

Testing the goal area navigation hypothesis against the re-navigation hypothesis: compass-orientation in the standard direction plus navigation back towards the last previous position

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(Med et dansk resumé: Forflytningsforsøg: Test af målområdenavigations-hypotesen mod den alternative re-navigations hypotese: Kompass-orientering i normaltrækretningen plus navigation tilbage mod den sidste position, hvor fuglen kom fra)

Abstract The question is how the compensatory orientation normally following a geographical displacement is established in medium- and long-distance passerine migrants. Rabøl (first 1969) proposed (1) a moving goal area navigation system, whereas W. Wiltschko (1973) proposed (2) a hybrid system between (a) vector orientation and (b) navigation back towards the position from where the birds were displaced. (2) is designated the re-navigation hypothesis by the present author and is here considered in its most simple single step form.

Juvenile migrant Spotted Flycatchers *Muscicapa striata* and Eurasian Blackcaps *Sylvia atricapilla* were captured and funnel-tested for orientation on Christiansø in the Baltic Sea. After a displacement 450 km WNW to Mors in NW-Jutland they were transported back to Christiansø and tested here for a second time. On Mors the birds were sometimes exposed in their cage for the sun and starry sky and always to the local magnetic field. However, because of bad weather we failed to carry out proper funnel-experiments on Mors. Anyway, that was not considered detrimental for the interpretation of the outcome of the tests.

The birds were southerly oriented on both occasions, and there was no statistically significant difference between the two sample mean vector. The results are indicative of the action of (1), i.e. a moving goal area navigation system. The predicted outcome of (2) was an about SW-WSW orientation on the second occasion on Christiansø.

Implicitly – as shown by his proposal – W. Wiltschko considered (2) a more simple and therefore more reasonable hypothesis than (1). However, scrutinizing the scenarios (including extending the one-step re-navigation situation to a multi-step situation like the moving goal area system) (2) develops into a parabolic pattern with much un-controlled variation including shortening of progress. In conclusion, both the single experiment (we certainly need many more) and theoretical considerations place (2) as an inferior hypothesis.

Introduction

The question is whether the migratory route in medium-/long-distance passerine migrants is genetically programmed as (1) vector orientation/clock & compass or (2) goal-area navigation

The goal area navigation hypothesis proposed by Rabøl (first in 1969) is about to go extinct because of distrust mostly resting in (a) selected counterevidence and inappropriate data treatments, and (b) preconceived attitudes including lack of appropriate testing.

Concerning (a): Single studies such as Perdeck (1958), Mouritsen & Larsen (2001) and Thorup *et al.* (2007) are held up against a meta-analysis as Thorup & Rabøl (2007). But selected cases cannot disprove a significant general tendency – in particular not when burdened with errors: (1) Perdeck (1958) is seldomly considered together with the more confusing contribution Perdeck (1967). When treated together, the clear patterns of juvenile birds using compass orientation and adult birds coordinate navigation break more or less down (Fig. 10 in Rabøl 1981, 1988, see also Holland 2014 concerning Perdeck 1967). (2) The procedure in the study by Mouritsen & Larsen (2001) is inappropriate and out of context: Longitudinal displacements in all probability cannot be simulated by presenting birds with a stationary planetary sky. (3) The data-treatment of the orientation of juvenile birds in Thorup *et al.* (2007) suffers in omission of several corrections and considerations (see Appendix 3 of the present paper).

Concerning (b): For two main reasons, leading people on the orientation-scene such as W. & R. Wiltschko and H.G. Wallraff always distrusted the goal area navigation hypothesis: (1) they were and are convinced that the stars are only used for compass orientation (I coupled goal area navigation and stars), and (2) they strongly believe that birds are unable to navigate towards what is inappropriately designated an ‘unknown/unbekannt place’. I agree. Neither birds nor humans can do that. However, the goal area is not necessarily unknown but just a position the birds never visited before. But of course – just like in humans – birds may in principle navigate if endowed with a flight plan. This plan is basically intrinsic but learned components are supposedly added already before the juvenile birds initiate their first autumn migration. Wallraff and W. & R. Wiltschko displaced a lot of pigeons but never migrant passerine birds. Therefore, their feeling for what is going on in such birds is probably not optimal. Anyway, W. Wiltschko (1973, first mentioned in Rabøl 1972).¹ proposed another compensatory mechanism (not a coherent system) than goal area navigation as responsible for the compensatory orientation following a displacement. This is the basic component in what I termed the re-navigation hypothesis: the compensatory orientation is a combination of compass orientation in the standard direction and “and a compensatory navigational response [...] directed towards the trapping place“ (Rabøl 1972). However, W. Wiltschko never understood and realized the full range and consequences in time and realm of his proposition (which may be named the extended re-navigation hypothesis).

¹ Independently – apparently without knowing Rabøl (1972, nor W. Wiltschko (1973) – Holland (2014) proposed the same hypothesis.

Therefore, dismissing the question whether migrant birds compensate a displacement or not, and just follow Thorup & Rabøl (2007) accepting ‘they do’, the question changes into ‘how they compensate the displacement?’ and testing the re-navigation hypothesis of W. Wiltschko/Holland contra the goal area navigation hypothesis.

Material and methods

For testing the re-navigation and goal area navigation hypotheses against each other we considered birds experiencing a clear starry night when tested in funnels following an exposure during sunset/early night in outdoor cages under a clear sunset sky and the emerging stars in early night.

Birds were trapped as grounded migrants on the island Christiansø in the Baltic Sea. The intention was to displace the birds as far as possible within the borders of Denmark. We selected a place on western Mors about 450 km WNW of Christiansø. This place is far from disturbing city lights. Birds should be tested first on Christiansø soon after the trapping, then displaced to Mors exposed for the starry sky and the natural magnetic field, and then tested here. This is the traditional procedure for a displacement experiment, but to carry it further into testing the re-navigation hypothesis a final step was added: transport back to Christiansø and testing here for a second time. If the birds make use of a goal area navigation system, the orientation in the two experiments on Christiansø should be about the same. If a re-navigation system were in charge, the orientation in the second Christiansø experiment should be as in the first Christiansø experiment (i.e. hopefully in about the standard direction of the population/species in consideration) plus orientation back towards Mors, i.e. WNW. Considering an example: if goal area navigation is the system and the standard direction is SW, we expect SW in the first and second experiment on Christiansø. If a re-navigation system is in charge, we expect $SW + WNW = WSW-W$ in the second experiment, provided that the two tendencies are expressed as vectors are of approximately the same strength. The directional difference between the outcomes of the two hypotheses would then be about 34° counter-clockwise in the re-navigation system. This is not much, so we had to look for other species with a standard direction counter-clockwise to SW. Lesser Whitethroat *Curruca curruca* is an obvious choice; it is a numerous migrant with a standard direction about SSE. The expected orientation in the alternative re-navigation system should thus be $SSE + WNW = SW$, i.e. the orientation should be about 68° clockwise of SSE which is the expected orientation, provided goal area navigation is carried out. However, according to our experience Lesser Whitethroats are often rather inactive in funnels. Therefore, we focused on Spotted Flycatchers with a standard direction a little E of S. The difference between the two hypotheses in the Spotted Flycatchers is about 61° , which looks acceptable as an average to distinguish when stochastic variation is included. However, perhaps it was not possible to trap sufficient numbers of Spotted Flycatchers, so we needed a back-up-species such as Eurasian Blackcap. However, Blackcaps are potentially tricky because of a migratory divide: to the W of longitude $12^\circ E$ the standard direction is about SW and to the E about SSE. Now Christiansø is situated on $15^\circ E$, and migrants here trapped in early September supposedly more or less solely belong to the

SSE population. Therefore, we intended to include Blackcaps to fill up for lack of Spotted Flycatchers.

The original plan was to displace birds from Christiansø first to Mors, then to Vidoy, Faroes, and finally back to Mors again. The birds should be tested in funnels on all four occasions. The intention was to use European Pied Flycatchers *Ficedula hypoleuca* and/or Common Redstarts *Phoenicurus phoenicurus* with a presumed migratory orientation of SSW-SW on Christiansø. On Mors the birds were supposed to orient about SE-SSE as a compensation for the displacement. Vidoy is situated about 1050 km NW of Mors and again we expect SE-SSE orientation. Back the second time on Mors we expect SSE-S orientation if a goal area navigation program should be carried out (the goal area has moved somewhat down the route). If the birds make use of a re-navigation system, we would expect an orientation between NW and the standard direction SSW-SW, i.e. a little S of W. The difference between the two systems is about 100° – in principle – making a distinction easy. However, we were not allowed to bring in birds from Denmark to the Faroes because of outbreak of bird flu in Europe.

The experiments started on Christiansø on 30 August 2018. The next morning the wind was northerly, and we collected three Blackcaps and four Spotted Flycatchers. On 2 September (weak winds from NE) we trapped further birds and 10 Blackcaps and 10 Spotted Flycatchers (from 31 August, and 2 September, all juveniles of the year) were placed in pairs in plastic baskets (for a description see Rabøl 2010, 2014). All birds were migrants which probably arrived to the island in late night/early morning on the date of trapping. The baskets were placed on the test site, the Bastion of the Queen in the SE-corner of the island. On 3 September the 20 birds in their baskets were exposed to the sunset and later a starry night sky for about two hours. On 4 September the birds were again exposed under the sunset/early night sky and two hours after sunset 16 birds were funnel-tested for one and a half hour during night under a clear starry sky. All birds were in good fatty condition.

On 7 September the birds were transported by ship and car to Mors in Jutland. The team arrived at 2200. The sky was overcast but between 0200 and 0300 in the night of 8 September the birds in their cages were exposed under a clear starry sky. Until 11 September we spent three further nights on the site, but it was not possible to carry out funnel experiments under a starry sky as all nights were mostly overcast, rainy and the wind was heavy. However, on the last night between 10 and 11 September the birds spent three hours outside in their cages and between 2255 and 2315 under a partly starry sky (cloud cover 3-4/8). The birds in the baskets were normally placed in a greenhouse experiencing the local magnetic field. During daytime in several prolonged periods, they observed the sun moving across the sky.

In the night of 9 September 16 birds were for more than three hours placed in outside funnels covered on top with a wooden plate board for protection against rain. If a starry sky, then appeared we were ready for testing. However, stars never appeared on the sky. Normally, birds in funnels covered with a wooden board during night – in almost total darkness – will make no activity (actually, they did; see next chapter).

On 11 September the birds were transported to Copenhagen and next day back on Christiansø. On 13 September the birds experienced a clear sunset and an early starry night in the baskets before transferred to and tested in funnels during a clear starry night. After one and a half hour the birds were released.

Results

The birds oriented very similarly on the first (4 September) and the second night (13 September) on Christiansø. The sample mean vectors were $178^\circ - 0.754$ ($P < 0.001$, $N = 14$), and $159^\circ - 0.736$ ($P < 0.001$, $N = 14$), respectively (Fig. 1). Applying the Watson-Williams two-sample test leads to no difference between the two samples (P about 0.30).

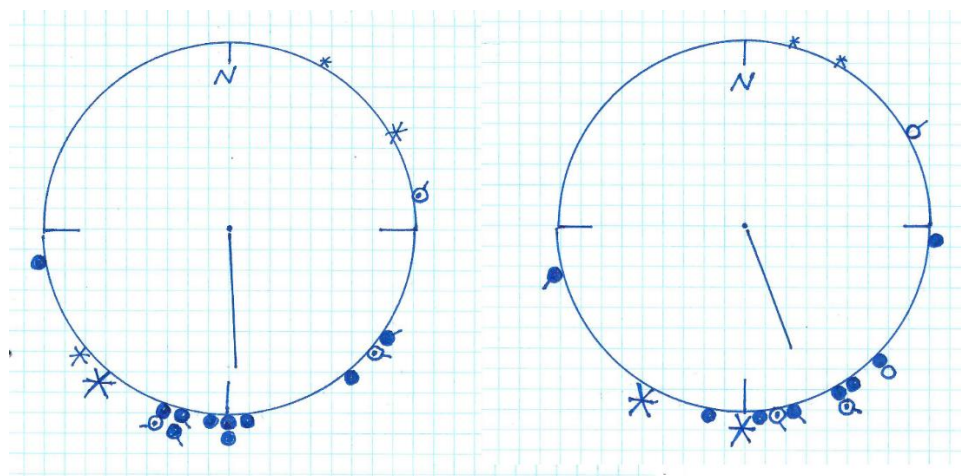


Fig. 1. The orientation on Christiansø 4 September (left) and 13 September 2018 (right). Each dot refers to the mean direction of the funnel activity of a Spotted Flycatcher or Blackcap (mark on the dots). A black, dotted or white dot refer to high, medium or low concentration, respectively. The two medium sized crosses in the left figure refers to a bird showing bimodal orientation with about the same amount of activity in both tops. A large cross refers to a bimodal activity with a dominating top. Such a top is included in the calculation of the sample mean vector. The two sample mean vectors are $178^\circ - 0.754$ ($P < 0.001$, $N = 14$), and $159^\circ - 0.736$ ($P < 0.001$, $N = 14$), respectively. *Orienteringen af Grå Fluesnapper og Munk (med streg på mærket) den 4. (til venstre) og 13. september 2018 (til højre). Der er ikke statistisk forskel på orienteringen på de to dage.*

Considered in more details: on 4 September we tested nine Spotted Flycatchers and seven Blackcaps. The sample mean vector of eight Spotted Flycatchers (a single bird not included displayed bimodal $60^\circ/230^\circ$ orientation) was $191^\circ - 0.846$ ($P < 0.01$). The sample mean vector of six Blackcaps was $156^\circ - 0.712$ ($P < 0.05$). On 13 September the sample mean vector of nine Spotted Flycatchers (a single bird was disoriented) was $158^\circ - 0.845$ ($P < 0.001$). The sample mean vector of the five Blackcaps was $162^\circ - 0.541$. The difference between the Spotted Flycatchers in the first and second

experiment was close to significance (P about 0.06, Watson-Williams two sample test). 10 individual birds (Spotted Flycatchers and Blackcaps) were oriented on both nights. The orientation on the second night as function of the orientation on the first night was $-26^\circ - 0.617$ ($P < 0.05$). The counter-clockwise rotation was not significant (the difference should have been about 42° in order to be significant at the 0.05-level according to the Confidence Interval Test).

Contrary to expectation, nine birds in the cloudy and rainy night of 9 September on Mors displayed significant migratory activity (as apparent from the scraping-patterns in the funnels). The activity level ranged from small/medium to very large (Rabøl 2010). Three birds were disoriented, and the sample mean vector of the remaining six birds was $253^\circ - 0.334$, i.e. the sample was disoriented. As the birds were tested in the local magnetic field, apparently a magnetic compass was not in charge.

Discussion

Rabøl (1969, 1970, 1972) proposed the goal area navigation hypothesis, which received some interest. However, already in Rabøl (1972) W. Wiltschko proposed an alternative explanation for the compensatory orientation following geographical displacements, named by me the re-navigation hypothesis. I remained open for other explanations of compensatory orientation (Rabøl 1978, 1980, 1994). Perhaps I should have defended my hypothesis more persistently (as suggested by the late E. Gwinner), but true science is to be open about competing hypotheses. Anyway, the present state is that the goal-area-navigation-hypothesis is on the fringe of eradication as evident by the survey of Holland (2014). Such a development is a pity for me personally but more importantly a major drawback for our understanding of migratory orientation in birds. Therefore, it is important to keep the scene alive considering new ways of hypothesis testing.

Commentary

Clearly, the very similar southerly orientation on both the first and second night on Christiansø is not compatible with the re-navigation hypothesis according to which we should expect orientation on the second night in about SW-W. On the contrary, the results are in accordance with the expectation of the goal area navigation hypothesis. Of course, this is not a proof of that hypothesis. We need many more experiments and an overall significant outcome as in the meta-analysis of Thorup & Rabøl (2007).

One may argue that the lack of funnel experiments on Mors weakens the conclusion above. However, the birds were exposed for what was considered sufficiently long time in their baskets under the clear starry sky on the night of arrival (and also 20 minutes on the last night) enabling them to star navigate. Furthermore, a sunny day sky was available for the birds in the greenhouse for some hours on two days and the local magnetic field all the time. Therefore, there is no valid objection that the birds in the second experiment on Christiansø were unable to navigate back towards Mors.

Perhaps people may argue that birds are only able to navigate towards a former position attained by themselves actively whereas a human transport – such as the one to Mors – are not enabling them to re-navigate. Again, this is a theoretically possible but not a constructive claim which invalidates any experimental approach in the future – and also former experiment such as Perdeck (1958).

In fact, there is nothing new under the stars: how to test the re-navigation/goal-area navigation hypotheses and appropriate experimental approaches were proposed already years ago:

- (1) Rabøl (1978, Fig. 4) considered a displacement which should be able to distinguish between goal area navigation and the alternative hypothesis. The system in mind was the Spanish population of Red-backed Shrike *Lanius collurio*, which in autumn, first moved ENE to Northern Italy, then ESE to Balkan, then SE from Greece to Egypt, and next S to Sudan. Birds from this population should be displaced to – say Firenze – from the breeding area or during the first part of the eastern leg. Staying in Firenze and tested there throughout autumn, the orientation should develop differently according to the two systems. This experiment still waits to be carried out. Perhaps the recent geolocator-experiments with Spanish Red-backed Shrikes (Tøttrup *et al.* 2017) could serve as an entrance.
- (2) Rabøl (1981) displaced migrant European Robins *Erithacus rubecula* trapped on Christiansø, Denmark to La Gomera, Canary Islands. Here the birds were kept and tested throughout October to December 1978. The centre of the wintering area of birds banded on Christiansø is about Barcelona in the direction of NNE-NE as seen from La Gomera. If the birds on La Gomera oriented towards a goal area moving on the migratory route the orientation should be NE shifting a little towards ENE in course of the autumn. According to the re-navigation hypothesis the orientation should shift clockwise from NE over E to SW (considering the navigational component diminishing with time), and of course a progress based on simple clock and compass orientation should be unaltered about SSW-SW orientation during all of the autumn. The orientation of the juvenile Robins on the average was significantly SE with an insignificant clockwise shift in course of the autumn, i.e. if anything it is in better (initial) accordance to the re-navigation hypothesis than to the goal area navigation hypothesis. The adult Robins oriented significantly a little W of S, i.e. apparently followed a simple clock and compass course. According to Wiltschko & Wiltschko (1999) this orientation of the adult Robins was unclear and difficult to understand. The right formulation is that the S-SSW orientation of the adult birds was clear and significant but not following the traditional expectation of navigation towards the wintering area NE of La Gomera but instead indicated an outcome of a clock and compass system. Obviously, this is an inconvenient scenario for supporters of the re-navigation hypothesis.

The views of Wallraff and W. & R. Wiltschko

These prominent and often cited scientists have strongly influenced the prevailing paradigm on the orientation/navigation scene. They also authored many surveys on orientation/navigation. For acceptance of a manuscript for publication much depended on the accept and goodwill of theirs. In the

years following Rabøl (1972), they paid some attention to the goal area navigation hypothesis but never accepted it and fairly early the hypothesis disappeared in their publications and as the sun-arc navigation hypothesis of Matthews (e.g. 1968) became a sort of ghost hypothesis almost only mentioned by the inventor. As earlier mentioned, the reasons for the rejection were mainly a) distrust in the connection between stars and navigation, and 2) disbelief in navigation towards what was incorrectly named an ‘unknown position’.

According to Wallraff in Rabøl (1972) birds cannot navigate towards an unknown area “The goal area model implies, however, an element of navigation towards an unknown area. As WALLRAFF (pers. comm.) has emphasized, this would have very important consequences regarding the orientational mechanism. Therefore, one should not accept it before having excluded other possibilities”. It is not clear what these “very important consequences” are, but certainly influenced by the pigeon universe of Wallraff, where the job of the displaced pigeons is to find their way back towards a known position, i.e. the loft. Wallraff (1977), referring to Rabøl (1970, 1972), said that claims about juvenile birds in their first autumn reacting on “absolute values of some navigational coordinates – should not be taken too seriously as long as they are not supported by unequivocal experimental evidence”. Wallraff (1983) characterized ideas about goal area navigation as “speculations”. On the more constructive scene, Wallraff (1972) hypothesized that the mechanism behind compensatory orientation could be comparison between the standard direction and the navigatory direction back towards the point of origin. In this way the bird could deduce whether it should compensate to the right or left. As long as the standard direction is unchanged this would be a potentially useful system, but many migratory routes shift direction, and in such cases the comparison made may sometimes lead to anti-compensatory orientation.

W. & R. Wiltschko also distrusted goal area navigation, as first expressed by the proposal of W. Wiltschko in Rabøl (1972, Fig. 7). W. Wiltschko (1973) repeats the points emphasized upwards: “Eine Navigation zu einem unbekanntem Ort ist jedoch recht schwer vorstellbar”. Wiltschko & Wiltschko (1978) commented on the displacement from Akerøya in the Oslo Fiord, Norway to Blåvand, westernmost Denmark and Christiansø, easternmost Denmark (Rabøl 1972). The birds displaced to Blåvand shifted clockwise from NNE-NE to SE in course of the period 25 August through 22 September, whereas the birds displaced to Christiansø shifted insignificantly from NW to W in the period 25 August through 7 September. This was considered by me to be suggestive of navigation towards a moving goal area. According to W. and R. Wiltschko: “Rabøl’s finding certainly suggest navigation to be involved, but the compensation involved could also be explained by a decreasing tendency to take reference back to a known stopping place [...] navigation to an unknown goal based on site-specific coordinates seems to be excluded by Perdeck’s (1958, 1967) results”. This is clever insight except for the last words.

Wiltschko & Wiltschko (1999) comment on the goal area navigation hypothesis as “die von angeborener Navigation zum unbekanntem Ziel anhand von Sternbildern ausgingen (z.B. Sauer 1957, Rabøl 1972, 1985, 1998) [...] vorgestellten Versuche sprechen jedoch dafür, dass Sterne erlernt werden und nur zur Kompassorientierung dienen” [in English: Sauer (1957) and Rabøl

(1972, 1985, 1998) claim the presence of inborn stellar navigation towards unknown goals. However, the experiments performed indicate that the stars (patterns and movements) are learned and only used for compass orientation]. Clearly, Wiltschko & Wiltschko have not understood nor accepted the significance of Rabøl (1998) concerning ‘displacements’ on the planetary ‘sky’. The grand mean vector based on 16 sample mean directions from the ‘displaced’ positions expressed in reference to stellar N is totally insignificant ($197^\circ - 0.154$), whereas the grand mean vector expressed in reference to a goal area in France ahead in the migratory route is very significant ($-11^\circ - 0.755$, $P < 0.001$). Recall that in these ‘displacements’ the azimuth direction towards stellar N of the planetary sky was unchanged all the time, i.e. if vector orientation in reference to stellar N is carried out the former grand mean vector should be significantly directed towards about SSW-SW. Clearly, it is not. The concentration is all too low.

Contrary to the goal area navigation hypothesis, the scenario of Wiltschko (1973) is not a coherent model for the whole autumnal migratory progress. The scenario of Wolfgang ‘invades’ the progress of a navigational system and (in the words of mine) claims “The next step or next few steps may be explained in another and simpler way not involving navigation towards an unknown goal”. However, in order to be a coherent model, Wiltschko has to start from the very beginning and see how his model evolves in course of the progress. Basically, his model is modified vector orientation and a migratory progress based in vector orientation/clock and compass spread parabolic from the start (Fig. 1 in the main paper).

In conclusion, Wallraff and W. & R. Wiltschko are mostly arguing and seemingly seduced by their own words “unknown” and “unbekannt”. The appropriate words are ‘a position/place the bird never visited before’. As we all know, a human navigator is able to navigate towards a position he never visited before. It just requires a sail or flight plan, and such a plan could in principle be laid down intrinsically in the birds just like the components, direction and distance (i.e. number of hours on migration) of the vector orientation model are implicitly supposed to be.

In the universe of Wallraff, a migrant bird is a sort of super-pigeon navigating by means of olfaction and visual piloting towards both the breeding and wintering site held together in between by vector orientation. This is obvious from Fig. 10.8 in Wallraff (2005). He also abandoned his former view (1974) about a PCD perceived as an inevitable outcome of the uncertainties in the navigational system. At present, he considers this ‘nonsense’ orientation as something else, not fully understood nor explained. Certainly, he is very far from something like goal area navigation in juvenile migrants.

The views of Holland

In an impressive survey, Holland (2014) proposed that compensation for geographical displacements – real or simulated – do not need to be founded in navigation towards a moving goal-area but could be the resultant between compass orientation in the standard direction and navigation towards the last experienced position. Holland does not seem to be aware that this is an old story already

proposed by W. Wiltschko in Rabøl (1972) and several times later by Rabøl (such as 1978, 1980, 1985 and 1994). Furthermore, Holland does not – as Wiltschko & Wiltschko – seem to realize the problems of the alternative hypothesis considered above. The re-navigation hypothesis has to be considered and simulated – and confirmed broadly by observational data – in order to be taken seriously.

In his survey about true migratory navigation, Holland (2014) is very cautious and reluctant to talk about navigation in juvenile birds. He grossly underscores the meta-analysis of Thorup & Rabøl (2007) where the significant tendency of compensation in juvenile birds tested under a starry sky is reduced to “juvenile birds may in some circumstances appear to make corrections for displacements”. He also forgets to refer to the significant case of navigation towards the wintering ground of satellite tracked juvenile Eleonora’s Falcons *Falco eleonora* (Gschweng *et al.* 2008), and there is no reference to Rabøl (1998) where nocturnal passerines compensated significantly for simulated displacements on a planetary starry sky. To his possible defence the authors of the falcon-paper never realized that the juveniles compensated in spite of the impressive picture of juvenile tracks converging towards the traditional wintering ground of the species during last half of the travel. Gschweng *et al.* only focused on the initial spread. Obviously, in this world of vector orienting referees Holland apparently did a lot of self-censuring in order to save his manuscript for publication.

The extended re-navigation system

Based in pure logic the migratory progress in an extended re-navigation system will be retarded and more dispersed compared with a vector orientation system simply because the re-navigational component in most cases will be directed more or less backwards compared with the standard component.

In order to simulate such a system, I considered a single sample (not much!) of six ‘birds’ starting in the same spot proceeding each five steps with 1) a standard direction probability distribution of $180^\circ - 0.84924$ and an airspeed of 30 km/h, 2) a wind vector distribution with $r = 0$ and a wind speed of 20 km/h and 3) a re-navigation vector directed towards the start position of the preceding step and an air speed of 30 km/h. In the first step, no re-navigation vector was included. Due to chance the winds selected were rather easterly; mean wind vector $104^\circ - 0.646$ ($n = 6$, $0.05 < P < 0.10$). However, this will not influence the general tendency.

(a) If no winds and no re-navigation, the mean vector was $184.86^\circ - 0.992$ and the mean progress (five steps) 144 km (s.d. 4 km). (b) If wind was added and no re-navigation, the mean vector was $174.17^\circ - 0.992$, and mean progress after five steps 149 km (s.d. 45 km). (c) If re-navigation was added, the mean vector was $169.50^\circ - 0.981$, and mean progress after five step 85 km (s.d. 36 km). In this case, 2/3 of the time the bird oriented standard, and 1/3 re-navigation. As expected, mean progress of (a) and (b) was about the same, whereas mean progress of (c) was significantly reduced (to about 60%). Furthermore, the directional variance in (c) was increased (from 0.992 to 0.981). Now, a single sample is clearly insufficient. However, I simulated another five cases now based in 10 steps each but unfortunately with a contemporary airspeed of 30 km/h in the standard vector and

20 km/h in the re-navigation-vector, meaning that the total airspeed contribution of the 'birds' was 50 km/h. This is unrealistic high, but the influence on the simulation was about the same as in the single five step sample as the reduction in progress of (c) compared with (b) was between 56 and 74% (mean 66).

The last – guessing – words could be, that goal area navigation not only is an advantage (gives more survivors) under the migratory progress, but also gives more genetic coherence/stability because the goal area moving birds from a certain area return with a higher probability next year than birds only endowed with a vector orientation program.

The view of Åkesson et al. (2021)

Åkesson *et al.* (2021) mention that a sample of juvenile White-crowned Sparrows *Zonotrichia leucophrys* trapped and tested in the breeding area spread more than adults, and also in another study juvenile satellite tracked Black Kites *Milvus migrans* spread more than adults. Such a development is axiomatic for the hypothesis of an initial clock-and-compass changing into a navigation system. However, it is not an unambiguous signal of an initial clock and compass system, because in a goal area navigation system the prediction/expectation is or could be the same.

According to Åkesson *et al.* (2021), all too few studies exist comparing the orientation and scatter in juveniles and adults. Anyway, I found another appropriate example not recognized by Åkesson *et al.* (2021): Pied Flycatchers were trapped as grounded migrants in autumn 2004 on Christiansø in the Baltic Sea (55°N, 15°E) and transported to Endelave (55°N, 10°E), where funnel experiments were carried out on starry nights during the next three weeks (Rabøl 2014). The experiments were designed to study the influence of the magnetic inclination shifted from the local inclination of +70° to 76.5° or 53° simulating geographical displacements towards N and S, respectively. Four juvenile birds were tested on three through six nights each (12 controls, 4 N- and 4 S-experimentals). Nine adult birds were tested on four through eight nights each (28 controls, 8 N- and 9 S-experimentals). As no influence of the magnetic treatment was found, controls and experimentals were combined. The results are presented in Rabøl (2014, Appendix 1.1). The grand mean vector of the juveniles was 189° – 0.893 (N = 4, P < 0.05), and of the adults 179° – 0.788 (N = 9, P < 0.01). The difference was tested with the Wheeler-Watson test. P was far from significance (P >> 0.20). The sample mean vector of the juveniles was 189° – 0.633 (N = 20, P < 0.001), and of the adults 177° – 0.611 (N = 46, P < 0.001). The difference was not significant (Wheeler-Watson, 0.10 < P < 0.20). Anyway, the important points are that both age groups oriented in about the standard direction and that the juveniles were not less concentrated.

Both juveniles and adults were too easterly oriented in reference to the expected standard direction on about SSW-SW. Probably, some compensation for the westerly displacement occurred (suggesting a goal area navigation system).

I also investigated the individual concentrations of juveniles ($N = 4$) and adults ($N = 9$). The means were 0.667 and 0.777 (and mean ranks for the combined sample 5 and 7.9), respectively. Applying a Mann-Whitney U-test, $P > 0.05$ for $U = 10$, the concentrations were not significantly lower in the juveniles. As the 13 individual mean vectors were in the 121° section between 124° and 245° , I applied a Mann-Whitney U-test to the individual directions. The more westerly orientation in juveniles was not significant ($U = 15$, and $P \gg 0.05$).

Thus, the Endelave experiments – contrary to most experiments and observations by Åkesson *et al.* (2021) – were not supporting the hypothesis that juveniles show a higher directional scatter than adult passerine birds.

Final commentary

If the only inherited migratory system of birds is vector orientation, and the birds after the first year change to a navigation system developed under the migratory progress in course of the first year – that's what people believe implicitly or explicitly – then one may wonder about the possible advantage of the transformation from vector orientation to navigation and the way natural selection is involved.

This means that birds – beside an inherited vector orientation system – have the potential for developing a navigation system – and which navigation system? It has to be efficient and therefore the ability to work over larger distances than within the short range of a visual or olfactory system (cf. above, the scenario of Wallraff 2005).

If it is essential that juvenile birds imprint on their start position before initiating their first autumn migration, one may guess that the system involved is based on magnetic and/or celestial cues, and in particular a N/S-gradient based on the altitude of the Polaris Star and/or solar arc angle is to be expected. Involvement of very precise internal clocks as representative for an E/W-gradient are certainly difficult to imagine, whereas the magnetic declination seems more acceptable for most people.

We need a lot of reasonable scenarios and simulations in order to see whether the transformation from inherited vector orientation to a learned navigation system works in context of natural selection – or perhaps rather under which conditions.

The crucial point is that natural selection is on the learned position(s) whereas heredity is on compass directions (and 'distances'). Clearly, the individual could improve its survival changing to learned navigation. However, its offspring acting in a compass system will perhaps not.

If a bird survived its first winter on a certain location, there should on the average be a higher probability of survival wintering here again the next winters – and navigation would improve this scenario better than compass orientation.

However, if the ‘good’ locations are scattered as islands within the whole wintering area of the population, a change from compass orientation to navigation may mean (next to) nothing for individual survival. Probably, an eccentric or central selection pressure on the population level is the precondition for a significant coupling between an inherited compass direction and a learned/imprinted goal position.

It is not rewarding to decide through speculation which system is the most probable. Displacements as the one from Christiansø to Mors and back again to Christiansø, and plots of recovery patterns (parabolic, ellipsoid, or parallel-sided) must be the ground for a judgement.

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Resumé

Forflytningsforsøg: Test af målområdenavigations-hypotesen mod den alternative re-navigations hypotese: Kompas-orientering i normaltrækretningen plus navigation tilbage mod den sidste position, hvor fuglen kom fra

For over 50 år siden fremsatte jeg målområdenavigations-hypotesen som en forklaring på unge nattrækkende småfugles efterårstrækforløb. Hypotesen går ud på, at fuglene til en bestemt dato skal befinde sig i et målområde, der starter i yngleområdet (eller hvorfra den unge fugl nu starter sit træk) og ender i vinterkvarteret. Jeg kaldte det for det vandrende målområde, fordi det i efterårets løb bevæger sig ned gennem trækrueten. Fuglene navigerer altså ikke fra starten af mod det fjerne vinterkvarter; det kommer først mod slutningen ad vejen.

Hypotesen blev modtaget med interesse, men også betydelig skepsis. Problemerne var flere: 1) Jeg blandede stjernnavigation ind i programmeringen af målområdets N/S og Ø/V koordinater. Især det sidste var – og er – kontroversielt, fordi det (i hvert fald tilsyneladende) kræver en meget nøjagtig tidssans af fuglene, hvad der på mange mennesker virkede usandsynligt. 2) Et andet problem var, at fuglene navigerede mod en position/et sted, hvor de ikke tidligere havde været. Det kan ikke lade sig gøre, fastslog kapaciteter som R. og W. Wiltschko og H.G. Wallraff. ‘Fuglene kan ikke navigere mod et ukendt sted’, sagde de med lidt andre ord. Jeg er ganske enig. Det kan mennesker heller ikke. Men et ukendt sted er ikke nødvendigvis synonymt med et sted, hvor man ikke tidligere har været. En pilot kan godt flyve til Los Angeles, selv om han ikke tidligere har været der. Det kræver blot en flyveplan, og trækfugle er udstyret med en medfødt, skitseret flyveplan, der udvikler og udvider sig i forbindelse med, hvad fuglene observerer i naturen omkring

sig både før og efter starten på trækket om efteråret (i modsætning til fx unge Traner *Grus grus*, Sangsvaner *Cygnus cygnus*, Hvide Storke *Ciconia ciconia* og Grågæs *Anser anser* følges unge nattrækkende småfugle ikke med deres forældre eller andre erfarne fugle på efterårstrækket).

Det, der lå til grund for min målområdenavigations-hypotese, var i første omgang ren spekulation. Sådan måtte det være; det ville næsten nødvendigvis give større overlevelse end hos trækfugle, der kun havde et kalender- og kompassystem til rådighed. Det første forsøg, der så bekræftede hypotesen, var en forflytning af Havesangere fra Blåvand til Ottenby på Øland (Rabøl 1969). Trækgæster fanget ved Blåvand var SSØ-orienterede og efter forflytningen til Øland SV-orienterede; de kompenserede – i hvert fald tilsyneladende – for forflytningen. Denne kompensation ind mod trækruten var 'beviset' for det vandrende målområde. Kompensationen var ikke rettet mod det fjerne vinterkvarter i Afrika. Den var heller ikke rettet i normaltrækretningen, der er SSØ i Vestjylland for Havesangere af den norske bestand, der fanges i Blåvand. Fuglene orienterede ikke SSØ, men SV i Ottenby rettet mod målområdets position p.t. Senere kom andre forflytninger til, og de fleste lod sig bedst fortolke ud fra målområdenavigations-hypotesen.

Allerede i Rabøl (1972) – og snart efter i egen publikation – fremkom W. Wiltschko (1973) med en anden forklaring på den kompenserende orientering efter en forflytning. Hans forklaring var, at denne orientering er et kompromis mellem normaltrækretningen fastlagt som kompasorientering og en navigation rettet tilbage mod det sted, hvor fuglen var flyttet fra. Han kunne også forklare en jævnt mod syd skiftende orientering efter forflytning fra Østfold (Akerøya) i Sydnorge til Blåvand og Christiansø, hvor fuglene blev holdt tilbage i flere uger og testet i tragtene flere gange i løbet perioden. I følge Wolfgang var det ikke navigation mod et vandrende målområde, men tendensen til orientering tilbage mod Norge var aftagende med tiden, og det betød, at normaltrækretningen derfor slog mere og mere igennem med tiden. Denne forklaring er mulig og ikke sådan at tilbagevise, men den er klart nok ikke gennemtænkt som et rimeligt system for hele efterårstrækket; den var tilpasset og rimelig som en enkelt eller få trins- forklaring. Tænker man i baner af hele efterårstrækket, vil de mange tilbagenavigationer mod tidligere besøgte steder næsten nødvendigvis give trækforløbet en betydelig extra spredning, forsinkelse og forkortelse. Det må komme an på en simulering, men en gennemgribende sådan er ikke foretaget endnu, selv om den i princippet er nem at lave. Nogle få, simple simuleringer passer dog med forventningerne.

Wallraff (1972) kom også med en anden forklaring end målområdenavigation for den kompenserende orientering efter en forflytning, som ikke virker urimelig i forbindelse med et retlinet trækruteforløb. Wallraff foreslog, at fuglen hele tiden har en navigatorisk 'snor' med udgangspunkt i, hvor den startede sit træk. Den kan så sammenligne retningen herimod med trækretningen baseret på kompasorientering. Er normaltrækretningen således SV og retningen tilbage mod udgangspositionen N, skal den kompensere til højre – fx mod NV – i forhold til normaltrækretningen. Wallraffs hypotese er ikke testet og ser ud til at munde ud i noget rod, hvis trækruten skifter retning undervejs, fx fra SV over SSØ til Ø, som den gør hos hollandske Brogede Fluesnappere (Ouwehand *et al.* 2016).

Det var en masse snak. Jeg skal nu berette om det forflytningsforsøg, som jeg foretog for at belyse hvilken af de to: 1) målområdenavigations-hypotesen eller 2) W. & R. Wiltschkos alternative, re-navigations hypotese, der beskriver bedst for et enkelt træktrin af efterårstræktruten.

Tidligere har jeg flyttet nattrækkende småfugle masser af gange (for en oversigt se Thorup & Rabøl 2007). Jeg har brugt tragtmetoden, hvor en gruppe fugle (normalt) er blevet testet på fangststedet (fx Christiansø) og så igen testet efter forflytningen til et andet sted (fx Blåvand). Der har været en signifikant gennemgående tendens til kompensation for forflytningen for unge nattrækkende småfugle, testet om natten, om efteråret og med stjerner på himlen. Så der er egentlig ikke længere så meget diskussion, om fuglene kompenserer. Slaget står om, hvordan de gør det.

De hidtidige forsøg kan ikke bruges til at skelne mellem min og Wolfgangs hypotese, og først i 2018 fik jeg ideen til et forsøg, der i praksis har potentialet til at kunne skelne. Forsøget går i al sin enkelhed ud på at flytte fuglen tilbage til fangststedet (i eksemplet nævnt ovenfor fra Blåvand til Christiansø) og teste dem her een gang til og så sammenligne orienteringen i det første og andet forsøg (på Christiansø).

Jeg havde først udtænkt et ret så ambitiøst forsøg med fangst på Christiansø, så forflytning til Mors, herfra forflytning til Viderø, Færøerne, og endelig flytning tilbage til Mors – og tragtforsøg alle fire steder. Det skulle i det afsluttende forsøg på Mors have resulteret i en over 90° forskel på orienteringen i de to systemer. Det var så smukt, men det kunne den ansvarlige færøske veterinær ikke se af frygt for fugle-influenza i de medbragte trækfugle, så det blev ikke til noget.

Jeg udtænkte så et simplere forsøg indenfor det egentlige Danmarks grænser: En 450 km forflytning fra Christiansø mod VNV til det vestlige Mors (Nes) i NV-Jylland. Færø-forsøget skulle have brugt SV-trækkere som Broget Fluesnapper og/eller Rødstjert. For at få en så stor som mulig vinkelforskel frem i orienteringen i følge de to systemer måtte jeg nu vælge en S eller SSØ trækkende art, og Grå Fluesnapper var det oplagte valg. Da jeg ikke kunne regne med at fange nok (helst 20) Grå Fluesnapper på de få dage, som jeg havde afsat, var jeg indstillet på at supplere med Munk, hvor der formentlig er kraftig dominans af SSØ-trækkere omkring 1. september. Senere er der måske mere islet af SV-trækkende Munke. Arten har jo en såkaldt trækdeler omkring længdegraden 12°Ø. Den 2. september 2018 endte jeg med at have 10 Grå Fluesnapper og 10 Munke – alle ungfugle – i burene, og da jeg helst ville bruge Grå Fluesnapper og ikke mere end 16 fugle ad gangen i testgruppen, blev den første test under en klar stjernehimmel udført på Christiansø den 4. september med 10 Grå Fluesnapper og seks Munke. Som det fremgår af Fig. 1 til venstre, var orienteringen meget klar i retningen lidt Ø for S. Det var flot; det lignede så afgjort normal orientering.

Den 7. september forlod vi Christiansø og kørte til Mors, hvor vi ankom kl. 22 om natten. Det var mest overskyet og blæste noget med lidt regn ind i mellem. Men der var varslet chance for stjerner, og fra kl. 2 til 3 om natten den 8. september var fuglene ude i deres bure frit eksponeret under en flot stjernehimmel. Det tager mange timer at sætte trage op til forsøg, så det kunne vi ikke nå. De næste tre nætter ventede vi på stjerner, der aldrig kom, bortset fra i en 20 minutters periode den

sidste nat, hvor fuglene i deres bure blev sat ud til beskuelse af stjernehimlen. Det blæste og regnede mestendels fra en overskyet nattehimmel. Fuglene stod i deres bure i et drivhus og kunne følge Solens gang nogle timer to af dagene, og de stod hele tiden i Jordens uforstyrrede magnetfelt, der var til fri afbenyttelse for de, der kan navigere efter det. Fuglene var ude i tragtene en af de regnfulde nætter, men efter over tre timer under regntæt låg, måtte jeg pille dem ud igen og putte dem tilbage i burene. Mod forventning havde ni ud af 16 fugle vist trækaktivitet og nogle af dem endog stor aktivitet i mørket under net og træplade. Seks af fuglene var orienterede men i spredte retninger. Gennemsnitsvektoren var $253^\circ - 0.334$, hvad der bedst fortolkes som manglende orientering af gruppen (0.334 er en så lav koncentration, at man ikke kan tillægge middeltretningen 253° nogen som helst betydning).

Den 11. september kørte vi tilbage til København, og næste dag var vi igen på Christiansø med fuglene. 13. september blev 15 fugle testet under en flot stjernehimmel, og de var signifikant SSØ-orienterede (Fig.1 til højre), altså lidt østligere (og til den 'gale' side set ud fra den alternative hypotese af Wiltschko) end i det første Christiansø-forsøg, men forskellen var ikke signifikant.

Konklusionen af forsøget er klar: Resultaterne er i god overensstemmelse med forventningerne ud fra målområdenavigations-hypotesen (hvor fuglene skal være ens orienterede i SSØ-S i begge Christiansø-forsøg) – og i meget ringe i overensstemmelse med den anden hypotese (hvor vi forventer SV-V-orientering i det andet Christiansø-forsøg), så Wolfgang Wiltschko lader ikke til at have ret. Men der skal selvfølgelig mange flere forsøg til, før der kan drages en mere sikker konklusion.

Den 13. september 2018 blev mit sidste tragtforsøg nogensinde; forsøg der startede i foråret 1967 på Hesselø, så jeg nåede at lave forflytningsforsøg i 52 år. Hvor mange og med hvor mange fugle har jeg ikke styr på, men jeg flyttede da til og fra Sverige i flere omgange, fra Norge to gange, til Færøerne, til Tjekkiet, til La Gomera (Kanarie-øerne), til Kenya og til USA, foruden mange gange på kryds og tværs i Danmark især mellem Christiansø og Blåvand.

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