Displacement experiments in night migrating passerines

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(*Med et dansk resumé: Forflytningsforsøg med nattrækkende småfugle*)

Abstract Compensatory orientation following real or simulated geographic displacements is to be expected if migratory progress in migrant passerines is programmed as navigation in one way or another. Here I report on an array of old, real displacements never published before and some new ones partly published in other connections. The displacement experiments strengthen the significance of compensatory orientation found by Thorup & Rabøl (2007). Next, mostly on an inspirational level for future investigations, follows a collection of three rather preliminary funnel experiments: 1) magnetic declination is manipulated to simulate geographic E/W displacements, 2) a prism mounted on top of the funnel tilts the view of the starry sky 4º towards S, and 3) a displacement is followed by a return-displacement to test the re-navigation hypothesis of W. Wiltschko (first proposed by him in Rabøl 1972 and later in Wiltschko 1973) that compensatory orientation is compass orientation in the standard direction plus navigation back towards the position from where the birds were displaced. In all three cases I found indications of goal area navigation. Furthermore, 4) the treatment of Thorup *et al.* (2007a) concerning reaction to the displacement of juvenile White-crowned Sparrows *Zonotrichia albicollis* in the US was scrutinized: the claim of vector orientation in the juveniles was not substantiated. The juvenile White-crowned Sparrows compensated partly for the displacement and thus navigated in some way that calls for more nuanced understanding of their migratory programme. Finally, various difficult issues and scenarios concerning goal area navigation are presented and discussed: calculation of actual goal area position; the concept of pseudo-navigation; the possible influence of clock-shifts; and the suitability of various substitutes for the natural stellar sky, including the simple '16-star-sky' of the Frankfurt-group.

Introduction

Over the course of the year, birds from a migrant population move around between the breeding area and one or several wintering areas and stopover sites.

In some species, the juveniles learn about and imprint on the migratory route through following the adults. However, in many passerines the juveniles migrate later in the autumn independently of their parents or other adults from their population. Therefore, the juveniles have to rely on an intrinsic programme which in interplay with the external world develops into a migratory system. The question is which system it is, and here people following the iconic contribution of Perdeck (1958) focus on two possibilities: one-direction orientation (compass orientation) which together with programmed information about time and distance constitutes 1) vector orientation or 2) coordinate (gradient) navigation. This second possibility may be either 2a) directed towards a (single) wintering area, or 2b) directed towards a goal-area which during the course of the season moves through the migratory route, sometimes resting for a while in the breeding area, one or several stopover sites, or one or several wintering areas (e.g. Rabøl 1985, Holland 2014).

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The two systems

Vector orientation

If the route is straight between the breeding area and a single wintering area, a vector orientation programme would seem sufficient. An example could be: a population of European Robins *Erithacus rubecula* from Sweden, Finland and the Baltic Countries on average breeding on the Åland Islands, SW-Finland, 60ºN, 20ºE, and on average spending the winter a little west of Barcelona in Spain, 42ºN, 0ºE. This is the mean recovery position of adult European Robins banded as migrants on Christiansø in the Baltic Sea (Rabøl 1981).

Following the loxodrome (constant compass-direction between two positions in reference to geographic N), the direction and distance between the two positions is 214.5º and 2427 km. If there is no directional variation in migratory direction, birds programmed to move towards 214.5º and covering 2427 km will (on average) end up in the centre of the wintering area. Such a journey could be programmed in reference to geographic N (the stellar sky or sunset and sunrise integrated) or magnetic N. The 2427 (≈ 2430) km corresponds to 81 hours in the air on migration if the constant airspeed of the birds is 30 km/hour. The 81 hours could translate into nine migratory steps on each nine hours (270 km) in duration. Considered superficially, a vector orientation programme seems to be sufficient and reasonable. However, there will always be directional and temporal variation both within and between individuals (Thorup *et al.* 2007b), and full wind-drift compensation seems utopia. Starting on the Åland Islands and simulating a vector-orientating population, progress will spread parabolic (Fig. 1). When the programme stops (and the birds are supposed to be at about 42ºN, 0ºE), say 70% of the birds will be around this position within an ellipsoid (Rabøl submitted) measuring perhaps 1000 and 800 km on the long and short axes, respectively. So, what seemed simple – requiring only a vector orientation system – is clearly not something very precise or accurate to rely on in the real world.

Goal-area navigation

Many bird-populations have longer and more complicated migratory routes than European Robins. An example is the Danish Gribskov population of Red-backed Shrikes *Lanius collurio* (Pedersen *et al.* 2020). The breeding position is 56ºN, 12ºE. In a geolocator-study (Pedersen *et al.* 2020), adult birds with geolocators from this population were followed in their annual cycle. First, the birds from Gribskov migrate to the Balkans (Belgrade on 44ºN, 22ºE is at about the centre) and stay in this stop-over site for some weeks, then move to a stop-over area in the Sahel/Sudan centred around 9ºN/ 27ºE. This may be considered the first wintering area. From here the birds move further south and winter for a longer time in Namibia/Botswana centred around 22ºS, 21ºE. In late winter (local summer), the birds migrate to East Africa towards their third wintering area centred around 2ºN, 40ºE. After some weeks the birds migrate a little E of N until about Baghdad (33ºN, 44ºE). On their way the birds seek out places to rest, but there are no long-time stop-overs in any particular area. The routes bend NW about Baghdad and the birds pass Belgrade again before proceeding to the breeding area in Gribskov. All four stop-over/wintering areas are rather large (between 560 000 and 1 400 000 km²) when considered as 70% ellipsoids (Rabøl submitted). It seems almost impossible that such a yearly cycle of migration could be achieved by relying only on a vector orientation programme. Furthermore, the area of the Sahel/Sudan wintering ground is much larger than the area of the following wintering ground: in a vector orientation system the area of the ellipsoids is bound to increase with distance.

In the above case one has to consider the possibility of a goal-area navigation programme. Such a consideration should be based on the outcome of reasonable simulations and – of course – geographical displacements to show whether the displaced birds compensate towards the (actual goal-area) on the migratory route.

The question is which system – vector orientation or coordinate navigation – is found in medium- and long-distance migrant passerine birds? The key to answering this question is geographic displacements, real or simulated. If the birds compensate for the displacement, this is an indication of a navigational system in action.

Summing up

The question is how the yearly cycle of movements and stop-overs in the migratory route is programmed. Real and in particular simulated geographical displacements are the key to revealing whether the migratory route is inherently programmed as vector orientation or as goal-area navigation, e.g. Rabøl (1985, 1994), Thorup & Rabøl (2007).

If birds compensate for displacements this would be considered as an indication of goal-area navigation. The problem is that what looks like compensatory navigation towards a moving goal-area could be rooted in several other systems, some of which are not even navigational. Alternatively, lack of compensatory orientation following a displacement is not a proof against the moving goal-area navigation hypothesis (because the conditions for carrying out navigation may be absent or suppressed). Therefore, one must carefully scrutinize each single case and make a balanced decision about the most plausible explanations.

In most autumns, when displacements were conducted with juvenile passerine migrants under a stellar sky, the birds tested in funnels compensated and thus behaved according to the goal area navigation hypothesis (Thorup & Rabøl 2007). However, what had seemed simple in the beginning changed to become more complicated or, expressed more accurately, become vulnerable to distortion by people with competing points of view (see Appendix 4). Regrettably, I contributed to the confusion by being open to all possibilities (Rabøl 1994).

Displacement experiments

The following is a rather heterogeneous collection of displacement experiments presented in the six appendices available online. However, what they all have in common is that compensations were observed which indicates that some kind of gradient/coordinate navigation was present.

The magnetic declination as an E/W-parameter

E/W-navigation on a spherical Earth is considered a difficult affair because, at a first consideration, time is bound to be involved and very accurate and precise biological clocks are not easily imagined. Biological clocks that only loose or gain a few seconds per day seem a fantasy but are necessary if they are to be useful for proper navigation over several months. Anyway, compensatory orientation following clockwise and counter-clockwise rotations on a planetary 'sky' suggested stellar-based E/W-navigation (Thorup & Rabøl 2007). Another – and of course not alternative – system could be rooted in the magnetic declination. Out of five samples, Kishkinev *et al.* (2013) and Chernetsov *et al*. (2017, 2020) found compensatory orientation in a single sample only that indicated navigation based in the magnetic declination. Kishkinev *et al.* (2013) interpreted the lack of compensatory orientation of displaced Reed Warbler in spring following sectioning of the ophthalmic branch of the trigeminal nerve as an indication of home area navigation mediated through this branch. In Appendix 1 funnel experiments of mine are presented with shifted declinations mimicking E/W displacements; compensatory orientation was observed in the single spring case but not in two autumn cases, which suggests a navigational response. Clearly, we are on the fringe of 'something' and further experiments are much needed, particularly during spring when the bird is close to the origin of the start-position of the previous year.

The stellar sky as seen through a prism

N/S-navigation seems to be easy to perform: just look at the altitude of the Polaris star and you know the latitude. Rabøl (1998) and Thorup & Rabøl (2007) found evidence of N/S-navigation in passerine birds tested under the natural starry sky or the 'stellar sky' of a planetarium. The stellar sky may be tilted along the N/S-axis to simulate a geographic displacement towards N or S. We did so by means of a prism mounted on top of a funnel. Appendix 2 presents autumn experiments which mostly simulated a displacement of 4º towards S. Some evidence of a stellar-based N/S navigation was found. However, the results were mostly better described by simple reverse compass-orientation while spurious directional reactions to the bilateral prism perhaps also sometimes played a role.

Displacement across the US

Thorup *et al.* (2007a) released White-crowned Sparrows *Zonotrichia leucophrys* that had been trapped on autumn migration in Washington State, transported eastward to New Jersey and equipped with radio-transmitters before release (Appendix 3). The adult sparrows oriented approximately W and very clearly compensated for displacement, thus indicating a navigational system. The mean juvenile track-direction was S-SSW and Thorup *et al.* (2007a) concluded there was no compensation for the displacement and therefore indication of a basic vector orientation system. However, if the tracks were corrected for drift by the wind, the mean heading turned W of SSW corresponding to $P = 0.05$ or < 0.01, respectively, in reference to a standard direction of S or SSE, respectively. Thus, the juveniles also compensated for the displacement, which indicated some kind of gradient navigation (and if the compass reference was magnetic N, the compensation was even stronger). Clearly, the conclusion of Thorup *et al.* (2007a) that the juveniles showed vector orientation was premature.

Testing Wolfgang Wiltschko's re-navigation hypothesis

Rabøl (e.g. 1969, 1994) claimed goal area navigation in juvenile passerine migrants. However, Wiltschko (first described in Rabøl 1972 and later in Wiltschko 1973) explained the compensatory orientation following a displacement as a compass orientation in the standard direction plus navigation back towards a former experienced position. In Appendix 4 a retour-displacement experiment is proposed and performed which in principle should be able to distinguish between the two systems. The single experiment published to date indicated the presence and action of a goal area navigation system.

Further displacements
Appendix 5 describes further displacements not included in Thorup & Rabøl (2007). These add to the significance of compensatory orientation following a displacement. In the autumn displacements (juvenile birds) conducted under the natural starry sky, compensation was carried out significantly in six cases, whereas significant counter-compensation appeared in two cases. Adding 6/2 to the 12/2 distribution in Tab. 2 in Thorup & Rabøl (2007), results in a 18/4 distribution. Applying a Chi-square test and testing against 11/11 results in a Chi-square = 8.91 and $P < 0.01$, i.e. the tendency to compensate is clearly significant.

Additions to Thorup & Rabøl (2007)

Appendix 6 is devoted to explaining and expanding difficult parts of Thorup & Rabøl (2007). In this contribution we found compensation for displacements of juvenile birds at least in autumn tested under a starry sky, i.e. a goal area navigation system was inferred. Appendix 6 considers four 'disturbing' or elaborating points:

1) How to indicate presence of compensatory orientation, and by means of (near) symmetrical test-sites find the position of the actual goal area? The procedure is explained using an example.
2) Coping with the process of pseudo-navigation. Compass orientation by reference to a star 'moving' on the southern sky in autumn under certain conditions may look like the outcome of a navigational process.
3) Evaluating the relevance of testing birds under a stationary planetary 'stellar sky', including the '16-star-sky' introduced by the Frankfurt-group (Wiltschko & Wiltschko 1976). There may be 'good' reasons for making the 'sky' stationary in the test-phase, but the real starry sky is not stationary, and we are on very uncertain ground indeed, when a simple '16-star-sky' – in particular if stationary – is substituted for the real starry sky.
4) Discussing whether light/dark phase-shifts in a navigational process can substitute for geographic displacements, real for birds tested under the starry sky or simulated for birds under a planetary 'stellar sky'. On first consideration this seems reasonable (and Emlen 1975 apparently was positive about this scenario). However, E/W-navigation based on the starry sky should be rooted in a rigid clock not vulnerable to light/dark phase-shifts, for otherwise it would be of no use. Furthermore, there is no experimental support for its existence. Emlen (1975) mentioned clock-shifted White-throated Sparrows *Zonotrichia albicollis* released and radio-tracked under a starry sky. But Emlen provided no data, only the remark that there was no effect. Rabøl (1970a, b, Appendix 6) clock-shifted Common Redstarts *Phoenicurus phoenicurus* and Garden Warblers *Sylvia borin* eight hours clockwise (autumn) and counter-clockwise (spring) without any effect (funnel tests under the natural starry sky). Related to this, Matthews (1968) found no influence of L/D-shifts on NW 'nonsense' orientation in Mallards *Anas plathyrhyncos* released on starry nights, whereas orientation shifted in the predicted way on sunny days, which showed the influence of a time-compensated sun-compass.

Vector-orientation in juvenile birds changing to navigation in adults

The question is whether 1) there is a shift from an inherited vector-orientation system (first autumn in the life of a bird) to a learned navigation system (the following autumns), or 2) there is no such shift but rather there is goal-area navigation right from the very start. 1) originates from the interpretation of the Perdeck (1958) displacement, whereas 2) traces back to Rabøl (1969). 1) is supported by other experiments such as Drost (1938) and (apparently) Thorup *et al.* (2007a; see also Appendix 3). 2) is supported by Rabøl (1998) and Thorup & Rabøl (2007).

If 1) is the case, the transition from vector orientation to navigation needs to be explained. Such an explanation seems straightforward: the bird imprints navigationally on the position of the wintering area (i.e. the area where the autumn migration stopped), and perhaps also on one or more (all) positions visited on the first autumn track. In spring, at least in the final steps, the bird navigates towards the position it left last year. During the following season(s) the bird navigates towards the wintering area and perhaps also former positions along the first autumn track. The transition from vector orientation to navigation is supposed to increase survival probability compared with a repetitional vector orientation progress. At first, this seems elementary and easily understandable evolutionary biology. However, perhaps it is not that easy. 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 the context of natural selection – or perhaps rather under which con-

Young birds migrating alone need to be able to perform goal area navigation. Otherwise far too many would succumb on their first migration. The question is how? Photo: Erik Biering.
Ungfugle, der trækker alene, skal kunne udføre målområdenavigation. Ellers ville alt for mange bukke under på deres første træk. Spørgsmålet er hvordan?

ditions. 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 2), one has to explain the inherited system of goal-area navigation. Rabøl (submitted) provides a possible explanation for gradual shifts in the programming of the moving goal area as gradual shifts in the Polaris altitude (latitude) and stellar time/rotational phase (longitude). For most people, this seems too complicated. However, if vector orientation occurs, then the basic elements, direction and (a representative of) distance must also be inherited and have to be explained.

Both 1) and 2) presume – implicitly or explicitly – that juvenile birds imprint in navigational terms on the fledging site or another/nearby site from where the birds initiated their first autumn migration, e.g. Wynn *et al.* (2022). This system could in principle be locally based on visual recognition of the landscape or on olfactory cues, regionally based on olfaction or magnetism, or globally based on magnetism or celestial cues. If 2) one should expect the latter. If 1) the first seems sufficient at least in short distance migrants.

Concerning the supposed transition from vector orientation to navigation in 1): progress in the first autumn is a chain of compass-steps only – perhaps with inclusions of navigation back towards the last start-position (Wallraff 1972) or one/some/all former visited positions on the route (Wiltschko 1973). These components of navigation towards experienced positions are used by Wallraff and W. Wiltschko as explanations for compensatory orientation following displacements. This kind of navigation leads to a parabolic spread of the population in consideration. Another complication with this extended re-navigation system (as designated in Appendix 4) is that it seems more – and unnecessarily – complicated compared with goal-area navigation: The capacity for developing navigation should be inborn as is the vector orientation system. In a goal-area navigation system, the system required is inborn and progress is 'locked' on the final goal, with mistakes during migration being fed back negatively.

Concerning 2), goal-area navigation: a chain of navigational steps from the very start. Such a system may be changed and improved through natural selection.

Nevertheless, displacement experiments provide the tool to find out which of the systems (or a mixture of them) best describe the results. The problem is to design appropriate experiments which make clear interpretation possible. Here the new variant of a displacement experiment as presented in Appendix 4 seems promising.

If the juvenile birds are endowed with a goal area-navigation system, the population proceeds within a belt or perhaps an ellipsoid (if navigation is towards the wintering area), and in many cases it should be possible to distinguish between these and the parabolic spread originating in a vector orientation system. Here the spread of Spotted Flycatchers *Muscicapa striata* (Thorup & Rabøl 2001) and Eleonora's Falcons *Falco eleonorae* (Gschweng *et al.* 2007) are clearly not parabolic but look like ellipsoids. Thorup & Rabøl (2001) present data from Marsh Warblers *Acrocephalus palustris* migrating within very narrow belts in E Africa as incompatible with a clock-and-compass programme. Even so, it is always possible to find affirmative 'proof' for something through examples where general and significant tendencies should be sought instead.

Accordingly, the present understanding of the presumed shift from vector orientation to navigation in juvenile passerine migrants seems insufficient. In the most recent contributions, Aakesson *et al.* (2021) and Flack *et al.* (2022), the authors are apparently unaware of the inherent problems of the qualitative shift from vector orientation to navigation short circuiting the process of natural selection.

Simulation of vector-orientation and goal area navigation

The following was calculated and illustrated by Henning Noer.

Vector-orientation

Consider a population of five birds starting in (0, 0) and moving 100 km in each of 25 steps towards W and 200 km towards S. The length of each step is 223.6068 km and if there are no uncertainties all birds end up in (-2500, -5000). Put another way: the total vector proceeded is 206.565° – 5590.17 km. For simplicity we consider the scene as a plane and not as a sphere like the Earth.

Now we introduce uncertainty by considering a circular distribution with a mean direction of 206.565° and a concentration, r = 0.84924. Consider a population of five birds each setting out on 25 migratory steps of length 223.6068 km. For each step we generate a random heading vector from the distribution 206.565° – 0.84924. The five routes generated are shown in Fig. 1. As we are considering a system based on vector-orientation, there is no final goal (-2500, -5000) but this position is marked with a cross in the lower left of Fig 1. None of the birds moved as far as to this 'goal'. What should be noted is the increasing spread between the birds with the number of steps. When considering the population, this spread could be designated as 'parabolic'. If random wind-vectors had been added for every step and no or partial compensations were carried out, the spread would have been much higher but still 'parabolic' and the mean progress in the direction of 206.565° would have been (approximately) the same.

Goal area navigation

Now we consider a population of five birds performing goal area navigation from (0, 0); the first step towards (-100, -200), the next towards (-200, -400), and the last step (no. 25) towards (-2500, -5000). This system also contains uncertainties on both the abscissa (-200 (0.0625), -100 (0.25), 0 (0.375), +100 (0.25), +200 (0.0625) and the ordinate (-100 (0.25), 0 (0.50), +100 (0.25). The probability of making a longitude error on 200 km W is 0.0625, and a latitude error on 100 km S is 0.25. Furthermore, to each step we have added a wind-vector (no compensation = full drift) with an average speed of about 20 km/h (the airspeed of the birds is supposed to be 30 km/h). More details are found in Rabøl (submitted). The progress of five birds following these conditions is shown in Fig. 2. The final goal (-2500, -5000) is shown in the lower left (red spot). The five birds come close to but none actually reach the final goal. Compared with the pattern of a vector orientation system in Fig. 1, the birds spread more between the single steps, but the overall picture is one of much less spread along the mean route – and there is no 'parabolic' spread but only spread within a narrow belt.

In conclusion both models can be modified so that the average bird reaches the final 'goal' or goal. But the shape of the progress of the population is typical: vector-orientation leads to 'parabolic' spread, whereas goal area navigation leads to spread within a 'belt' which after a few steps normally becomes narrower than in the case of spread due to vector-orientation. If the birds navigate all the time towards the final goal, the spread (not shown) will be 'ellipsoid', i.e. at approximately half way, it looks 'parabolic' but then gradually changes and becomes more and more concentrated towards the final goal.

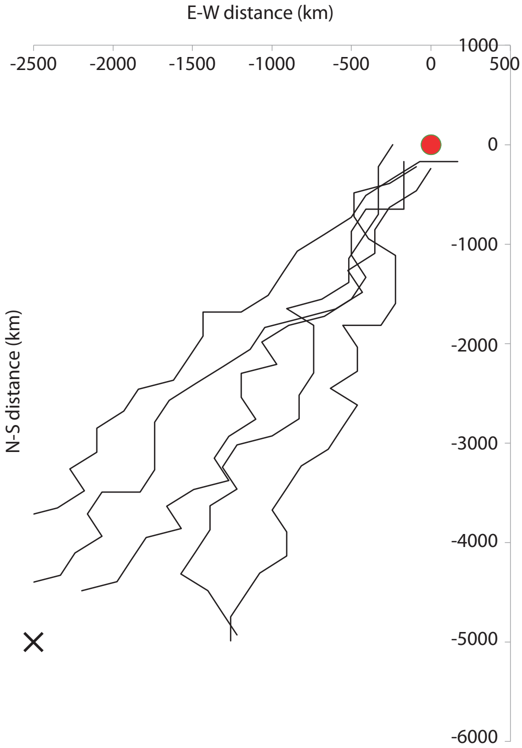

Fig. 1. Vector-orientation. Five 'birds' start in (0, 0) and in each of 25 steps move 100 km towards W and 200 km towards S. The length of each step is 223.6068 km and the mean direction 206.565º. If there are no uncertainties all birds end up in (–2500, –5000). Now we introduce uncertainty through considering a circular distribution with a mean direction of 206.565º and a concentration, r = 0.84924, and a population of five 'birds' each performing 25 migratory steps of length of 223.6068 km. For each step we generate a random heading vector from the distribution 206.565º – 0.84924. The five routes generated are shown. As we are considering a system based on vector-orientation there is no final goal (–2500, –5000) but this position is marked with a cross in the lower left.

Vektor-orientering. 'Trækforløbene af fem virtuelle 'fugle'. For hver 'fugl' startende i (0.0) er der genereret 25 træktrin, hver med en længde på 223,6068 km og en retning, der varierer tilfældigt følgende en gennemsnitsvektor på 206,565⁰ – 0,84924. Trækforløbet for bestanden udvikler sig som en 'parabel'.

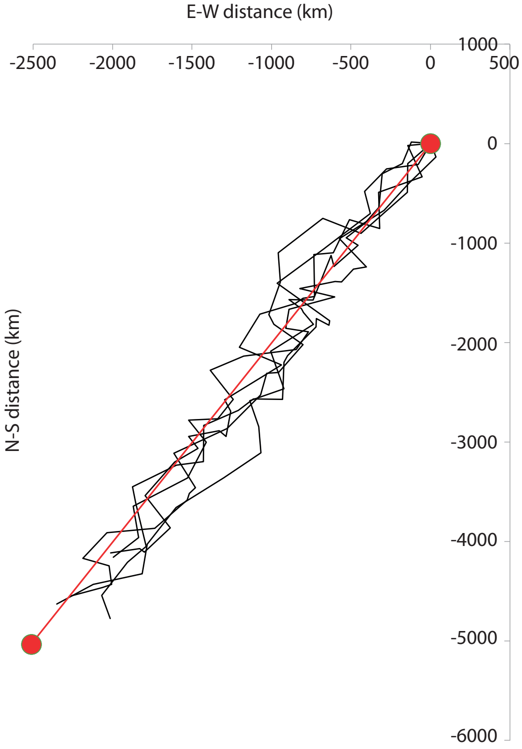

Fig. 2. Goal-area navigation. A population of five 'birds' perform goal area navigation from (0, 0); first step towards (-100 km, -200 km), next towards (-200, -400), and the last step (no. 25) towards (-2500, -5000). This system contains uncertainties on both the abscissa (-200 km (0.0625), -100 km (0.25), 0 km (0.375), +100 km (0.25), +200 km (0.0625)) and the ordinate (-100 km (0.25), 0 km (0.50), +100 km (0.25)). To each step is added a wind-vector (no compensation = full drift) with an average speed of about 20 km/h (the airspeed of the birds is supposed to be 30 km/h). The progress of five 'birds' following these conditions is shown. The final goal (-2500, -5000) is shown in the lower left (red spot). The five birds come close to, but none reach the final goal. Compared with the pattern of a vector orientation system in Fig. 1, the 'birds' – even including wind drift – spread out less, i.e. within a more narrow band.

Målområdenavigation. En bestand på fem fugle starter i (0, 0) og det første træktrin er rettet mod (-100 km, -200 km), det næste mod (-200 km, -400 km), osv., det sidste mod -2500 km, -5000 km). Der er indlagt usikkerheder på både bestemmelsen af abscissen og ordinaten. Der er også indlagt vindafdrift og manglende kompensation for vindafdrift. På trods af vindafdriften spreder 'fuglene' hen ad vejen mindre i navigationssystemet, end de gør i et vektororienteringssystem.

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Resumé

Forflytningsforsøg med nattrækkende småfugle

Fuglenes reaktion på geografiske forflytninger – reelle eller simulerede – er nøglen til en forståelse af trækfuglenes orienterings-system. Jeg antager, at der er et medfødt program, der efter sit frembrud er i stadigt samspil med omgivelserne. Ungfuglene oplærer sig løbende. Nogle gange er de voksne fugle ledsagende og vejledende, men for de fleste arter og specielt de nattrækkende småfugle lærer ungfuglene sig selv op.

I mange år – siden generaliseringen af hollænderen Perdeck's (1958) ikoniske Stære-forflytnings-forsøg – har de allerfleste træk- og orienteringsforskere troet på et medfødt trækprogram kaldet vektororientering (eller kalender & kompas) basalt set bestående af en kompasretning og en afstand/træklængde.

I vektororienteringssystemet kan retningen evt. skifte undervejs, og vektorlængden/afstanden er at opfatte som en kombination af en flyvehastighed og et vist antal flyvetimer. 30 km i timen og 100 flyvetimer i løbet af efteråret giver således en træklængde på 3000 km. Så stopper fuglen sit træk og befinder sig forhåbentlig i et passende vinterkvarter. Problemerne med at effektuere et sådant system i denne verden, hvor bjerge, ørkner, have og vinde forskyder, forlænger eller forkorter trækket, der i forvejen er præget af ukontrolleret fastlæggelses- og fastholdelses-variation, er åbenbare – også for tilhængerne af hypotesen, så man taler nødigt om det, men forestiller sig situationen reddet af et mirakel: Vektor-orienteringen forvandler sig undervejs i fuglens liv til navigation. Hvordan det sker, ved man ikke rigtigt bortset fra den sædvanlige generelle/upræcise forklaring med 'natural selection', hvor de uegnede sies fra og dør, og de bedst egnede overlever og arver riget. Problemet er bare – som omtalt af Thorup & Rabøl (2001) – at der i et sådant system efter alt at dømme vil være en alt for stor dødelighed til at fuglene i bestanden ender op i de snævre trækruter og begrænsede vinterkvarterer som mange artsbestande rent faktisk færdes i. 90 % af de unge Kærsangere skal således dø undervejs på efterårstrækket, men det gør de ikke, hvad der er en indikation på, at navigationen er med fra starten af og sikkert i en ufuldstændig form, der bliver forbedret hen ad vejen.

Skiftet fra retning og afstand til position i et navigationssystem er en kvalitativ udbygning. Man forestiller sig, at trækfuglen undervejs indprenter sig positionen af fx Nordstjernens højde over horisonten (en N/S-koordinat), og misvisningen (en Ø/V koordinat) for gunstige rastesteder undervejs, og til sidst for vinterkvarteret. Næste år gentager fuglen så sit trækforløb, nu gennem navigation mod de indprentede positioner undervejs, men der sker ingen forbedring/ændring af det ruteforløb, der startede som vektororientering. Nogle trækforløb (med tilhørende vinterkvarter) er imidlertid bedre end andre i den forstand, at fuglens overlevelseschance er/har været større. Vektororienterende fugle spreder sig som bestand betragtet parabolsk derudad omkring normaltrækretningen (Fig. 1), og man må forestille sig en selektion mod nogle trækruteforløb og vinterkvarterer, men hvordan de ligger i forhold til ungfuglebestandens spredningsforløb ved man ikke, men de fleste forestiller sig nok (på grund af selektion mod fløjene), at de voksne fugles parabolske trækruteforløb er smallere end ungfuglenes. Fuglen kan så i de følgende år navigere sig frem mellem sine tillærte positioner fastlagt navigatorisk, men det trækprogram, den overleverer til sit afkom, vil stadig være vektororientering. Sådan et system kan måske fungere for en skandinavisk Rødhals, der trækker et par tusind kilometer stort set retlinet mod SW. Men hvad med de Brogede Fluesnappere og Rødryggede Tornskader (Rabøl submitted, Appendiks 2), der trækker mange tusind kilometer ad ruter, der ofte skifter retning undervejs. Det svarer nærmest til en sejlbåd, der kun har et kompas og et ur til rådighed og starter i Endelave Havn først i august, og som skal være fremme i Mumbai i Indien først i november. Hvordan skulle det kunne lade sig gøre?

Når en ung Rødstjert *Phoenicurus phoenicurus* fanget på Christiansø den 1. september testet om natten i en tragt viser SV-orientering, er det så fordi, den 1) orienterer sig i relation til et magnet- eller stjernekompas, eller fordi den 2) navigerer mod et mål 300 km mod SV? Ja det kan man i princippet finde ud af ved at flytte fuglen 450 km mod V til Blåvand og tragtteste den igen. Viser den uændret SV-orientering, så ligner det 1) kompasorientering. Orienterer den sig mod 120 grader, er det derimod tegn på 2), for målet 300 km SV for Christiansø ligger i retningen ca. 120 grader (ØSØ-SØ) set fra Blåvand.

Nu skal der mere end én fugl og ét forsøg til at vise en generel tendens, men laver man mange forsøg med mange fugle forflyttet i mange forskellige retninger, og er der som i tilfældet med Rødstjerten en gennemgående tendens til at kompensere for forflytningerne, ja så har man som gjort af Thorup & Rabøl (2007) sandsynliggjort et tilstedeværende navigationssystem kaldet målområdenavigation, hvor den gennemgående navigation er rettet mod et vandrende mål fremme i trækruten. Først på efteråret ligger dette mål langt fra vinterkvarteret.

Til artiklen hører seks uddybende appendikser, som er tilgængelige on line:

Appendiks 1 er om mine forsøg på Christiansø, hvor den magnetiske misvisning[1] blev ændret fra +3° til henholdsvis +15° og -9° svarende til en position på samme breddegrad, men med en længdegrad henholdsvis ved Uralbjergene og ved Færøerne/Island. Hvis fuglene navigerer og bruger misvisningen som Ø/V-koordinat, skal vi derfor forvente en orientering med fremtrædende henholdsvis V- og Ø-rettede kompenserende tendenser. To forsøgsserier om efteråret viste ikke tegn på misvisningsnavigation, men det gjorde forårsforsøgene i betydelig grad. Derfor muligvis misvisningsnavigation om foråret.

Appendiks 2 er om mine prismeforsøg og en simuleret breddegradsforflytning 4° mod S. Ved hjælp af prismer anbragt oven på tragtene så fuglene nede i tragtene op gennem prismet på efterårsstjernehimlen over Christiansø, der som udgangspunkt var tippet 4° mod S. I stedet for den sædvanlige SV-orientering, var der en gennemgående tendens til orientering Ø for N, hvad der mere tydede på omvendt kompasorientering end egentlig stjernenavigation (V for N). Det er dog ikke ligetil at skelne mellem de to muligheder. Noget skete i hvert fald, som ikke bare var at opfatte som en reaktion på det bilaterale prisme, dvs. rettet mod den tynde prismekant mod N og/eller væk fra den høje prismekant mod S.

Appendiks 3 er en revurdering af Thorup *et al.*'s (2007a) radiosporings-forflytningsforsøg fra det vestlige til det østlige USA med voksne og unge Hvidkronede Spurve *Zonotrichia leucophrys*. Forfatternes konklusion er, at de unge fugle ikke kompenserede for forflytningen og dermed viste tilbage til vektororientering som det medfødte trækprogram. Diverse

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[1] I Danmark i øjeblikket peger mN 3° til højre for geografisk N, og misvisningen er +3°. Ved hjælp af kunstige magnetfelter kan mN forskydes mod højre eller venstre og dermed simulere en geografisk forflytning mod henholdsvis Ø og V.

korrektioner for vinddrift og en mere realistisk vurdering af normaltrækretningen og kompasreferencen (geografisk N eller magnetisk N) viser dog en klar kompensatorisk orientering ikke bare for de voksne fugle, men også for ungfuglene. Det kan vanskeligt tydes som andet end indflydelsen af et medfødt trækprogram med et navigatorisk indhold.

Appendiks 4 handler også om en revurdering, denne gang af en fastlåst, gammel indvending om orienterings/navigationssystemet bag en kompensation for en geografisk forflytning. Wiltschko (1973) forkastede tanken om målområdenavigation og forklarede kompensationen i det enkelte træktrin som et vektorkompromis mellem 1) kompasorientering i normaltrækretningen og 2) navigation tilbage mod positionen, hvorfra fuglene blev flyttet. Jeg kalder det et re-navigationssystem. W. & R. Wiltschko har dog aldrig forsøgt at videreudvikle denne kompromisorientering til at gælde for hele trækforløbet (det udvidede re-navigationssystem). Hvis de havde gjort det, ville de have fået et mere eller mindre forkortet, 'parabolsk' spredende og ikke godt beskrivende trækforløb.

I en forbedret version af et traditionelt forflytningsforsøg har man mulighed for at teste W. Wiltschko's alternative enkeltstep-hypotese: Den forbedrede version går ud på at gøre som hidtil men dertil at flytte tilbage til udgangspositionen og teste her igen for anden gang. I efteråret 2018 fangede jeg Grå Fluesnapper og Munk på Christiansø. De blev testet her, og derefter forflyttet mod VNV til Mors og derfra tilbage til og testet igen på Christiansø. Resultaterne støttede målområdenavigationshypotesen, da der ikke var forskel på den sydlige orientering i de to Christiansø-forsøg. I følge Wiltschko's hypotese skal orienteringen i anden omgang på Christiansø være signifikant medurs-drejet i forhold til første gang, sådan ca. mod SV-VSV, hvis den er S i første omgang. Der skal naturligvis mange flere lignende forsøg til, før fortolkningen af resultatet kan generaliseres, men den meget foreløbige konklusion er, at fuglene målområdenavigerer.

Appendiks 5 omhandler forsøg ikke medtaget i Thorup & Rabøl (2007), samt nyere forsøg og en genbetragtning af forsøg #11 i Thorup & Rabøl (2007).

W. Wiltschko var redaktør på tidsskriftet Behav. Ecol. Sociobiol. og kasserede 10 af mine forflytningsforsøg, som utilstrækkeligt dokumenterede. Det var rigtigt nok, og det har jeg så gjort nu og dertil tilføjet yderligere tre forflytninger til Endelave mest med adulte fugle, dertil tre nyere forflytninger til Færøerne.

De nye forsøg bekræfter og udbygger blot konklusionen fra Thorup & Rabøl (2007): Ungfugle testet med stjerner på himlen og om efteråret kompenserer på hensigtsmæssig vis for geografiske forflytninger, hvad der tyder på et medfødt målområdenavigationssystem (18 forsøg viste statistisk signifikant orientering til den kompensatoriske side ($P < 0.05$ i hvert forsøg), medens fire forsøg var signifikant ikke-kompenserende. En 18/4 fordeling er signifikant forskellig ($0.001 < P < 0.01$) fra en ligelig 11/11 fordeling).

Appendiks 6 uddyber fire vigtige områder og problematikker i forbindelse med Rabøl (1997) og Thorup & Rabøl (2007).

Det første belyser med et eksempel, hvordan man i en metaanalyse med mange forflytningsforsøg kan behandle data, så det viser sig, om der er en signifikant gennemgående tendens til kompensation.

Som det andet punkt omtales begrebet pseudonavigation, der i princippet kan optræde i forbindelse med kompasorientering i forhold til en stjerne, der som Solen bevæger sig medurs hen over sydhimlen. Bemærkningerne har formentlig især planetarierelevans – og så vidt jeg kan se kun om efteråret (Fig. 2), især hvis fuglen er nyfanget og allerede testes samme/næste nat efter fangsten under en Ø/V-skiftet planetarie-'stjernehimmel'.[2] Er fuglen indstillet på at holde en tidskompenseret vinkel i forhold til en stjerne, der her og nu står i 170°, og man så viser den en 'stjernehimmel' 30° mod Ø, så skifter kursen i forhold til stjernen – der har rykket sig 30° i sin vandringsbue – til 200°, hvad der ligner et navigatorisk respons. Men reaktionen ligger automatisk i kompasleddet og ikke i navigationsdelen. Hvis den ændrede orientering er noget til meget større end de 30°, så ligner det et udslag af navigation. Det er ret indforstået og svært det her. Beklager.

Det tredje punkt er kommentarer til test under en ikke-roterende planetarie-'stjernehimmel', samt det primitive derivat af en sådan, den såkaldte '16-stjerne-himmel', introduceret og især brugt af Frankfurt-gruppen. Min konklusion er, at man ikke kan forvente at få navigatoriske responser frem under en ikke-roterende 'stjernehimmel' (og især ikke, når den slet ikke ligner en rigtig stjernehimmel).

Angående '16-stjerne-himlen': Fuglen står i sit bur eller tragt i bunden af en dyb cylinder, hvor cylinderens 'låg' kan roterer. På undersiden af 'låget' og et stykke fra rotations-punktet i midten er der 16 lyspunkter, anbragt i otte 'bundter' af to tæt ved periferien. Burene/tragtene – normalt fire ad gangen – er anbragt i et kors excentrisk i forhold til rotationsaksen i bunden af cylinderen, hvad der formenes i rimelig grad at imitere en nordlig stjernehimmel set af fuglene i deres bure/tragte nede i bunden af cylinderen. Som regel har der været en indledende bur-fase med en roterende '16-stjerne-himmel', hvorefter fugle er overført til tragte i samme position, men nu under en ikke-roterende/stationær '16-stjerne-himmel'. Er du forvirret? Det er fuglene måske/måske ikke, men det er godt nok meget at udsætte dem for og bede dem om at reagere på en entydig, let fortolkelig måde.

Cylinderen er 2 m høj, og fuglene – i øjenhøjde – i deres tragte/bure er formentlig hævet 20 cm over bunden. Diameteren af cylinderen er omkring 1.5 m, og midten af de fire tragte/bure står omkring 50 cm N, Ø, S og V for rotationsaksen. Det betyder, at fuglene ser rotationspunktet på 'himlen' 74.5 ° over vandret/horisonten (tangens 180/50). Hvis orienteringen er SV i forhold til rotationspunktet i S-tragten, så er den NV i Ø-tragten, NØ i N-tragten og SØ i V-tragten (Wiltschko & Wiltschko 1976, Able & Able 1990).

Fjerde punkt har med faseskift i lys/mørke rytmen at gøre, og spørgsmålet om hvorvidt sådanne faseskift kan substituere geografiske forflytninger[3]. Forsøg foretaget bl.a. af mig viser, at det kan de øjensynlig ikke.

Angående faseskift: Hvis man fx erstatter det stedlige, naturlige lys/mørke skift kl. 17 og kl. 7 med et lys/mørke skift kl. 15 og kl. 5 svarer det principielt til, at man har flyttet fuglene 2 timer/30° mod Ø. Hvis fuglene ser op på den stedlige, uforandrede stjernehimmel vil de måske fortolke dens omdrejningsfase som et signal på en forflytning to timer mod V (1912 km på 55° N) og reagere med at ændre en SSV-trækretning til E-ESE,

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[2] For gentagne planetarieforsøg med de samme 'burfugle' er pseudo-navigation givetvis ikke så forventelig, men mere en teoretisk mulighed.

[3] Se Rabøl (1988) side 33-39 og 44-46; side 47-68 beskæftiger sig også med problematikken.

så er det en indikation på, at de stjernenavigerer (og at metoden kan substituere en geografisk forflytning 30º mod V). Hvis fuglene efter behandlingen er uændret SSV-orienterede, så er det et tegn på, at behandlingen ikke virker, og faseskiftet i lys/mørke rytmen kan ikke substituere en geografisk forflytning.

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Appendix 4: https://pub.dof.dk/link/2023/1.2.appendiks4
Appendix 5: https://pub.dof.dk/link/2023/1.2.appendiks5
Appendix 6: https://pub.dof.dk/link/2023/1.2.appendiks6

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