first years under my mild but not always democratic leadership. Anyway, HN survived and together we developed a passionate interest in Skylark migration and the influence of wind on bird migration, in the case of the Skylarks not least the prominent amount of over-compensation, so-called headwind migration.

Later, HN studied the wind-influenced waders passing Blåvandshuk, the westernmost point of Denmark. His work was released in a mammoth-treatment of 718 pages (Noer 2017). Part of this report was published as Noer (2019). Much earlier, HN published an important paper on the influence of the wind vector and flock size on the airspeed of migrating waders (Noer 1979). Together, we authored Rabøl *et al.* (1971), Rabøl & Noer (1973), and Geil *et al.* (1974). The last two papers became well cited and influential.

Both of us studied biology, and HN also mathematics at the University of Copenhagen. A few years after HN graduated, he attained a job at the Game Biology Station, Kalø, whereas I continued as a

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[3] Part of a sentence in the title of Thorup *et al.* (2019) appears as a judicial masterpiece: "young cuckoos respond to long-distance displacements as adults", i.e., no claim of navigation, but a neutral observation only. Clearly – if true – a referee cannot object to such a descriptive statement.

lecturer in Copenhagen. For many years our contacts were rather sporadic, but in December 2015 I contacted HN because of his skills in mathematics and programming. I has a good sense of numbers and trigonometry with some insight into statistics, but certainly I am not a mathematician. Now I wanted to simulate the outcomes of the orientation systems of migrating birds based on vector orientation (CC) and goal area navigation (NAVGA) for a comparison of the 'goodness' of the two systems, and HN was the guy who could help me.

Once again, we became a happy 'marriage' because of our differences and mutual respect. I was the outgoing person, and HN translated my visions, though certainly not without much resistance and discussion forcing both of us to think twice and re-evaluate many times to the borders of our patience and mental capacities. Then HN suddenly passed away in October 2018 (Kiørboe *et al.* 2019) in the middle of a complex and unfinished process, and I had to make the compilation alone, in spite of my obvious limitations. Nevertheless, valuable insights had been achieved and these – though imperfect – have to be communicated because of their potential significance for understanding the field of bird migration and orientation. I apologize for the sketchy presentation ending up without more precise conclusions.

CC and NAVGA

As described in Rabøl (2023), vector orientation/clock & compass (CC) leads to a 'parabolic' progression of a migratory population. CC is vector orientation in itself, i.e., without any influence of wind-drift. If wind vectors are added, the outcome widens out still (more) 'parabolic'. Rabøl (2023) also exemplified how navigation towards a moving goal area (NAVGA) leads to a narrower, 'parallel-sided' progression of the population. Furthermore, Rabøl (2023) claimed that navigation directly towards a distant goal such as the wintering area leads to an 'ellipsoid' progression on the population level.

Progression on a 'flat' Earth

After some initial trials with a mean direction in SSW, we started simulations in a flat/planar level, considering a population of 'birds' moving 100 km west and 200 km south for each migratory step, finishing after 25 steps. If all 'birds' do the same all the time, this means that following a vector orientation program (CC) the virtual birds would all end up in the same point 5590.17 km away in the direction of 206.565°. If following a goal area navigation program (NAVGA), the end goal after 25 steps would be the position (2500 km to the west and 5000 km to the south). If no between- or within-individual variation occur, all 'birds' following either system would thus end in the same point, which – technically – is not a goal/position for the CC 'birds': it is just the determined vectorial outcome.

To start, we introduced the following within-individual directional variation for each step: SE 0.05, SSE 0.10, S 0.20, SSW 0.30, SW 0.20, WSW 0.10 and W 0.05, leading to a mean vector of 202.5° – 0.84924 (no between-individual variation). Sometimes we added passive drift/zero compensation by the wind, or partial compensation for drift by the wind. We considered a wind-vector distribution with a directional concentration, r = 0 (i.e., all directions had the same probability of being selected by each individual 'bird' (out of 3000) in each step). Furthermore, an average wind-speed of 21.15 km/h (0 (0.02), 5 (0.05), 10 (0.10), 15 (0.15), 20 (0.25), 25 (0.20), 30 (0.12), 35 (0.07), and 40 km/h (0.04)). If the wind speed exceeds 40 km/h, the 'birds' will not set out. The airspeed, of the 'birds' was set to 30 km/h. HN developed a system of partial compensation for wind drift, and also a system of contour ellipsoids with 70% and 95% probability limits for inclusion of 'birds' (normally 3000) after N steps of progress. No variation in number of steps, step-length and between individuals were considered. Of course, such variations occur in the natural world. Later, JR simulated a simple full compensation system for wind drift, but such 'birds' never proceeded all the way down – and if they did, the airspeed, sometimes would have had to be unrealistically high. Furthermore, the necessary calculations seem impossible for a bird to carry out (never say that!), and if strict calculations are replaced by rough estimations, 'birds' (in a system with full compensation for wind drift) necessarily would end up into a 'parabolic' spread of positions.

Progress on spherical Earth

Later, we simulated the progress on a sphere and calculated loxodromic courses following specifications in Rabøl (1988). Soon, European Pied Flycatchers from the Netherlands (Ouwehand *et al.* 2016) became our prime model population: wintering in the Ivory Coast apparently within narrow limits and separated from other European populations (Britain, Finland, Czech Republic and Norway). Adult birds of the Dutch population were equipped with geolocators, and the more than 6000 km long autumn migratory route first went to the northwestern part of The Iberian Peninsula and then offshore along the West African coast 2500 km towards SSW until about Cabo Blanco in Mauretania. From there they moved SSE to Sierra Leone (about Freetown), and then finally 600 km towards east into the state of the Ivory Coast.

Unfortunately, we never finished these simulations. To start, we ran into problems using the Wrapped Cauchy as our circular distribution type. As the responsible mathematician, HN insisted on solving these problems in detail, and much time was used in vain before he finally turned to a wrapped normal distribution, which worked better. As it turned out, in CC (no winds) we needed very high concentrations (about r = 0.99) before 'CC-birds' turned up in the stop-over sites and the final wintering area to a reasonable degree. With wind – and no compensation for wind-drift – only a single (out of 3000) wind-drifted 'birds' succeeded to reach the wintering area. With partial compensation, CC 'birds' performed better, but still all too few 'birds' succeeded to a reasonable degree. Wind-drifted 'birds' using goal area navigation performed better than CC birds with partial wind compensation, and many more turned up in the wintering quarter. Because of the unrealistically high r = 0.99, and much more built-in single-step variation in the NAVGA progress (see Appendix 1), CC 'birds' in no winds performed better than NAVGA 'birds'. Unfortunately, HN passed away before simulations of navigating 'birds' with partial wind-compensation were initiated.

When making general conclusions from simulations, the species/population of the birds in mind should be a typical one. However, the population of Dutch Pied Flycatchers was perhaps not the obvious choice because different populations of Pied Flycatchers winter within very restricted and different areas. At least, the three wintering areas (Sudan, Southwest and East Africa) of Danish Red-backed Shrike are much more extended and widespread (Pedersen *et al.* 2020 and below). Also, Danish breeding populations of Willow Warbler *Phylloscopus trochilus* (Lerche-Jørgensen *et al.* 2017) and Common Redstarts *Phoenicurus phoenicurus* (Kristensen *et al.* 2013) behave differently, and birds from the same population apparently winter everywhere along a latitudinal belt several thousand kilometres long. Thus, it seems difficult to talk about a typical route/wintering area of a long-distance passerine migrant species and set standards for the real-world latitudinal and longitudinal spread.

Two further points, relating to the CC-system are:

If 223.6088 km is used as the step-length, all birds should orient in 206.565° in order to proceed 5590.17 km, i.e., r = 1.00. Even in the very high concentration of r = 0.99 the ‘birds’ lag behind (if r = 0.99, the step-length should be 223.6068/0.99 = 225.9 km in order not to lag behind). If r = 0.84924, the step-length should be about 263 km. Nevertheless, natural selection may ‘interfere’ and select for an appropriate step-length.

A wind-vector concentration of 0 is utopian. If, e.g., the mean wind-vector is 45° – 0.30, the population mean vector would change from 206.565° – 5590.17 km to 201.78° – 4484 km (length of wind vector 0.3 times 21.15 km divided by 30 times 5590.17 = 1182.32 km, and the laws of cosines and sines applied).

Clearly, the only possible way for passerine birds to compensate drift by the wind in the long run is by means of navigation – and the narrow parallel-sided migratory routes mostly found (cf. Thorup & Rabøl 2001) point towards a system based on goal area navigation.

Simulation of vector orientation

For the CC ‘birds’, and in a flat/planar world, the initial choice by JR would be a step-length of 240 km (corresponding to eight hours in flight and an airspeed of 30 km/h), a mean direction of SSW (202.5°) and – as mentioned – a discrete circular probability distribution: SE (0.05), SSE (0.10), S (0.20), SSW (0.30), SW (0.20), WSW (0.10) and W (0.05). The sample mean vector is 202.5° – 0.84924. The conditions were changed and the ‘birds’ – as already mentioned – were set to move 100 km W and 200 km S for each step. Here the step-length is 223.6068 km and the mean direction 206.565°. On the sphere, we maintained the discrete probability distribution and the concentration 0.84924 for the CC ‘birds’. Later, we tried other sample concentrations such as an even +/- 10° around the mean (i.e., every direction within this 20° range has the same probability). The sample mean vector concentration in this case is (about) 0.9944. We also used modified normal distributions with r = 0.80, 0.95, 0.98, 0.99 and even tried – inspired by cross-axes orientation – a discrete four-mode distribution. When turning to the sphere, to start we focused on the Wrapped

Cauchy distribution (and r = 0.99), which, however, caused problems. Finally, HN changed to a Wrapped Normal (r = 0.99). Concerning the wind-vector we considered all wind directions to have the same probability, i.e., r = 0. We already presented the wind-vector distribution considered with r = 0 and an average wind-speed of 21.15 km/h.

Simulation of goal-area navigation

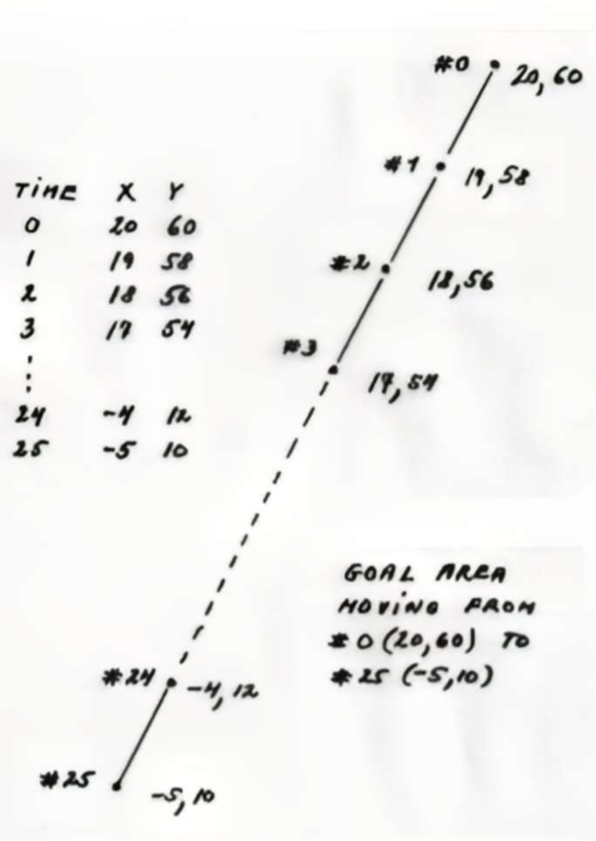
The scenario below is the initial approach of JR sent to HN for inspiration. The scenario in mind was a migrant bird initiating the flight at 60° N, 20° E bound for a wintering area in 10° N, 5° W. The 'birds' make use of goal area navigation, and the first goal area was situated at 58° N, 19° E, and four days and nights later the goal area was at 56° N, 18° E and so on. A total of 25 steps were considered, and because of spherical Earth, the loxodromic steps were not of equal length, the first being 229.47 km and the last 247.55 km.

However, we started simple with a flat Earth and instead of degrees, kilometres were considered: on each migratory step the 'bird' moved 200 km south and 100 km west, i.e., a step-length of 223.6068 km and a direction of 206.565°. Total length will be 5590.17 km.

As a first approach, we considered the progress in calm/no wind. It was tempting to think in longitudes and latitudes, and therefore JR still attained the numbers from the start and end goal, (20°, 60°) and (-5°, 10°), respectively, but took away the degrees. As shown in Fig. 1, the 'birds' started in "0" (20, 60) and the first step is initiated when the goal area arrives at "1" (19, 58). Over the course of 25 steps, the goal area moves in a straight line to "25" (-5, 10). The question is how accurate the 'bird' can estimate the abscissa and ordinate. JR guessed that the probability distribution of the latter followed the binomial distribution as -1 (0.25), 0 (0.50), +1 (0.25), where the unity 1 used correspond to 100 km. Concerning the abscissa – and with the stellar sky in mind (Appendix 1) – at least two probability distributions have to be combined: (a) the time on the 'stellar watch', i.e., an angle between a star(pattern) and Polaris, and (b) time for local midnight. As a first approach JR combined (a) and (b) as (-1 (0.25), 0 (0.50), +1 (0.25)) times (-1 (0.25), 0 (0.50), +1 (0.25)) = -2 (0.0625), -1 (0.25), 0 (0.375), +1 (0.25), and +2 (0.0625). Later, further expansions were carried out.

Now JR drew random, paired numbers according to the probabilities of the abscissa and ordinate above; the first six were (-1, +1), (0, +1), (-2, -1), (-1, -1), (-2, +1), and (0, 0).

As the 'bird' stayed a long time in '0' (20, 60), no uncertainty was assumed in the first step towards '1' (19, 58). Furthermore, it was assumed that the 'bird' was unable to establish and maintain a track very accurately but just used the nearest 'cardinal direction' (N, NNE, NE … NNW) in reference to its estimate. The direction between '0' and '1', 200 km S and 100 km W, is 206.565° and the 'cardinal-direction' chosen was thus SSW (202.5°). Now the 'bird' migrates 240 km (2.4 entities, eight hours per step, and airspeed, 30 km/h) in this direction and ends up in 1a (Fig. 2). 223.6068 km/step was the natural choice, but 240 km was used in order to keep in approximate touch with the goal area. Here the 'bird' would stay for four days and start up a new migratory step



TIME	X	Y
0	20	60
1	19	58
2	18	56
3	17	54
⋮		
24	-4	12
25	-5	10

Fig. 1. Goal area moving 25 steps in a plane from #0 (20. 60) to #25 (-5. 10).
Målområde der starter i #0 og over 25 trin ender i #25 (-5, 10).

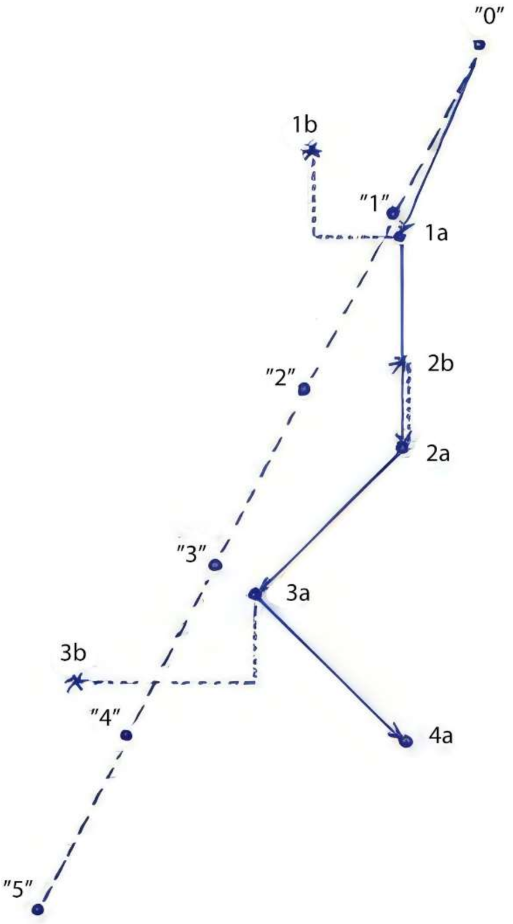


Fig. 2. First migratory steps in sequence of a moving goal area.
De første træktrin af et målområdenavigationsforløb.

intended for goal area ‘2’ (18, 56). However, its position was estimated with the errors +1 in the ordinate and -1 in the abscissa (take a look at the array of errors above). This means that the ‘bird’ believes its position is 1b (Fig. 2). The direction from 1b towards ‘2’ is 182°, and the ‘bird’ therefore migrates 240 km towards the cardinal-direction 180° – from position 1a, because its actual position is 1a and not – as it believes – 1b. The ‘bird’ ends up in 2a, and after 4 days it has to migrate towards goal area ‘3’. However, it believes it is in 2b (ordinate/abscissa, +1/0). The direction from 2b towards “3” is 222°, i.e., the ‘bird’ migrates 240 km towards SW (225°). It ends up in 3a, but believes the position is 3b (ordinate/abscissa, -1/-2). From here the direction towards goal area “4” is 139°. Therefore, the ‘bird’ migrates 240 km towards SE (135°) from 3a towards 4a, and so on. The steps are shown in Fig. 2 and rest on graphic readings, not calculations. However, in the real world normally there is a wind-vector, and the birds drift by the wind. I already gave the wind-speed probabilities in km/h and a random wind-direction distribution, i.e., r = 0. As an example, an air-speed vector on 202.5° – 2.4 and a wind-vector on 104° – 1.6 combines to a track-vector on 166.31° – 2.68 (calculated by means of the laws of sines and cosines).

The influence of wind

Since about 1960, we studied the visible, diurnal bird migration: first Eurasian Skylarks on spring migration at Knudshoved, easternmost Funen; later shorebirds, in particular Eurasian Oystercatchers *Haematopus ostralegus*, Red Knots *Calidris canutus* and Dunlins *Calidris alpina* in July-August along the west coast of Jutland, mostly at the westernmost point, Blåvandshuk. JR also studied the autumn migration of Hooded Crows *Corvus cornix* and Chaffinches *Fringilla coelebs* on Hesselø, a remote, small island in Kattegat about 30 km from the nearest land (Rabøl 1967). Together we analysed movies of bird-echoes on a PPI-radar screen (e.g., Geil *et al.* 1974) and observed how the bird-echoes drifted by the wind.

Summing up our experiences with bird migration and wind: Even during daytime, at low altitudes and along coastlines, birds cannot (except in the very short run) compensate fully for the drift by wind: full compensation (in the long run and in a CC system) is an unrealistic fantasy conceived at a writing desk. Nevertheless, the Skylarks often locally over-compensate, and the diurnal migration is sometimes – in time and space – dominated by headwind migration at low altitudes. On Hesselø, the immigrating birds arrived against the wind following a wind-drifted approach over the sea. They also left the island heading against the wind (Rabøl 1967). The shorebirds at Blåvand struggled to follow the coastline (Noer 2017). Anyway, if relying on clock-and-compass and compensation of wind-drift in an open system, in the long run, the birds will be lost: goal navigation of one or another kind has to be included at least sometimes in the migratory progress.

In principle, a diurnal low-altitude migrant while on the ground may establish the wanted course and select a row of items on the ground pointing in this direction. When airborne, the bird starts to drift by the wind but then must keep an eye on the ‘row’ of items and all the time add new items ahead (comparable to migration along a coastline). In this way, the bird may compensate to a high degree – but what to do at higher altitudes, over the sea, during night and within clouds? There is no way to avoid drifting with the wind.

If a bird migrating over the open sea heads towards an island – say – 5 km away, it would proceed in an arcuate curve and arrive at the island (Hesselø) into the headwind. The obvious question is why the bird is not changing its heading in such a way that the track proceeds in a straight line towards the island. The answer is that it seems impossible to do so only ‘equipped’ with a distant point, the island in the sea of ‘nothing’. However, Alerstam (1982) hypothesized that birds over the sea could compensate partly using the moving waves as a directional reference, so – possibly – the sea is not necessarily ‘nothing’.

No wind compensation

JR used the following simple example to understand the situation. The flying vector was 180° – 30 (km/h), and the wind vector variable in direction: 0°, 20°, 40° … 320°, 340°, whereas its length always was 20 (km/h). The first vector combination considered was 180° – 30 and 0° – 20. The resulting track vector is 180° – 10. Then 180° – 30 and 20° – 20. The track vector is 148.60° – 13.13. And so on; a total of 18 track-vectors emerged. The sum-vector of these is 180° – 540, i.e., the same as the sum of 18 flying/track-vectors in calm/no-wind (all vectors 180° – 30, 18 times 30 = 540). Conclusion: if r in the distribution of wind-directions is 0, and the wind speed is constant and on average lower than the airspeed, then full drift by the wind makes the birds – with much scatter – end on average in the very same position as in calm/no-wind.

Partial compensation for wind-drift

HN in the flat considered a heading vector of 202.5° – 30 (km/h) in combination with wind-vectors with directions all the way around (1°, 2°, 3°, … 78°, … 219°, … 360°) and airspeeds 0, 5, 10, 15, 20, 25, and 30 (km/h). He was then able to set up equations and calculate simple rules for changing the heading direction. HN came to the following conclusion, where 202.5° could be changed to be any preferred flying direction. Using these corrections, the area of the contour ellipsoids of CC + wind was significantly reduced considering CC + partial compensation for wind-drift:

1. If wind-speed is 40 km/h or higher, no migration would be initiated.
2. If the wind-vector is estimated to cause progression for eight hours less than 50 km in the intended direction, migration should not be initiated.
3. If the wind-vector is between 20° and 160° from the right in relation to the preferred heading direction, the bird turns its heading-axis 20° towards the right if the wind-speed is 10 km/h, and 40° to the right if the wind-speed is 15-35 km/h. If the wind is to the left side, the opposite is done.

Later, HN changed the calculations/scenario to the sphere considering contour ellipsoids in terms of degrees and not kilometres (Tab. 1).

Tab. 1. Calculation of contour ellipsoids on a flat plain. **a** and **b** are the two half axes in km and **Area,** viz., the area of the ellipsoid in square km. Start in (0.0) and end in (-2500. -5000) after 25 steps. The concentration was high – about 0.9944 – derived from an even circular distribution where all directions between -10° and +10° had the same probability (the mean 0° is transferred to the mean in the distribution considered, i.e. 206.565°).

Beregninger af kontur ellipser i et todimensionelt plan. ***a*** *og* **b** *er det halve af ellipsens to akser i km og* **Area** *er ellipsens areal i kvadrat km. Start i (0,0) og slut i (-2500, -5000) efter 25 trin. Koncentrationen var høj, 0,9944 stammende fra en cirkel fordeling hvor alle retninger mellem -10° og +10° havde den samme sandsynlighed (gennemsnittet på 0° kan forskydes til gennemsnittet i en enhver betragtet fordeling, fx 206,565°).*

System	a	b	Area
CC	172	8	4,291
CC with full wind-drift	989	923	2,869,387
CC with partial compensation for wind	763	478	1,145,805
NAVGA	120	97	36,598
NAVGA with full wind-drift	622	308	601,747

Full directional compensation for wind-drift

HN was not involved in these considerations. JR took over, the heading vector was considered to vary in direction but not in speed. In combination with a wind-vector, a track-vector should then arise always directed towards 180°. The calculations were based on the law of cosines: $c^2 = a^2 + b^2 - 2ab\cos C$. As an example, a wind-vector of 20° – 20 was used, then b = 20 (directed towards 20°), a = x (directed towards 180°), C = 160°, and c = 30. We end up in a quadratic equation, where the reasonable solution is x = 10.42. The 17 other track-vector lengths were calculated in a similar way. The sum of all 18 track-vector lengths = 473.76, which is a little less than 88% of 540 (the sum of the 18 flying/track-vectors in calm/no-wind; mean track-vector = 26.32 km/h). Conclusion: If full (directional) compensation for wind-drift, the birds would proceed 88% of the way towards the 'goal' (recall, there is no real goal; the birds are not navigating).

Full vector compensation for wind-drift

If full compensation for both direction and step-length of the track-vector (i.e., all track-vectors 180° – 30), then the airspeed has to be changed accordingly. If r = 0 in the distribution of wind directions for a given region, and the average wind-speed over the years is constant, then evolution may adapt the time spent migrating in such a way that the birds on average attain the 'goal'. However, in the real world where the wind-vector varies in both direction, speed, time and altitude, accurate compensations would be impossible. The calculations are – probably – too complicated to carry out for a passerine bird. Anyway, birds only estimate but the total of many estimates may appear as a calculation.

I calculated the airspeed, vectors for a constant wind-speed of 20 km/hour, and for opposed and following winds, the airspeed should be 50 km/h and 10 km/h, respectively, which appears rather unnatural. The mean airspeed was 33.44 km/h. The sum-vector of all 18 vectors was 180° – 540, not surprisingly corresponding to the mean track-vector 180° – 30 km/h. It looks more plausible to think that the bird tries to keep a constant airspeed than a constant groundspeed.

Further considerations

Loxodromes or orthodromes?

When considering vector orientation/navigation on a sphere (the Earth being an approximate sphere), one could ask whether the programming should follow in an orthodromic or a loxodromic system. Sometimes there may be many kilometres to save following an orthodrome instead of a constant angle loxodromic course. Minimizing distance and thus saving energy would seem to be an important evolutionary strategy. However, the correspondence of several very long migratory pathways – e.g., of shorebirds from N-Siberia migrating over many longitudes westwards to Mauretania – to great circle routes (orthodromes) does not necessarily mean that the birds navigate in a great circle system[4]. An orthodromic course may be programmed as a chain of shifting loxodromes. Years ago, Rabøl (1976) considered the possibility of reverse great circle navigation into Europe by Siberian Pallas' Leaf Warblers *Phylloscopus proregulus*. However, later he turned sceptic and at present do not really know what to believe (Appendix 3). If large E/W-differences between actual position and goal, orthodromic estimations are not possible/straightforward as a direct sensory contact with the distant goal seems out of context. Finally, there is no need for orthodromic navigation in the context of normal goal area navigation because in a NAVGA system the actual goal should never be distant away but only – say – from a few hundred up to one thousand kilometres.

However, loxodromic navigation (at least in a human perspective) is simpler because it means that the compass course between two points is held constant irrespective of the number of steps: in the case of the orthodrome, the course (in reference to geographical N) changes gradually except in the special cases where the two points are located on the Equator or on the same longitude. If navigation is not between two far-separated points but the goal is close to – say up to 500-800 km away – then the difference in degrees and distance is very small, typically only a few degrees/km. Recall, goal area navigation is normally between two nearby positions. However, orthodromic navigation seems the obvious choice if navigation is between the start- and endpoint such as, e.g., the hypothetical case of Willow Warblers navigating from eastern Siberia to East Africa (Sokolovskis *et al.* 2018; see also fig. 1 in Rabøl 2023). In Appendix 3, I finally reach the

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[4] An analogy could be birds following what appears to be a magneto-clinic course (Kiepenheuer 1984). Apparently, S. Åkesson in several papers, e.g., Åkesson & Bianco (2016), considers magneto-clinic compass orientation a realistic possibility. I have my doubts, but we must await the outcomes of simple experiments with shifting magnetic inclinations in the same sample of birds conducted by researchers with the appropriate magnetic equipment.

conclusion that an orthodromic system seems more probable than a mixed loxodromic/mirror-image system concerning the routes of vagrant *Phylloscopus* warblers within Europe and further SW.

Comparison of the variance in CC and NAVGA

HN was much concerned about the variance in these two systems: If we compare the area of their contour ellipsoids, the build in variance should be the same – whatever that means because the two systems are not straightforwardly compared concerning variance.

What do we understand by variance?

In the beginning, we used a sample concentration, r = 0.84924 for the CC system. JR – without investigation and any deeper considerations – simply assumed the single-step variance was higher in the NAVGA system, and his general attitude was one of favouring the CC system. If the variance was lower in CC than in NAVGA (no winds), and the latter described better (smaller contour ellipsoid area after a few – say 5 to 8 – steps), we were on the right side by concluding that goal-area navigation was the 'better' system.

If using -1° (0.25), 0° (0.50), +1° (0.25) as the establishment variation in the ordinate, and -2° (0.0625), -1° (0.25), 0° (0.375), +1° (0.25), +2° (0.0625) for the abscissa, how much variance will these introduce. One possible method to determine this is to calculate the product of the two distributions. The combined probability of +1° (ordinate) and -2° (abscissa) is thus 0.25 multiplied by 0.0625, equating to 0.015625. Similarly, the probability for hitting (0°, 0°) is 0.50 multiplied by 0.375 equating to 0.1875. Summing all the probabilities for the 15 combinations yields 1.00. Assuming that an entity of 1° corresponds to 100 km, consider a bird 240 km (on migratory step of eight hours times 30 km/h) to the N of (0°, 0°) perceived as a goal area position, one can then draw lines to all 15 positions and calculate the 15 directions considering these as a probability distribution: the mean vector is 180° – 0.9203, i.e. the concentration is significantly higher than 0.84924 used in the CC system.

If we expand the two binomial distributions from -4° to +4° (abscissa/longitude), and -2° to +2° (ordinate/latitude), the 45 directions (following the method mentioned above) lead to a sample mean vector of 180° – 0.8627, i.e. now we are close to r = 0.84924. However, we never performed that expansion (concerning the initial, incomplete NAVGA calculations from the Netherlands to the Ivory Coast we used a 7 (longitude) by 5 (latitude) expansion (Fig. 3). In fact, the stringent mathematician HN was not involved in these considerations and might have disliked them.

Nevertheless, in almost all later analyses we used a much higher r (mostly 0.99) for the CC system, so certainly this system described best (as also displayed by the much smaller area of the contour ellipsoids for CC compared with the one for NAVGA; however, corresponding NAVGA simulations with wind-drift described better than corresponding CC simulations).

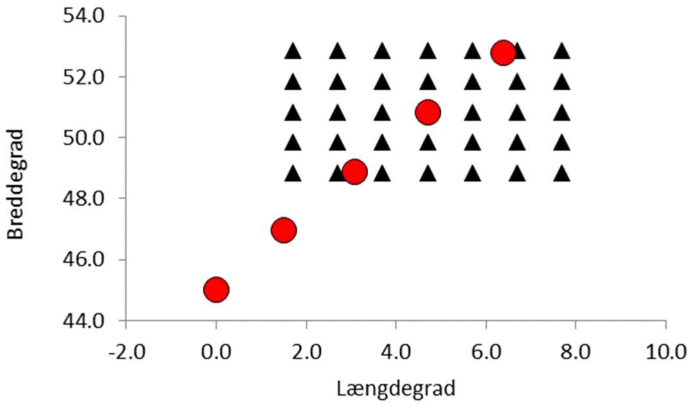

Fig. 3. “Breddegrad” and “Længdegrad” mean latitude and longitude, respectively. The uncertainties in the first step (out of four) from Drentje to Bordeaux. In the longitudes -3° (0.015625), -2° (0.0625), -1° (0.234375), 0° (0.3125), +1° (0.234375), +2° (0.0625), +3° (0.015625), and in the latitudes -2° (0.0625), -1° (0.25), 0° (0.375), +1° (0.25), +2° (0.0625). The “bird” starts in the upper red dot and navigates towards the next red dot towards SW. Only 12 “birds” out of 100 (100 times 0.3125 times 0.375) end up here.

Usikkerhederne med hensyn til fastlæggelsen af det første målområde efter starten fra Drentje mod Bordeaux. Fuglene starter i øverste højre røde plet og navigerer – med usikkerheder – mod den næste røde plet SW derfor. De sorte trekanter viser placeringen af de kombinerede binomiale sandsynligheder.

Kilometres or degrees?

When describing CC and loxodromes on spherical Earth, we operated with kilometres. However, turning to NAVGA, degrees were considered. A navigating bird almost necessarily must operate in degrees and fraction of degrees – in particularly in case of celestial navigation. However, in the case of degrees, the area of contour ellipsoids increases towards Equator. For example, at Equator the area of a 1° times 1° N/E/S/W square is twice the area of a 1° times 1° rectangle at 60° latitude.

Contour-ellipsoids

In order to compare the goodness/fit of different systems such as CC with wind-drift and partial compensation for wind-drift, and corresponding simulations with NAVGA, we needed a measure of the area encompassing, say 70% of the positions of the simulated ‘birds’ after, say, 25 steps.

HN elaborated such a ‘test-statistic’ named a contour-ellipsoid. Fig. 4 shows the positions of 1000 ‘birds’ after 25 steps in a CC-system. Each single step was a vector; the direction was a stochastic output from the sample distribution of 202.5° – 0.84924. The distance of the step-vector was always 240 km. The correlation between x1 and x2 was -0.67. Now the dots were transformed in reference to two axes, y1 and y2, where the correlation between y1 and y2 is 0. The process is the same as in

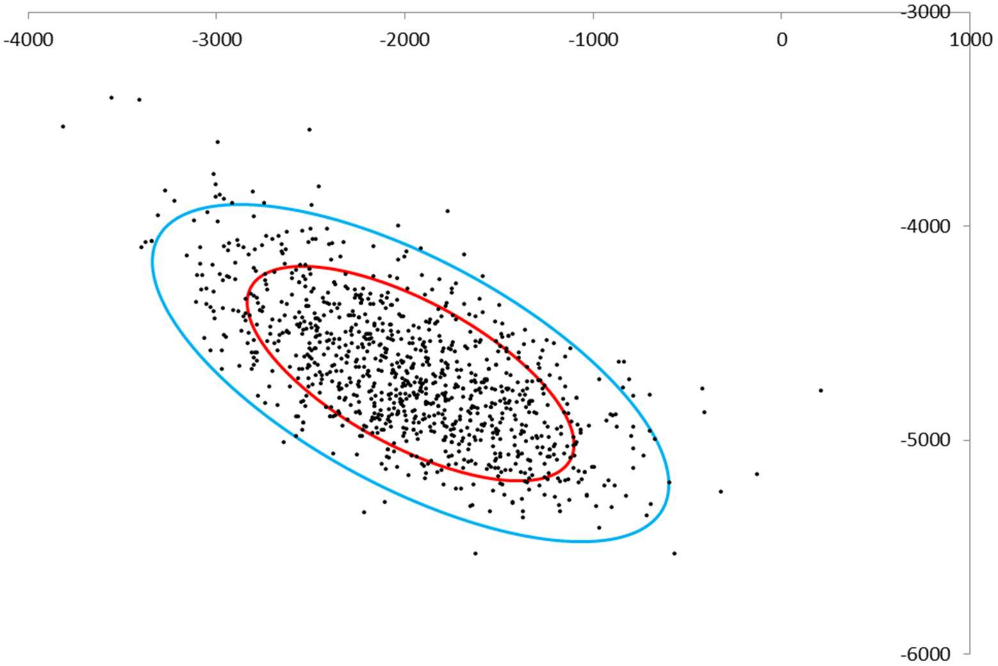

Fig. 4. Contour-ellipsoids based in 70% (red) and 95% (blue) confidence intervals. The horizontal and vertical axes show E/W and N/S in km, respectively. 25 steps in a CC-system, mean direction 202.5° – 0.84924. The step-length is 240 km. Obviously, 240 km per step is too short for the sample to proceed 6000 km. The sample progress is about 5100 km towards (about) 202.5°.

70 % og 95 % konturellipser i et vektororienteringssystem med 25 steps og en sample mean vector på 202,5° – 0,84924 (step længde 240 km). Den vandrette og lodrette akse viser Ø/V og N/S afstande i km. Som det ses, er tyngdepunktet ikke 6000 km (24 gange 240 km) væk fra startpunktet, men ca. 5100 km. Retningen fra startpunktet (0,0) er dog stadig meget tæt på 202,5°.

a Principal Components Analysis (PCA). This makes it possible to treat the distributions of y1 and y2 as bivariate normal distributions and calculate, e.g., the 70% and 95% confidence interval ellipsoids. Finally, these ellipsoids are transformed back to the distribution of x1, x2 (Fig. 3). Figs 5 and 6 show corresponding figures for a CC with wind-drift (CCW) and partial compensation for same (CCWPC), respectively. The point is that the distributions are not normal but appear more or less like a sausage or banana.[5] However, this probably does not seriously invalidate the goodness of the contour-ellipsoids calculated.

Remember, the area of a circle is π times r square. Now, the circle is a special kind of ellipsoid, and the area of an ellipsoid is π times (a) (half the long axis) times (b) (half the short axis). If nothing else is specified, we always refer to the 70% contour ellipsoid. Tab. 1 shows a first example. The area (km²) is very low in CC because of very high (r) and no wind. When wind is added, the variance increases enormously. When partial compensation for the wind is carried out, the scatter is

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[5] In the simulations, all 'birds' start in the same position, and all move the same length per step and the same number of steps. There is no variation between 'birds'. Clearly, this is a CC-system, and the question is whether the fitness to a NAVGA-system could be applied without corrections, but the mathematician HN never proposed or carried such out.

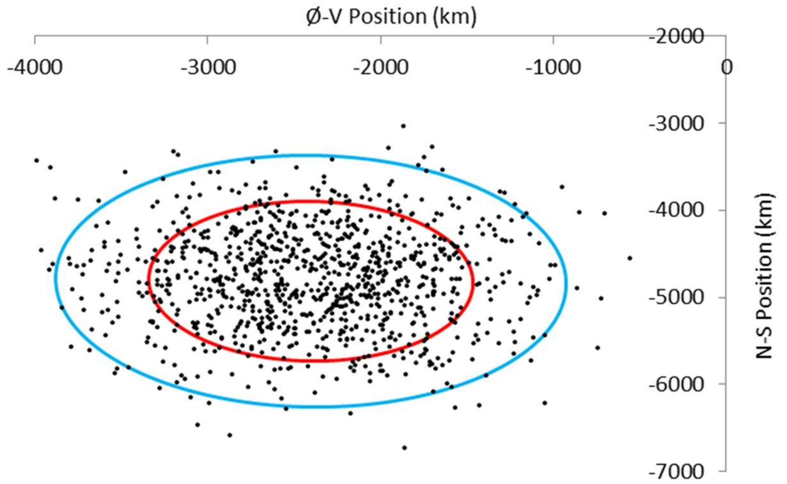

Fig. 5. The area of the corresponding (to Fig. 4) 70% contour ellipsoid for CCW after 25 steps is 2,682,944 km^2. Ø-V means E-W.

Arealet af den korresponderende 70% kontur ellipse (til Fig. 3) for CCW efter 25 træktrin er 2682944 kvadrat km.

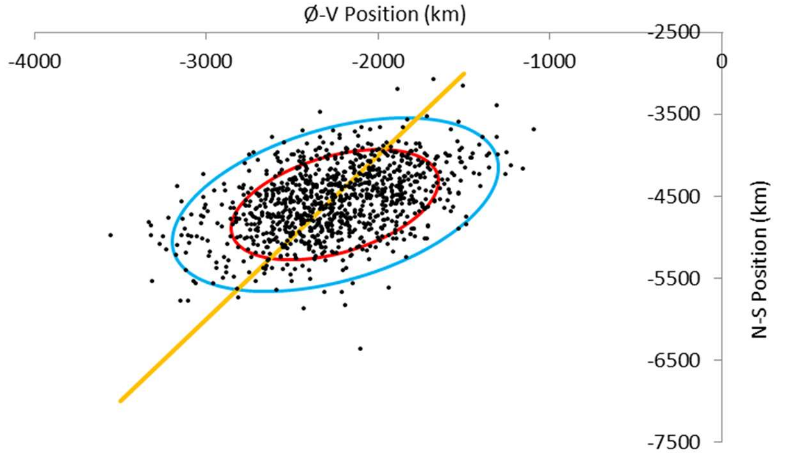

Fig. 6. The area of the corresponding (to Figs 4 and 5) 70% contour ellipsoid for CCWPC (CC partial compensated wind drift) is 1,145,805 km^2. It is 41% of the area of CCW (wind drifted CC) (Fig. 4). Anyway, there is still far down to NAVGAW (wind drifted NAVGA), where the 70% contour ellipsoid covers 595,863 km^2. The yellow line connects (0.0) and (-2500.-5000). It should be noted that the center of the contour-ellipsoids is about (-2300.-4700), i.e. PC slows down the progress a little, whereas wind drift in itself (Fig. 5) apparently does not.

Kontur-ellipserne når der er delvist kompenseret for vindafdrift (CCWPC). Arealet af 70 % ellipsen er godt 1.000.000 km^2, medens det for vinddriftet målområdenavigation (NAVGAW) er lidt under 600.000 km^2.

reduced between two and three times compared with wind-drift. The spread in NAVGA is clearly higher than in CC because additional variation on the determination of the longitudes and latitudes is added. However, even without compensations for wind-drift, NAVGA describes better than CC with partial compensation for wind drift.

Tab. 2 shows other examples. Already without wind it is clear that CC 80 describes badly. In this context, CC 80 + wind drift is utterly bad. NAVGA is much better, and NAVGA 95 + wind drift appears marginally sufficient.

Tab. 3 is a third example referring to calculations on a spherical plane with a start in 60° N/20° E and a final goal (25 steps) in 10° N/5° W. The entity was degrees. Loxodromes were considered and (r) was 0.99. The area of CC + wind drift is about[6] 4,500,000 km² looking just horrible. NAVGA + wind drift is not that bad (815,000 km²).

Tab. 2. Other examples: Again, reactions in a flat plane projection. Now using a Wrapped Cauchy distribution and two different concentrations considered: r = 0.80, and r = 0.95.
Andre eksempler. Reaktioner i et todimensionelt plan på baggrund af en ′Omviklet′ Cauchy-fordeling, og med to forskellige koncentrationer: 0,80 og 0,95.

System	a	b	Area
CC 80	748	733	1,722,803
CC 95	375	374	440.690
CC 80 + winddrift	1213	1201	4,578,330
CC 95 + winddrift	1013	1011	3,218,820
NAVGA 80	706	308	684,236
NAVGA 95	345	132	142,834
NAVGA 80 + winddrift	1033	519	1,685,049
NAVGA 95 + winddrift	730	339	779,115

Tab. 3. Calculations of area of contour ellipsoids in degrees.
Beregning af kontur ellipse arealer i grader.

System	a	b	Area
CC	2.34	0.16	1.14
CC + winddrift	12.93	9.15	371.74
NAVGA	1.12	1	3.52
NAVGA + winddrift	6.23	3.44	67.3

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[6] 1° of latitude corresponds to 111.111 km, whereas 1° longitude corresponds to 111.111 km times cos latitude. In the present case 10° longitude is very close to 1° latitude (109.423 km).

An example based on Pied Flycatchers from the Netherlands

The breeding population of European Pied Flycatchers at Drentje, the Netherlands (52.8°N, 6.4°E), is well studied and according to geolocator-studies of Ouwehand *et al.* (2016) the wintering area is mostly restricted to Guinea and the Ivory Coast. All birds considered were adults from the start of the experiment. Most adult birds (if still alive, and in particular, the males) return to the breeding area of the preceding year and are available for a recapture. Tagged juvenile birds are almost never recaptured probably because most/all disperse from their fledging site before departure on autumn migration from another more or less nearby site. to which they return next spring.

In an appendix table to Ouwehand *et al.* (2016) we found the medians of the longitude and latitude of the winter positions of six Drentje Pied Flycatchers. As outlined below in the section of the Red-backed Shrike the 70% ellipsoid area, and the two semi-axes (a) and (b) could be estimated by means of formulas presented in Batschelet (1978). Half the short and long axes were 158 and 336 km, respectively, i.e., the area was about 167,000 km^2. Adamik *et al.* (2023) give seven winter-positions of Pied Flycatcher from Drentje, and we estimated the area of a 70% contour ellipsoid to 173,000 km^2. The mean position of the 7 birds was 9.18° N/7.01° W. Adamik *et al.* also listed the wintering longitudes of further 27 Dutch flycatchers. The mean for all 34 birds was 7.32° W (probably, the Dutchmen abandoned the corresponding latitudes because of too high uncertainty in the latitude estimations).

When departing from Drentje, the birds presumably first migrated to somewhere near Bordeaux (45° N, 0° E), then to the NW corner of the Iberian Peninsula (42° N, 7° W). Here the flycatchers spent some time filling up their fat reserves before the next very long non-stop migration offshore the West African coast to Cabo Blanco in Mauritania (21° N, 17° W). From here the flycatchers supposedly moved SSE to about Freetown in Sierra Leone (8° N, 12.5° W), and finally about E to the Ivory Coast (8° N, 7° W). Bordeaux, N-Portugal/NW-Spain, Cabo Blanco, and Freetown thus involve four bends of a 'dog-legged' migratory route. The question now would be whether the migratory system was based in CC or NAVGA?

If the migratory system is CC

We first (Tab. 4) considered a CC-system: the number of steps was set to 16. The routes follow loxodromes. Note that in a CC system there are no goals. So, when we specify the coordinates, these have a (sort of) reality for NAVGA-birds, but not for the CC-birds.

Tab. 4 refers to CC-birds where the loxodromic flying direction in the first four steps is 208.27°, and the distance intended to cover 246.02 km/step. If the airspeed, of the bird was 30 km/h this would translate to 8.20 hours of flight per step.

HN made simulations in CC with no wind, CC with wind-drift, and CC with partial compensations for wind-drift. The calculations were in loxodromes, wrapped Cauchy, and $r = 0.99$. The simulated numbers of 3000 pairs of longitudes and latitudes were figured following four, six, seven, thirteen and sixteen steps with the positions of Bordeaux, Northern Portugal, Cabo Blanco, Freetown and

Tab. 4. Presumed migratory progress (16 steps) from Drentje, the Netherlands to the wintering ground in the Ivory Coast.
Det antagede trækforløb (16 trin) fra Drentje i Holland til vinterkvarteret i Elfenbenskysten.

Migratory leg	**Distance km**	**Loxodrome direction**	**Number of steps**	**Step-length**
Drentje-Bordeaux	984.08	208.27°	4	246.02
Bordeaux-Portugal	655.14	239.42°	2	327.57
Portugal-Cabo Blanco	2514.82	201.90°	1	2514.82
Cabo Blanco-Freetown	1523.03	161.51°	6	253.84
Freetown-Ivory Coast	605.16	90.00°	3	201.72
Total	6282.23		16	

the Ivory Coast in mind. The strict mathematician HN considered the patterns of plots as not usable for calculating contour ellipsoids so these never materialized from his side. However, from the tables that HN left behind, JR considered the first 50 pairs in each series and calculated means and standard deviations for longitudes and latitudes after sixteen steps.[7] Using the method of Hotelling (Batschelet 1978; see below in the section of Red-backed Shrike), I first calculated the long and short semi-axes, a and b of the CC simulations with wind. Then plotting the 50 pairs of longitudes and latitudes and using the slope to estimate a 70% contour ellipsoid by eye. The long and short semi-axes were 26° and 16.9°, respectively, corresponding to 2886 km and 1875 km, respectively. The area of the contour ellipsoid was then calculated as tremendous 16,999,943 km².

Turning to the CC with partial compensation for wind, simulations of 50 pairs of longitudes and latitudes the long and short semi-axes were found to be 10.5° and 8.8°, respectively corresponding to 1166 km and 977 km, and the 70% ellipsoid area as 3,578,846 km². Clearly, partial wind drift compensation improved the description significantly. However, the area was still far too high to be taken as an acceptable indication of the goodness of a CC system with partial compensation for wind. For a second sample – using 50 other pairs of longitudes and latitudes – the 70% ellipsoid area was 2,974,271 km².

Not surprisingly, a CC-system with r = 0.99 described very well as a plot of the 50 pairs of longitudes and latitudes resulted in semi-axes of 160 km and 74 km, and an ellipsoid area of very modest 37,196 km². However, a CC-system with so high concentration and without influence of a wind vector for so long distance and time is not compatible with real world conditions.

The CC plot with partial compensation for wind appeared less so with 2-5 (out of 50) remarkable outliers. In the CC plot, six outliers were prominent, two of which were not in the line of the long semi-axis. Anyway, about 35 positions were in the very tight cluster. Probably, this reflects the influence of a sometimes going-wild 'behaviour' of the Wrapped Cauchy distribution, as suspected by a frustrated HN on several occasions.

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[7] For the eyes of mine, the CCW plot looks totally appropriate for a contour ellipsoid calculation.

The migratory system is NAVGA

Now, we turn the attention to ‘birds’ performing NAVGA. The question is how they do. As an example, and a first approach, HN considered how to specify the positions of the three goal areas between Drentje and Bordeaux. He started in Drentje on 52.8° N, 6.4° E, then added the loxodromic vector on 246.02 km directed towards 208.27° and in this way found the end-position of step 1. Next step started here and again a loxodromic vector of 208.27° - 246.02 km was added and the end position of step 2 was determined, and so on. However, goal areas calculated in this way seem outside reasonable capacities of real birds, which probably ‘think, compute and react’ more in terms of latitude and longitude. The difference in latitude between Drentje and Bordeaux is 7.8° and four steps means 1.95° per step. In the same way the difference in longitude e is calculated as 1.6° per step. Using degrees instead of kilometres both the distance and loxodromic direction shift between steps in NAVGA. However, this means nothing because in NAVGA – in contrast to CC – it is not critical to use the ‘right’ step-length; the bird just use an appropriate, constant length, e.g. 240 km (8 flying hours), and in every ‘bend’ fill up by keeping the goal area position constant for e.g. the last two steps as exemplified below (Tab. 5).

Tab. 5. Start from Drentje in a NAVGA system (see the text).
Start fra Drentje i et NAVGA system. Se teksten.

#0 52.8°N 6.4°E	#4 45.0°N 0.0°	#8 42.0°N 7.0°W
#1 50.85°N 4.8°E	#5 45.0°N 0.0°	#9 42.0°N 7.0°W
#2 48.90°N 3.2°E	#6 45.0°N 0.0°	#10 42.0°N 7.0°W
#3 46.95°N 1.6°E	#7 43.5°N 35°W	And so on

Concerning NAVGA and Dutch Pied Flycatchers, HN only ran a single simulation using the Cauchy distribution and $r = 0.99$. Contour ellipsoids were not calculated, and a table was not presented to me. On the basis of a figure presented to me of 1000 simulated positions the ‘birds’ were on the average after 16 steps about 200 km W of the position 8° N/7° W in the Ivory Coast. About 70% of the dots were within 2.7-3 longitudes and 1.5-2 latitudes. In terms of an ellipsoid this means a long semi-axis of 158 km and a short semi-axis of 97 km, and an area of 48,148 km^2 – which is less than the estimated CC ellipsoid of 117,000 km^2 of the six Drentje-birds. Unfortunately, HN never presented a corresponding figure for NAVGA birds with wind.

Further notes

The very long step between Portugal and Cabo Blanco could be considered in two ways:

1. In case of CC: One single track; wind-vectors and PC as already outlined. The long track from Portugal to Cabo Blanco is 2514.82 km, and in case of no winds could be covered in a single 83.83 hour-step at an airspeed of 30 km/h. The loxodrome would be directed towards 201.9°. The loxodromic vector could be broken up in three sub-steps with the following lengths and

time in air (airspeed 30 km/h): a) 603.6 km and 20.12 hours, b) 1106.6 km and 36.89 hours, and c) 804.8 km and 26.83 hours.

2. In case of NAVGA: Two intermediate goal areas, where the ‘birds’ are not grounded but reorient in air (on positions 37° N/9.5° W and 28° N/14° W).

(2a) In the first sub-step from Portugal towards 37°N/9.5°W the birds would be selective concerning the wind-direction at start: Only start-winds between 300° over N through 100° were accepted. For an even start-wind distribution the sample mean vector is (abt.) 20° – 0.67.

(2b) In the next sub-step towards 28° N/14° W covering 1100 km the ‘birds’ arrived to the belt of westerly winds supposedly with the following distribution: sample mean vector 270° – 0.313: (0°) 0.12, (45°) 0.08, (90°) 0.04, (135°) 0.08, (180°) 0.12, (225°) 0.16, (270°) 0.24, (315°) 0.16, or alternatively a von Mises distribution, r = 0.30). In the calculations we have to remember wind-directions are denoted from their direction of origin, i.e. a wind from W contributes with a wind-vector directed E.

(2c) In the last sub-step towards 21° N/17° W the birds come into the trade-wind belt and inspired of a wind rose figure from La Laguna, Tenerife in Ceballos & Ortuno (1976) the following bi-modal wind-direction distribution with a major peak in 330° (NW-NNW) and a minor peak in 150° and the following frequencies were envisioned: (0°) 16.5, (10°) 12, (20°) 9, (30°) 6, (40°) 4.5, (50°) 3, (60°) 0, (70°) 1, (80°) 1.5, (90°) 2, (100°) 3, (110°) 4, (120°) 5.5, (130°) 7, (140°) 8.5, (150°) 10, (160°) 8.5, (170°) 7, (180°) 5.5, (190°) 4, (200°) 3, (210°) 2, (220°) 1.5, (230°) 1, (240°) 0, (250°) 3, (260°) 4.5, (270°) 6, (280°) 9, (290°) 12, (300°) 16.5, (310°) 21, (320°) 25.5, (330°) 30, (340°) 25.5 and (350°) 21. The major peak is three times bigger than the minor peak and considered separately the sub-sample concentration around the two not overlapping peaks is 0.836 of both. The mean vector of the total distribution is 330° – 0.418 (or 150° – 0.418 if considered as a wind-vector).

Clearly, a start-wind being on the average a following wind, and then two side-winds from – on the average – W and NW-NNW will displace the ‘birds’ towards ‘SE’ compared with the no-wind flying/track vector of 201.9° – 2515 km.

How to compensate? Well, if the average windspeed is 20 km/h and in (1) the mean vector concentration 0.67 of the winds between 300° and 100° (airspeed of the birds 30 km/h), and the time in air is 20.12 hours, a following wind contribution of 269.6 km should be added; i.e. the mean vector length towards 201.9° changes to 603.6 + 269.6 = 873.2 km. (2) To the air-speed vector of 201.9° – 1106.6 km a wind-vector of 90° – 221.3 km (20 km/t times r = 0.3 times 36.89 timer) should be added. The resultant is a track-vector of 190.56° – 1044.4 km. (3) To the flying-vector of 201.9° – 804.8 km should be added a wind-vector of 150° – 225.4 km (r = 0.42 times 20 km/h times 26.83 hours). The resultant is a track-vector of 191.3° – 960.4 km.

If the three track-vectors (1), (2) and (3) were added together, the resultant would be 194.2° – 2867 km. This would, as expected, be ‘SE’ (152° – 504 km) of the no-wind CC-flying/track vector 201.9° - 2515 km.

The following correction – well within the capacity of natural selection – could be to start from Portugal towards 209.6° (the difference between 201.9° and 194.2° = 7.7° added to 201.9°). Furthermore, a reduction in flying time with a factor 2515/2869 = 0.88. I.e. flying time of the three legs: (1) 20.12 times 0.88 = 17.71 hours, (2) 32.46 hours and (3) 23.61 hours. Unfortunately, HN never came to simulations when the long step from Portugal to Cabo Blanco was divided into three, so the specifications given above are mostly to the inspiration for what to do for other people. HN preliminary only carried out a few NAVGA-simulations (see below) on basis of Tab. 6A below (first part, not including the division of the long track in three).

Tab. 6A. NAVGA simulation in degrees of the track from Drentje to Ivory Coast.
NAVGA-simulering i grader af forløbet fra Drentje til Elfenbenskysten.

Position	**Latitude**	**Longitu.**	**Lat. shift**	**Lon. shift**
#0	52.8°N	6.4°E		
#1	50.85°N	4.8°E	-1.95°	-1.6°
#2	48.90°N	3.2°E	-1.95°	-1.6°
#3	47.95°N	1.6°E	-1.95°	-1.6°
#4	45.00°N	0°E	0°	0°
#5	45.00°N	0°E	0°	0°
#6	45.00°N	0°E	0°	0°
#7	43.50°N	3.50°W	-1.5°	-3.5°
#8	42.00°N	7.00°W	-1.5°	-3.5°
#9	42.00°N	7.00°W	0°	0°
#10	42.00°N	7.00°W	0°	0°
#11	21.00°N	17.00°W	-21°	-10°
#12	21.00°N	17.00°W	0°	0°
#13	21.00°N	17.00°W	0°	0°
#14	18.83°N	16.25°W	-2.17°	-0.75°
#15	16.66°N	15.50°W	-2.17°	-0.75°
#16	14.50°N	14.75°W	-2.17°	-0.75°
#17	12.33°N	14.00°N	-2.17°	-0.75°
#18	10.16°N	13.25°N	-2.17°	-0.75°
#19	8.00°N	12.50°W	-2.17°	-0.75°
#20	8.00°N	12.50°W	0°	0°
#21	8,00°N	12.50°W	0°	0°
#22	8.00°N	10.67°W	0°	0°
#23	8.00°N	8.84°W	0°	0°
#24	8.00°N	7.00°W	0°	0°
#25	8.00°N	7.00°W	0°	0°
#26	8.00°N	7.00°W	0°	0°

If the long step is divided in three, the following arises (Tab. 6B).

Tab. 6B. #14 is the same as #12 in Tab.6A, i.e. #15, #16 … correspond to #13, #14 and so on. *#14 er det samme som #12 i Tab. 6A, det vil sige #15, #16 … svarer til #13, #14 og så videre.*

Position	**Latitude**	**Longitud.**	**Lat.shift**	**Lon. shift**
#11	37.00°N	9.50°W	-5°	-2.5°
#12	28.00°N	14.00°W	-9°	-4.5°
#13	21.00°N	17.00°W	-7°	-3°

Mortality on migration

HN simulated 3000 ‘birds’ progressing CC in a calm/no-wind starting in the Netherlands in order to elucidate how many reached within a reasonable distance from the wintering area in the Ivory Coast. The results are shown below, and we also defined what we considered reasonable boundaries for the four ‘bends’ on the route. Obviously, whether the ‘birds’ arrive to the wintering area depends much on the concentration of the directional probability distribution. However, even the high concentration of 0.99 resulted in what appears to be too few surviving ‘birds’ and when a wind-vector is added, probably none of the wind drifted ‘birds’ and a few only of the ’birds’ drifting partially for the wind will arrive to the wintering area. In the present computation the ’birds’ were allowed to continue even if they came outside the borders of the intermediate ‘bends’ – therefore the somewhat bouncing numbers. Not surprisingly, after the long sea-crossing, Cabo Blanco becomes a bewildering site in particular.

If CC and r = 0.99, the centre of ‘birds’ when finished is only lagging a little behind the final destination. Probably, the same holds true in wind drifted CC ‘birds’– but with a much larger spread around the centre.

For each ‘bend’ we defined a ‘target area’, e.g. on six latitudinal degrees and eight longitudinal degrees. In order to proceed towards the next ’bend’ the birds should have been within this area. The ‘target areas’ were: 1) Bordeaux 43°/47° N and 2° W/3° E, 2) Portugal 43.5°/40° N and 9°/4° W, 3) Cabo Blanco 22°/17° N and 18.5°/15° W, 4) Freetown 10°/5° N and 14°/9° W, 5) Ivory Coast 10°/5° N and 9°/5° W.

HN considered 3000 starting ‘birds’ from Drentje, the Netherlands, and following a wrapped Cauchy distribution and r = 0.99, the following CC ‘birds’ survived until and inclusive Bordeaux, Portugal, Cabo Blanco, Freetown and the Ivory Coast: 2905, 2837, 2395, 2284 and 2163, respectively. However, a CC-system with r = 0.99 is probably unrealistic.

In the material left by HN in an (for me) understandable form, I found only a single table (Tab. 7 below), which show the area of 70% contour ellipsoids at the Ivory Coast following simulations in CC and NAVGA with the corresponding values for wind-drift and r = 0.80 or 0.95 for a wrapped Cauchy (or wrapped normal; I am not sure).

Tab. 7. 70% contour ellipsoid areas in square km of the wintering area
70 % kontur-ellipse arealer af vinterkvarteret i kvadrat-kilometer

System	**No wind**	**With wind, W**
CC, r = 0.80	1,722,803	4,578,330
CC, r = 0.95	440,900	3,218,820
NAVGA, r = 0.80	684,236	1,685,049
NAVGA, r = 0.95	142,834	779,115

Clearly, in order for the population to be stable in the long run, the flycatchers must be navigators – and in a more skilled way than proposed by me.

Red-backed Shrikes from Denmark

Pedersen *et al.* (2020) followed the migration of the Gribskov breeding population of adult Red-backed Shrikes using geolocators. As seen in Figs 7 and 8, the birds first migrate towards the Balkans. Then, after a stop-over there, the birds migrate to what must be considered the first wintering ground in Sudan. The next wintering ground is much further south in Namibia/Botswana.

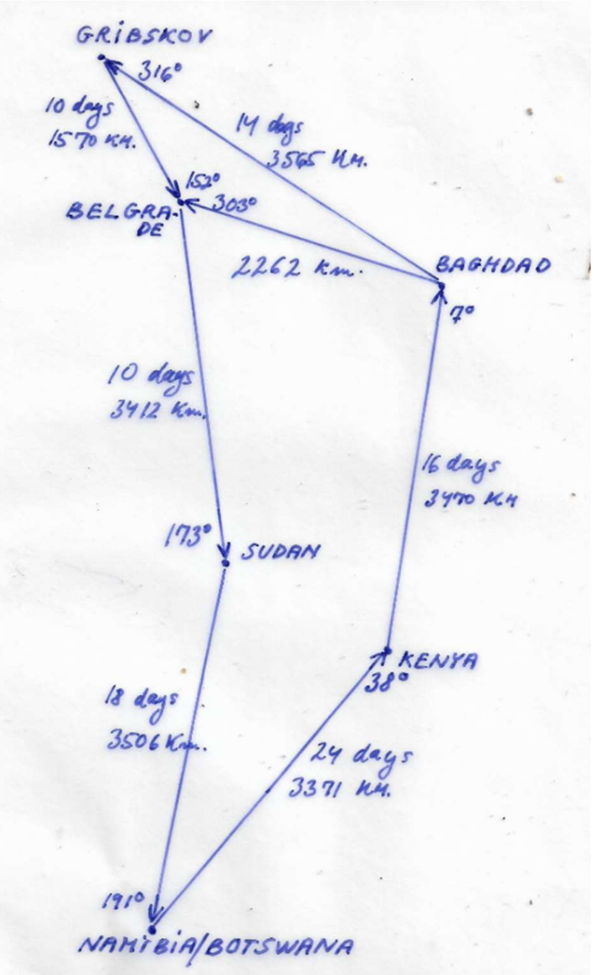

Fig. 7. Loxodrom-directions and -distances between the mean positions of breeding area, stop-over sites and wintering grounds in the Gribskov population of Red-backed Shrikes. Also, numbers of days between departure and arrival to a certain position are denoted.

Gribskovbestanden af Rødrygget Tornskade. Loxodrom-retninger og -afstande mellem vigtige rast- og overvintrings-områder og retningsskiftet ved Bagdad. Der er også vist, hvor mange døgn (dage), der forløber mellem afgangen fra et punkt til ankomsten i næste område.

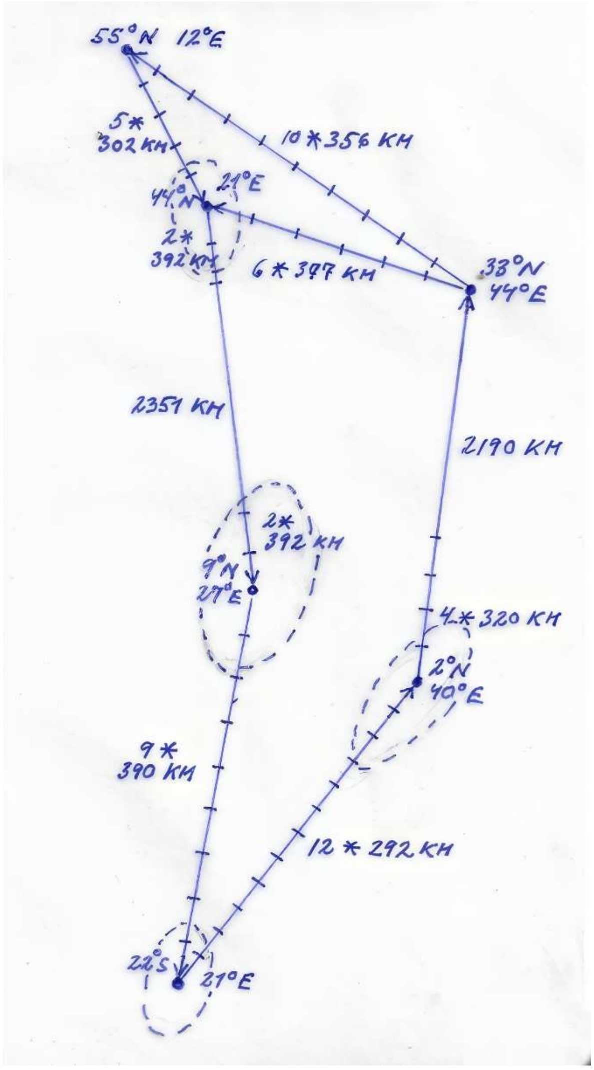

Fig. 8. The Gribskov-population of Red-backed Shrikes. Estimated number of migratory steps, 45 (or 44) short ones (between 292 and 392 km), and two very long (2351 and 2190 km) crossing inhospitable zones. The mean positions of breeding area, stop-over sites and wintering grounds are denoted in latitude and longitude. Also shown the approximate size of the stop-over area in Eastern Europe and the three wintering areas.

Det formodede antal træktrin – i alt 45 (44) korte (mellem 292 km og 392 km) og to lange træktrin (2351 og 2190 km) ved Sahara-/Arabien-overflyvningerne. Gennemsnits-positionerne af yngleområde, rasteområder og vinterkvarterer er angivet med bredde- og længdegrader.

Following a long stay there, the birds migrate to East Africa to a stop-over area, which could be considered the third wintering ground. From there, the birds migrate towards north to about Baghdad, where they bend northwest towards the Danish breeding ground.

Simulations

The figures and tables below are calculated/estimated based on fig. 1 and tab. 3 in Pedersen *et al.* (2020). For possible CC and NAVGA simulations, see Figs 7 and 8 and tables below. The hatched areas in Fig. 8 roughly follow the range of records within the stop-over site and three wintering areas.

In the following, (a) shows the breeding position, bends on route, or centre of stop-over/wintering ranges. (b) the range and (c) the direction and length of the loxodrome towards the next site/centre of range. (d) shows the possible number of migratory steps and their length.

(c) and (d) could be the base for a possible CC simulation:

Gribskov: (a) 56° N/12° E. (c) 152° – 1510 km. (d) Five steps of 302 km each.

Belgrade: (a) 44° N/22° E, (b) 35° – 50° N/17°E – 27° E. (c) 173° – 3919 km. (d) First two steps of 392 km each, then a single long step of 2351 km, terminated by two steps of 392 km each.

Sahel/Sudan: (a) 9° N/27° E, (b) 19° N – 5° N/20° E – 33° E. (c) 191° – 3506 km. (d) Nine steps of 390 km each.

Namibia/Botswana: (a) 22° S/21° E, (b) 14° S-26° S/17° E – 25° E. (c) 38° – 3371 km. (d) 12 steps of 292 km each.

East Afrika: (a) 2° N/40° E, (b) 3° S – 7° N/34° E – 45° E. (c) 7° – 3470 km, (d) first four steps of 320 km each, then a single long step of 2190 km.

Baghdad: (a) 33° N/44° E. (c) 303° – 2262 km, (d) six steps of 377 km each.

Belgrade: (a) 44° N/22° E. (c) 332° – 1510 km, (d) Five steps of 302 km each.

Gribskov: (a) 56° N/12° E.

If the birds migrated directly from Baghdad to Gribskov, the message would be:

Baghdad: (a) 33° N/44° E. (c) 316° – 3565 km, (d) 10 steps of 356 km each.

Gribskov: (a) 56° N/12° E.

The huge Sahel/Sudan area signals that the much smaller Namibia/Botswana area should be approached by means of NAVGA and not CC, considering an airspeed of 40 km/h. Perhaps no one should wonder because the birds are adults having spent at least one previous winter in southern Africa, but if the first winter of the juvenile birds was bounded in a CC-system, natural selection would have been strong against outsiders. The question is whether the migration from Namibia/Botswana towards East Africa is founded in NAVGA or CC? Possibly, from East Africa towards Baghdad only CC is involved. From Baghdad the birds – also the juveniles – in all probability navigate towards the Gribskov breeding position.

Tab. 8 lists the goal area positions based on NAVGA simulation.

Contour ellipsoids

HN was not involved in the following. He never calculated contour ellipsoids on real data but only considered ellipsoids originating from simulated data. He left instructions about the principles behind the calculations, but I do not possess the necessary skills to proceed his way. However, a passable road for me appeared to be Batschelet (1978) and his treatment of the bivariate normal distribution, the confidence ellipse and the Hotelling test. Though not always the same scenario, the approach was considered usable for calculating ellipses comparable to the contour ellipsoids of HN.

As a first step, I plotted the 17 geolocator mean positions of the individual shrikes wintering in Namibia/Botswana (Pedersen *et al.* 2020). Then I used the formulas on p. 11 in Batschelet (1978) for calculating the two semi-axes (a) and (b) of the confidence ellipsoid using the 95% F-value (F2, 15 = 3.68). Initially and naively, I guessed this would lead to the semi-axes of the 95% confidence ellipsoid of HN. However, this expectation was not met, but I soon discovered that inclusion of different F-values resulted in a constant a/b ratio. From here, it was a matter of trial and error to find the appropriate F-value, with corresponding semi-axes and an ellipse drawn by eye encompassing about 70% of the points. Then the area could be calculated as (a) times (b) times π.

Tab. 8. Red-backed Shrike. NAVGA simulations. Coordinates in blue refer to a route in spring from Baghdad over Belgrade to Gribskov. The black coordinates subsequently refer to a route from Baghdad directly to Gribskov. This route crosses the Black Sea at its widest and possibly a 200 km detour via Belgrade was selected.

Rødrygget Tornskade. NAVGA-simulering. Koordinatsæt i blåt refererer til en forårsrute fra Bagdad over Beograd til Gribskov. Sort koordinatsæt vist efterfølgende refererer til en rute fra Bagdad til Gribskov. Denne rute krydser over Sortehavet, hvor det er bredest, så muligvis vælger fuglen en 200 km længere omvej over Beograd (blå koordinater).

56°N/12°E
53.6°N/14°E
51.2°N/16°E
48.8°N/18°E
46.4°N/20°E
44°N/22°E
40.5°N/22.5°E
37.0°N/23.0°E
16.0°N/26.0°E
12.5°N/26.5°E
9.0°N/27.0°E
5.56°N/26.33°E
2.11°N/25.67°E
1.33°S/25.00°E
4.78°S/24.33°E
8.22°S/23.67°E
11.67°S/23.00°E
15.11°S/22.33°E
18.56°S/21.67°E
22.00°S/21.00°E
20°S/22.58°E
18°S/24.17°E
16°S/25.75°E
14°S/27.33°E
12°S/28.92°E
10°S/30.50°E
8°S/32,08°E
6°S/33.67°E
4°S/35.25°E
2°S/36.83°E
0°N/38.42°E
2°N/40.00°E
4.82°N/40.36°E
7.64°N/40.73°E
10.45°N/41.09°E
13.27°N/41.45°E
33.00°N/44.00°E
34.83°N/40.33°E
36.67°N/36.67°E
38.50°N/33.00°E
40.33°N/29.33°E
42.17°N/25.67°E
44.00°N/22.00°E
46.4°N/20°E
48.8°N/18°E
51.2°N/16°E
53.6°N/14°E
56°N/12°N
35.3°N/40.8°E
37.6°N/37.6°E
39.9°N/34.4°E
42.2°N/31.2°E
44.5°N/28.0°E
46.8°N/24.8°E
49.1°N/21.6°E
51.4°N/18.4°E
53.7°N/15.2°E
56.0°N/12.0°E

Anyway, increasing Batschelet's F2, (n-2) to 20, an ellipse was drawn encompassing 11 to 12 positions matching an about 70% ellipsoid. Transforming degrees to kilometres the two semi-axes were calculated as 618 km and 290 km which times π resulted in an area of 563,036 km². The ellipse is cantered in the means of longitudes and latitudes, and the shape and orientation of the ellipse is the same independently of the F-value.

Applying the same procedure to the Sahel/Sudan distribution – obviously covering a larger area than the Namibia/Botswana distribution – and using F2, 16 = 20, (a) and (b) were estimated as 709 and 615 km, respectively, and the almost circular ellipse covered 1,369,844 km² encompassing 10 positions, three were on the borderline and five outside the borderline, i.e., this area should be roughly comparable to an area of a 70% contour ellipsoid.

Considering the East African distribution and using F2, 14 = 18, I calculated an ellipse with five positions outside probably close to a 70% contour ellipsoid. (a) and (b) were estimated as 734 and 339 km, respectively, and the area 781,710 km².

I also calculated the two semi-axes and the about 70% contour ellipsoid area of the stop-over region of Balkan. (a) and (b) were estimated to 744 km and 544 km, respectively, and the area as 1,271,516 km².

The most important observation is that, if relying on a CC-system, the area covered in Namibia/Botswana would have to be greater than the Sahel/Sudan area. However, very clearly the opposite was found, supporting the idea of a NAVGA system.

Other European Pied Flycatcher populations and populations of Common Redstarts and Willow Warblers from Denmark

The autumn migration pattern of Danish populations of Redstart and Willow Warbler (Kristensen *et al.* 2013, Lerche-Jørgensen *et al.* 2017) appear clearly different from both the Pied Flycatcher and Red-backed Shrike populations (Fig. 9). The Redstarts migrate southwest through Spain and inland coastal West Africa to about Dakar and then bend east to a rather large wintering area. The Willow Warblers also arrive close to east of Dakar and then, over the winter, move in ESE direction up to about 3000 km. There seems to be no site fidelity between the years, and the 70% contour ellipsoid (not calculated) seems to be much larger than in the case of the Redstarts.

Concerning the Redstarts, apart from a very westerly bird wintering about 16° N/14.5° W, the 70% contour ellipsoid area of the remaining six birds was 232.245 square km and the mean position 13.7° N/3.8° E. One should note that the area is not much larger than in the case of the Pied Flycatchers, and that all the birds were adults at least in their second year.

Adamik *et al.* (2023) also informed about the geolocator tracked positions of a) English, b) Czech and c) Finnish populations of Pied Flycatchers:

a) Breeding site in SW-England near Exeter 50.6° N/3.7° E (N = 24). Mean wintering position 10.99° N/10.60° E (calculated JR) and 70% ellipsoid area of winter positions (estimated JR) 130,000 km².

b) Mean breeding site position of two nearby populations in Bohemia and Moravia was 50.29° N/16.54° E (N = 8). Mean wintering position 11.09° N/7.14° E (calculated JR) and 70% ellipsoid area of winter positions 195,000 km² (estimated JR).
c) Breeding site in SW-Finland near Turku 60.2° N/22.2° E (N = 4). Mean wintering position 11.32° N/10.73° E (calculated JR) was very close to the mean wintering position of the English birds.

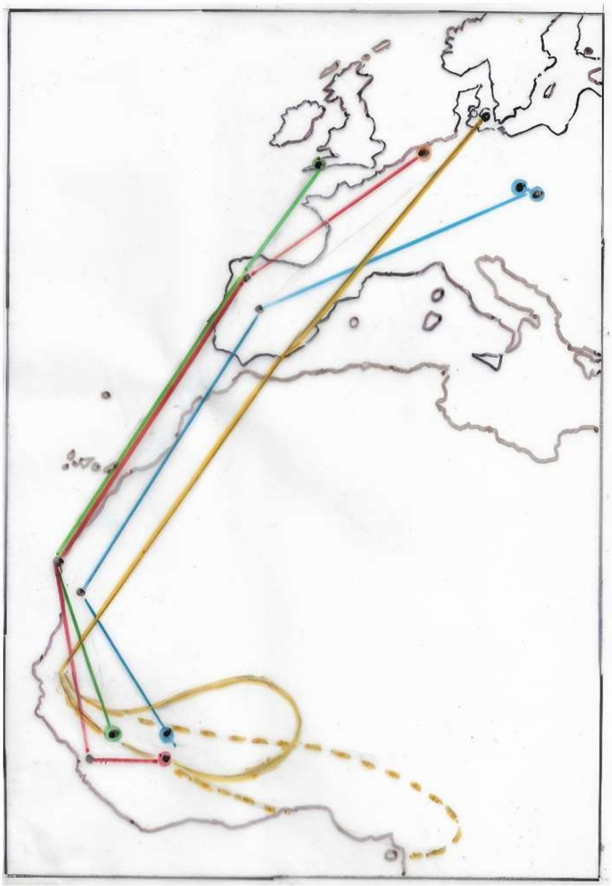

Fig. 9. Autumn migratory routes and mean wintering areas of three different populations of Pied Flycatchers *Ficedula hypoleuca*. Green shows autumn route and wintering area of an English population, red a Dutch population, and blue two nearby Czech populations. The orange/brown line from Denmark to about Dakar in Senegal denote the track of two breeding populations of Redstart and Willow Warbler. The wintering area of the former is encompassed within the fully orange/brown line, whereas the hatched orange/brown line encompasses the wintering area of the Willow Warbler. *Efterårstrækrute og vinterkvarter af tre forskellige bestande af Broget Fluesnapper (grøn en engelsk bestand, rødt en hollandsk bestand og blåt to nærliggende tjekkiske bestande kombineret. Danske bestande af Rødstjert og Løvsanger trækker ret direkte mod Dakar i Senegal (orange/brun). Herfra fortsætter Rødstjertene mod Ø til vinterkvarteret (fuldt optrukken), medens Løvsangernes vinterkvarter spreder flere 1000 km mod ØSØ (stiplet).*

In particular, the Pied Flycatchers appear to follow the predictions from NAVGA well. The Redstarts and Willow Warblers possibly only show latitude navigation. The Red-backed Shrikes perhaps only CC as part of the migration back to Europe (+ final navigation towards the fledging area in Denmark). NAVGA appears to be the system behind the migration to southern Africa, perhaps first from Sahel/Sudan, but it seems unreasonable that navigation first turns up at this stage.

However, the lesson to be learned is – as always – that one should not generalize too much based on the pattern of a single species/population. Not surprisingly, there seems to be a lot of variation and adaptation between the species/populations.

The wind-vector revisited

Obviously, our wind-vector distribution is vulnerable to criticism – it is not natural that the wind-drifted vector shifts stochastically between the 'birds'. In the real world, the bird populations migrate more or less at the same time in the same weather. We should have considered and used natural winds. Furthermore, individual variation in airspeed, direction and number and length of steps should also be introduced. However, we do not believe this will seriously affect the main claim: CC without wind and a very small within and between individual directional variation (say, r = 0.99 and r = 1, respectively) may function. But wind drifted CC – non-compensated or partly compensated – is not a possible way for a successful migration. Some kind of navigation must be involved.

Resumé

Simulering af vektororientering og målområdenavigation hos nattrækkende småfugle

Dette appendiks, udformet som en selvstændig artikel, blev til som et samarbejde mellem Jørgen Rabøl (JR) og Henning Noer (HN). HN døde et par år inde i projektet, så JR blev nødt til at afslutte projektet alene. Hans indsigt i matematik var begrænset, men stor nok til, at han mente at kunne præsentere de uafsluttede analyser på en måde, der kunne være til inspiration for andre træk- og orienterings-forskere indenfor området. HN var både biolog og matematiker, og dertil god til at EDB-programmere i Borland Pascal 7.0. JRs input til HN gik i al sin komplicerede enkelhed ud på at simulere to mulige trækrute-forløb (fig. 1 i Rabøl 2023), CC[8] og NAVGA[9], for at se hvilket af systemerne, der beskrev empiriske[10] trækrute-forløb bedst muligt. Simuleringerne gik mestendels ud på at slippe 3000 virtuelle 'fugle' løs fra samme udgangsposition, og så se på, hvor de meldte ind at være undervejs og efter et vist antal træktrin.

CC er det simpleste orienterings-system, som man kan forestille sig. Problemet med CC er, at det er et åbent system; der er ikke har indbygget kompensationsmuligheder for retningsfejl og vindafdrift. De hober sig derfor op og bliver større og større. Så efter – fx – 25 træktrin med vind på, ender

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[8] **CC** står for Clock & Compass, også kaldet vektor-navigation eller (mere korrekt) vektor-orientering. Rabøl (1988) kalder det kalender & kompas-orientering. Fuglene fra en bestemt bestand tænkes genetisk udstyret med (1) en trækretning, fx SV fastlagt i forhold til et eller flere kompasser, såsom Solen, solnedgangen, stjernehimlen eller Jordens magnetfelt. Dertil (2) et udtryk for afstanden til vinterkvarteret, såsom 25 træktrin af varighed på hver otte timer, der med en egenhastighed for fuglen på 30 km/timen giver en vejlængde på 25 gange 8 gange 30 km = 6000 km.

[9] **NAVGA** står for **NAV**igation mod et vandrende målområde (**G**oal-**A**rea). I NAVGA starter fuglen ikke med at navigere mod sit endelige mål, hvilket i denne forbindelse vil sige vinterkvarteret. Målet starter så at sige i udgangs-positionen og bevæger sig så ned gennem trækruten og ender i vinterkvarteret. Målet er bestemt af værdierne i (mindst) to parametre/koordinater, der fx kan være Nordstjernens højde over horisonten (svarende til breddegraden) og et mere eller mindre kompliceret samspil mellem fuglens tidssans/indre ur og stjernehimlens omdrejningsfase (svarende til længdegraden).

[10] Empirisk vil sige kendt ud fra genfund af ringmærkede fugle, og især – i de senere år – positioner estimeret ud fra GPS og lyslogger/geolocator-registreringer.

fuglene ikke indenfor snævre grænser svarende til, hvad man ved om vinterkvarterets udstrækning hos fugle fra en rigtig bestand, men måske indenfor et område, der er flere 1000 km i både N/S- og Ø/V-lig udstrækning. Dette indikerer, at CC ikke kan give en fuldgyldig forklaring på fuglenes orienteringssystem. Der må et system til med indbyggede kompensationer for retningsfejl og vindafdrift. Spørgsmålet er så, om det er NAVGA eller om det er et forløb mellem først CC og senere navigation mod vinterkvarteret.

I vores simuleringer startede vi simpelt i et (todimensionelt) plan, og med 25 træktrin; i begge systemer fra positionen (0,0).

I CC bevæger 'fuglene' sig – som udgangspunkt inden der blev lagt variation ind – i hvert trin 200 km mod S og 100 km mod V, hvad der svarer til en retning på ca. 207° (omkring SSV) og en afstand på 224 km. Vi lagde derefter variation ind i retningen, men ikke i andet såsom antal træktrin eller trinlængder. Vi indlagde heller ikke variation mellem individerne. Retningsvariation angiver man normalt med et reciprokt udtryk for variationen, der kaldes koncentrationen, r. Den første r, vi undersøgte effekten af, var 0,84924, der fremkom ud fra følgende diskrete retningsfordeling med en middelretning i SSV (202,5°) og følgende sandsynligheder for valg af flyveretning således: SØ 0,05, SSØ 0,10, S 0,20, SSV 0,30, SV 0,20, VSV 0,10 og V 0,05. Sandsynligheden for at en fugl vælger en flyveretning mod V er således 0,05 (5 %), medens den er 30 % for en SSV-retning. Senere brugte vi mestendels r = 0,99 i forbindelse med en teoretisk fordeling såsom den 'Omviklede' Cauchy. Vi er her meget langt fra de r-værdier (0,47 og 0,665), som henholdsvis Rabøl (1978) og Mouritsen (1998) opererede med. I disse størrelser var der – implicit – indbygget variation fra vindafdrift, hvad der ikke er i 0,849 eller 0,99, hvor vindafdrift bliver lagt på efterfølgende. En bestand, der CC-orienterer, spreder sig 'parabolsk' med antallet af træktrin, som vist på fig. 1 i Rabøl (2023).

I NAVGA navigerer 'fuglene' fra (0,0) i første trin mod (-100 km, -200 km). I andet trin mod (-200 km, -400 km), og i sidste og femogtyvende trin mod (-2500 km, -5000 km). Også her er der lagt variation ind med hensyn til positionsbestemmelsen. Den første kombination *af variation*, vi forsøgte os med, var -200 (0.0625), -100 (0.25), 0 (0.375), +100 (0.25), +200 (0.0625) i længdegraden/abscissen og -100 (0.25), 0 (0.50), +100 (0,25) i breddegraden/ordinaten. Senere ekspanderede vi den sidste (binomial fordeling) en gang og den første op til to gange uden de store effekter. Det vi fandt var, at en NAVGA-orienterende bestand spreder sig stort set parallelsidet, dvs. indenfor et bælte som vist på fig. 2 i Rabøl (2023). Om virkelige bestande gør dette, ved vi meget lidt konkret om; vi formoder, at de gør det, og at der i hvert fald er 'flaskehalse' undervejs i forløbet, som indiceret fx af det snævre bælte, hvorigennem Kærsangeren *Acrocephalus palustris* passerer i Ø-Afrika (Thorup & Rabøl 2001).

Det vigtigste redskab til at forstå 'godheden' af CC- og NAVGA-simuleringerne, er HNs introduktion og brug af kontur-ellipser. Efter et vist antal træktrin har de 3000 'fugle' spredt sig, og det er naturligvis for uoverkommeligt og uoverskueligt at se på dem allesammen. Punktskyen skal koges ned til noget håndterbart, og her kommer kontur-ellipserne i spil. Punktskyen fremtræder mere eller mindre elliptisk (eller banan-formet), og ved hjælp af passende transformationer og tilbage-transformationer af data kan man beregne fx 70 % og 95 % af kontur-ellipsen indeholdende hhv. 75 % og 95 % af punktskyen, der igen kan udtrykkes ved halvdelen af den lange akse (a), halvdelen af korte akse (b) og ellipse-arealet (a) gange (b) gange π (i km eller grader). En 70 % ellipse betyder, at 70 % af 'fuglene' er indenfor ellipsen. Helt enkelt fortæller (fx) 70 % ellipse-arealerne, hvordan CC og NAVGA fungerer, uden eller med vindafdrift eller med delvis kompensation for samme, og med forskellige koncentrations-værdier (r) i retningsfordelingen. På den måde kan vi i forskellige tabeller sammenligne i hvilken grad, fuglene når målområderne, som vi mener at kende ud fra ringmærkning og GPS/geolocator-data.

Efter de indledende og meget vigtige øvelser på en flad jord gik vi nu over til at betragte en sfære. Over større afstande må man tage hensyn til Jordens krumning og med hensyn til nogle forhold regne i grader og ikke i kilometer. Retning og afstand mellem to punkter på en kugleflade kan udtrykkes gennem en loxodrom eller en orthodrom. Sidstnævnte udtrykker den korteste vej mellem to punkter på Jorden og følger en såkaldt storcirkel. Retningen mellem to punkter på Ækvator og på alle længdegrader (uden pol-passager) skifter ikke kurs undervejs, men det gør den mellem alle andre to punkter på Jorden. En loxodrom skifter ikke kurs undervejs (i forhold til geografisk N), men afstanden mellem punkterne bliver større end for orthodromen bortset fra i special-tilfældene nævnt ovenfor, hvor de er lige store.

Hvis fugle bruger NAVGA, vil de – normalt (med bl.a. sibiriske gæster i Europa som mulige undtagelser; se Appendiks 3) – være tæt på (indenfor 1000 km af) målområdet, hvorfor det virker mest oplagt at regne i loxodromer, og som sagt så gjort.

Som det fremgår af diverse tabeller – især Tab. 6A over de formodede træktrin af Broget Fluesnapper fra Holland til Elfenbenskysten – opererer vi i grader, fordi det vil være det eneste naturlige at gøre i det virkelige liv for en trækfugl, der agerer navigatorisk. Vi skal her huske, at afstanden mellem breddegraderne er konstant = 111,111 km = 10.000 km/90°, medens afstanden mellem to længdegrader – på samme breddegrad – er 111,111 km gange cosinus til breddegraden. Det betyder, som eks., at afstanden mellem to længdegrader på 60°N er det halve af 111,111 km = 55,555 km (cosinus 60° = 0,5).

Vi går i detaljer med at se på data fra en hollandsk bestand af Broget Fluesnapper og en dansk bestand af Rødrygget Tornskade. I begge tilfælde er det adulte fugle, der følges, idet ungfugle mærket med geolokatorer i praksis ikke lader sig genfange. Desværre er det i et resumé ikke muligt at komme ind på for mange detaljer og udredninger, men det korte af det lange er, at udfaldet af et CC-trækforløb med vind-afdrift virker helt utilstrækkeligt, idet alt for få fugle når frem til vinterkvarteret. For – formentlig urealistisk – meget høje værdier af r (0,99) ligger beregningerne for CC med delvis vind-kompensation tæt på det mulige, og det gør NAVGA med vind-afdrift i endnu højere grad. Jokeren i spillet er vindvektorfordelingen. I den af os brugte fordeling er gennemsnit-vindstyrken 21,2 km/timen, hvad der er klart under fuglenes antagede egenhastighed (30 km/timen). Alle vindretninger er antaget lige hyppige. Det er de ikke, og det vil i snit formindske overensstemmelsen mellem forudsigelser og virkelighed. Men hvis vindstyrken er for høj, og de rigtige fugle er vindvektor-observante og -udvælgende, så vil det kunne forbedre resultaterne med vind eller delvis vind-kompensation en hel del. Moderne model-forskere såsom

Åkesson & Bianco (2017) opererer med (tæt på) virkelige vindvektorer fra de højder, hvori trækket formodes at udspille sig. Men også her er der godt med gætterier inde.

Det afsluttende punkt kunne måske være, hvorfor trækfugle ikke bare kompenserer fuldstændigt for vindafdrift i CC-systemet. Svaret er – i al sin enkelhed – at det kan de ikke under nogen omstændigheder. De vil så gerne, og de prøver rigtig meget, men uanset hvad, driver de for vinden og ikke bare lidt, men meget over store afstande. Kun lokalt og i de lave trækhøjder kan dagtrækkende arter som Sanglærker kompensere for vindafdriften og her forekommer sågar – kortvarigt i tid og sted – overkompensation for vindafdriften, såkaldt modvindstræk. Men vindafdrift er normalt ikke noget problem i praksis. Det er det kun i hovedet på vektor-orienterede trækforskere. I det virkelige liv kan trækfuglene kompensere ved at navigere, og sådan er det bare!

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