Appendix 3 for J. Rabøl 2023: Displacement experiments in night migrating passerines. – Dansk Orn. Foren. Tidsskr. 117: 37-46.

Juvenile White-crowned Sparrows compensate for displacement from western to eastern US: correction to Thorup *et al.* (2007)

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(*Med et dansk resumé: Kompensation for V/Ø-forflytning af unge Hvidkronede Spurve*)

Abstract Following the traditional interpretation of Perdeck (1958), it is generally predicted that juvenile passerine migrants are genetically endowed with a vector-orientation (clock-and-compass) program, which later in life changes into goal navigation. The displacement experiment of Thorup *et al*. (2007) confirmed this scenario. However, a different result emerges if the orientation is re-analysed in relation to magnetic N (instead of geographic N), if the standard direction is SSE (and not S), and if wind drift was taken into account. A proper treatment demonstrated that juvenile birds compensated significantly, indicating some sort of navigation. Thus, the traditional view of juveniles only performing vector-orientation cannot be maintained.

Introduction

Migrant White-crowned Sparrows *Zonotrichia leucophrys* trapped in autumn at a stop-over site, Sunnyside in Washington State were transported all across US east to Princeton, New Jersey and released equipped with radio transmitters (Fig. 1). The positions of the released birds were recorded continuously during the subsequent week. At Sunnyside the birds were supposed to be on their way towards the wintering area further south and southeast. The question was whether the released birds in New Jersey were 1) on their way back towards Sunnyside, the migratory route or the wintering area (SW US and NW Mexico), or 2) oriented on a southerly course assumed to be the standard direction in Sunnyside. 1) is indicative of the process of coordinate/gradient navigation, whereas 2) indicates the outcome of a vector orientation system.

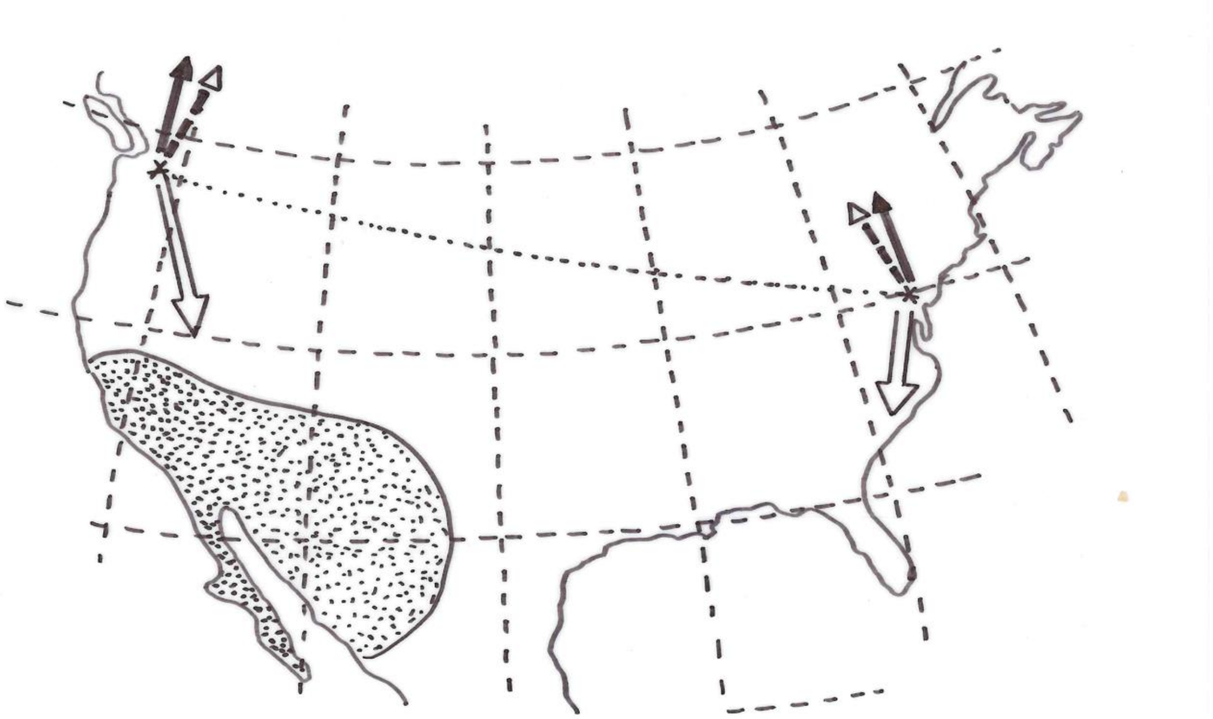

Fig. 1. White-crowned Sparrows trapped on migration at Sunnyside, north-western US, were transported (towards 100º, loxodrome, dotted line) to Princeton, eastern US, where they were released equipped with radio transmitters. The normal wintering area (dotted) is situated between directions SE and S (in reference to geographic N) as seen from Sunnyside, and SSE (158º) could be considered as a reasonable standard direction (thick white arrow to the west/left). Following the displacement and on basis of radiotrackings and corrections for wind-drift the mean headings of the juveniles end up in about 214º (thick white arrow to the east/right) in reference to geographic N (thick black arrow). The compensatory orientation in reference to geographic N and the standard direction is +56º, and in reference to magnetic N (hatched, white arrowhead) +84º (the magnetic declination was +15º at Sunnyside and -13º at Princeton).

Hvidkronede Spurve blev fanget som trækgæster ved Sunnyside i det nordvestlige USA og transporteret til Princeton i det østlige USA. Her blev de sluppet fri med påsat radiosender. Den omtrentlige normaltrækretning ved Sunnyside antages at være SSØ (tyk hvid pil) i forhold til geografisk N (tyk sort pil). Fra Princeton bevægede ungfuglene sig først mod SØ og senere V for S, og den gennemsnitlige beregnede flyveretning til sidst var SSV-SV (214º). I forhold til geografisk N kompenserede ungfuglene således +56º, og i forhold til magnetisk N +84º. Misvisningen ved Sunnyside er +15º og ved Princeton -13º (retningen mod magnetisk N er vist med stiplet pil med hvidt hoved).

Results and interpretations

The initial dispersal/migration more than 5 km away from the two release sites was SE in the juveniles and SW in the adults (Fig. 4 in Thorup *et al.* 2007). Here the directions mentioned are in reference to geographic N (gN).

The mean vector from the release sites towards the final recorded positions (more than 25 km away) were 192º – 0.990 (N = 9, P < 0.001) in the – juveniles, and 252º – 0.931 (N = 8, P < 0.001) in the adults (Fig. 3 in Thorup *et al.* 2007).

Thorup *et al.* 2007) focused on the orientation from the release sites towards the final positions without considering the possible significance of the initial orientation, and in spite of some reservations and reasonable considerations they concluded that the juvenile birds did not compensate the displacement and therefore displayed vector orientation in the standard direction. In fact, 192º – because of the high concentration – deviated significantly (P < 0.05) from due S considered to be the standard direction in Sunnyside. So, according to the definition by Thorup & Rabøl (2007) the deviation is significant to the compensatory side and therefore in a formal sense without possible reasonable objections indicative of a navigational process.

However, the orientation of the juvenile sparrows after the displacement was not considered in the details deserved – probably because of the significant difference between adults and juveniles, and the fact that the adults very clearly compensating for the displacement.

First, the standard direction at Sunnyside is said to be S. However, the wintering area as seen from here is situated towards about SSE and SE in reference to gN and mN, respectively (the magnetic declination is about +15º). Therefore, 1) the initial SE-response of the juveniles in the Princeton area could be perceived as unchanged standard orientation (in particular if considered in reference to mN; the magnetic declination is about -13º) – and the final 192º direction (in reference to gN, and 205º in reference to mN) as a compensatory response according to the definition of Thorup & Rabøl (2007).

A second possibility not considered 2) is that the juveniles navigated towards the wintering area – in Sunnyside as well as in Princeton – using magnetic N as the compass reference. Thorup *et al.* (2007) do not discuss the possible presence and significance of 1) or 2).

An additional approach not considered by Thorup *et al.* (2007) is the following: As mentioned, the initial dispersal/migration in the juveniles was SE (a). This means that the final positions as seen from SE of Princeton (b) – on the average towards 192º as seen from the release site – must be clockwise to 192º. If setting the relative lengths of a) and b) as 1 to 5 (a cautious estimate), the final positions as seen from the south-easterly positions on the average should be about 203º. Certainly, this looks like a compensatory response suggestive of at least some degree of navigation.

The track vector of a migrating bird is the sum of the wind-vector and the flying/airspeed-vector. The direction of the latter should be a better measure of the intended direction of the bird than the track-direction – if the bird is not compensating for the wind-drift. To my best knowledge most experts on the scene (e.g. McLaren *et al.* 2012) assume that, at least when in the air, there is no or only some partial compensation for the wind-drift. In order to proceed along this line of investigation I needed wind-data for the Princeton area for the period 17 to 27 September 2006 where the sparrows were released and radio-tracked. The following link was used: . The wind pattern was rather constant in the period considered with westerly winds very dominating. As an average for the period a wind-vector of WSW and 10 km per hour is a reasonable figure. If the airspeed of the sparrows is 30 km/h a track-direction towards 203º means an about 217º flying/airspeed-direction. 217º is clearly compensatory – and thus indicative of at least some navigation in the juveniles – compared with a standard direction somewhere between SE and S. However, such a 'calculation' is only tentative and should be followed up by a more stringent analysis as done below.

Kasper Thorup kindly supplied me with the radio-tracked positions of the 15 adult and 15 juvenile birds released at Princeton. Sometimes the birds were tracked on actual migration but mostly the positions were of grounded birds. Sometimes there were minutes or a few hours between successive positions but mostly these were separated by one day, two days or even more. Therefore, it is nearly always impossible to measure anything like a track vector of a migrating bird. However, given a reasonable constant wind vector in the period between two successive positions – and calculating the direction in between (as an estimate of the track-direction) – one is able to calculate the direction of the flying/airspeed vector, assuming an airspeed of 30 km/h and no compensation for wind-drift.

Considering the juvenile birds – and no more than three days after the release and a distance between succeeding positions of at least 10 km – the following 15 'tracks' of eight individuals fulfilling the conditions above were found. The directions were 81º, 112º, 156º, 174º, 201º, 202º, 203º, 204º, 204º, 205º, 206º, 219º, 222º, 224º, and 309º. The sample mean vector is 197º – 0.708 (N = 15, P < 0.001). Two further 'tracks' almost fulfilled the demand of 10 km (9.7 and 9.6 km). Here the 'track'-directions were 276º and 353º. Including these, the sample mean vector was 205º – 0.589 (N = 17, P < 0.01). The 'step'-lengths varied between 11.3 and 38.6 km (mean 20.2 km). Including 9.6 and 9.7 km the mean decreased to 19.0 km.

The airspeed-directions (headings) calculated were: 79º, 125º, 166º, 187º, 210º, 211º, 211º, 211º, 212º, 213º, 214º, 214º, 232º, 233º, and 294º. The sample mean vector is 206º – 0.736 (N = 15, P < 0.001). Considered by the confidence interval test and in reference to S, 26º is just compensatory (P = 0.05). However, is the standard direction more reasonably set to SSE the difference of 48.5º is significantly compensatory (P < 0.01).

If the two short-distance 'tracks' are added, the two directions 280º and 350º change the sample mean vector to 214º – 0.625 (N = 17, P < 0.01).

In their Fig. 4 Thorup *et al.* (2007) consider the directions of nine juveniles from the release site "to the first observed position to > 5 km from the release site". One of these birds (no. 583-o) first reached these positions after five days and then after an almost 25 km step towards SW. I have omitted this bird and only considered the other eight birds the sample mean vector of which was 121° – 0.734 ($P < 0.05$). I calculated the track-direction of these birds from the south-eastern positions to the final positions. The sample mean vector was 199° – 0.971 ($P < 0.001$) – as mentioned, the sample mean vector of these birds from the start towards the final position was 191° – 0.992 ($P < 001$).

Considering the adult birds, nine 'tracks' (in eight birds) were found. Adult no. 735-o moved towards 129° and 140°. This bird is mentioned by Thorup *et al.* (2007) as moving downwind in a very strong NW-wind, 42 km/h. In the weather table of Princeton, the wind is labelled as about WNW 9 to 15 km/h in the period considered, but apparently Thorup *et al.* measured the wind closer to the two tracks. The other seven 'tracks' were directed towards 34°, 237°, 255°, 264°, 267°, 283° and 308°. The corresponding airspeed-directions were calculated as 136° and 151° (no. 735-o), 26°, 247°, 247°, 248°, 267°, 271° and 298°, i.e. the sample mean vector of the six westerly birds shifted from 269° – 0.927 to 263° – 0.949. We should note that after calculation of the airspeed-directions the difference between juveniles and adults diminished, though the adults still compensated more clearly and significantly.

Discussion

Thorup *et al.* (2007) do not preclude the possibility that juveniles were allowed more time, or a shorter distance of displacement to show compensatory navigation. Probably, if it had not been for the comparison with adults, the authors would have given more attention to the compensatory shift made by the juveniles. However, the superficial fit to the firmly accepted Perdeck (1958)-scenario probably influenced the interpretation.

Why do Thorup *et al.*[1] not present the evidence for compensatory orientation shown by the juvenile birds? Why no attempts to correct for the wind-drift? Why set a standard direction towards S (in reference to gN) for the Sunnyside birds when SSE is more reasonable? Why not consider the possibility of a magnetic compass in a two-step navigation process? Using a magnetic compass makes compensation clearer. Why not for comparison include the results of the many displacements using

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[1] Kasper Thorup recently told me that before any results materialized, a decision was made that only the straight directions between the site of release and the last recorded position of the birds should be considered. The reason was that it will always be possible to make some corrections changing the observations in one or another direction to the benefit of a preferred hypothesis. However, the choice of a standard direction towards due S (and not more reasonable SSE) is questionable. Geographic N (and not magnetic N) were bound to skew the interpretation towards vector orientation. Anyway, the procedure chosen may be all right for a comparison between adults and juveniles, but certainly not considering whether the juveniles compensated for the displacement or not. However, the adults and juveniles were released at two different sites; juveniles about 7 km NE of adults. Because of the small distance Thorup *et al.* conclude "thus, local effects on the birds' orientation could be excluded". Perhaps, perhaps not.

the funnel method (Thorup & Rabøl 2007)? It is too smart to leave out the grand majority of results just by definition of methods (i.e. funnels).

Thorup *et al.* (2007) refers to Thorup & Rabøl (2001, 2007) but refrain from considering the results of displacements using the cage/funnel-method. This is problematic because the conditions in funnel experiments are closer to radio-tracked short-distance displacements than these compared with long-distance recoveries of ringed birds such as Perdeck (1958). In this connection Perdeck (1958) is almost always selected in contrast to the much more unclear results of Perdeck (1967) – as realized recently by Holland (2014). Thorup & Rabøl (2007) reviewed all funnel/cage experiments of geographical displacements (or simulated 'displacements' in planetariums). The conclusion was that juvenile passerines compensated at least in autumn under a stellar sky and in general somewhere ahead on the migratory route. This reaction is indicative of the process of stellar-based gradient/coordinate navigation towards a (moving) goal area.

Thorup *et al.* (2007) considered the cage/funnel method as inferior to release experiments and radio-tracking, and Muheim *et al.* (2006) is referred to for demonstrating the inferiority of cage/funnel testing. However, Muheim *et al.* demonstrated nothing, and forgot to inform about the significant influence of even weak winds on the tracks of short-distance radio-tracked birds as in the present investigation. Furthermore, cage/funnel testing is until now the only way to investigate birds under the 'stellar sky' of a planetarium, and in manipulated magnetic fields.[2] No doubt, long-time and long-distance satellite tracking of migrant birds is an improvement of cage/funnel testing – for a pure description of the migratory progress – but perhaps not as a tool for revealing the cues and systems involved. However, until now passerine birds like European Robins *Erithacus rubecula*, Garden Warblers *Sylvia borin* and European Pied Flycatchers *Ficedula hypoleuca* are too small to carry a strong enough radio-transmitter allowing satellite tracking. However, surprising results are already available from larger bird species such as Eleonora Falcons *Falco eleonorae* (Gschweng *et al.* 2008), where juvenile birds independently of adults – at least from about Equator clearly navigated towards their final wintering destination in the northern part of Madagascar.

The displacement across US was (according to Thorup *et al.* 2007) the first long-distance displacement performed using radio-tracking of passerine birds. Previously, Rabøl (1981, 1993) using the funnel-method long-distance displaced Robins from Denmark to La Gomera, Islas Canarias, and

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[2] Wallcott & Green (1974) published a much-cited paper about pigeons released equipped with a magnetic coil system on top of the head and around the neck which was supposed to (and in particular interpreted by other scientists) as inverting the magnetic inclination lending support to the hypothesis of a magnetic inclination compass (as introduced by and in the sense of Wiltschko & Wiltschko 1972). However, the resulting magnetic field did not invert the inclination and the reverse orientation observed must be caused by something else (Rabøl 1988).

Pied Flycatchers, Garden Warblers and Lesser Whitethroats *Curruca curruca* from Denmark to Naivasha, Kenya, respectively. As in the US displacement both adults and juveniles were included. These two studies are almost never referred to, probably because they do not fit into the nice 'Perdeckian' paradigm how adult and juvenile birds should behave. Certainly, the results are not easy to interpret. However, if any difference between juveniles and adults the orientation of the former looked more indicative as the result of a navigational act.

La Gomera (28ºN, 17ºW) is situated about 4000 km from Christiansø (55ºN, 15ºE) in the Baltic Sea, where the Robins (7 adults and 17 juveniles) were trapped as grounded migrants on 23-24 September 1978. The birds were transported to La Gomera in early October where experiments were carried out until early December. The great circle direction from Christiansø is about 230º. The center of gravity of the ringing recoveries of Robins banded on Christiansø is about Barcelona in the direction of about 215º. Some birds winter in Morocco and Algeria, but only the most distant reach a latitude about Las Canarias. The expectation following the displacement was that the adults should orient about NE – directed towards their former wintering area. Perhaps the juveniles also navigated towards the wintering area – or a little more NNE towards the migratory route in western Europe. However, the expectation of most people would probably be a SSW-SW course of the juveniles in the standard direction. None of these expectations were met (Rabøl 1981). The adults orientated S-SSW and the juveniles ESE, and the difference was very significant. It looked like the adults just proceeded in about the standard direction whereas the juveniles were aware of the displacement towards W but not the displacement towards S. The reader should consult the paper for more detailed information. Fig. 10 in the paper should also be consulted for a more nuanced point of view of the orientation of the displaced adult Common Starlings *Sturnus vulgaris* of Perdeck (1958, 1967). In short, only about half the adult Starlings moved towards the wintering area, and probably many of these did not navigate in a strict sense.

Twenty Pied Flycatchers (10 adults, 10 juveniles), seven Lesser Whitethroats (all juveniles), and 18 Garden Warblers (10 adults, 8 juveniles) were trapped on Christiansø in the Baltic Sea as grounded migrants from 23 to 27 August 1987 (Rabøl 1993). 9 September the birds left Copenhagen by air to Nairobi, Kenya. Naivasha is situated on 1ºS and 36ºE, and the magnetic inclination is about -23º, i.e. inverted compared to Denmark. By applying bar magnets close to the boxes the birds were transported in a strong, heterogenous magnetic field in order to prevent the birds from establish the direction of the displacement in reference to the magnetic field. As the Robins on La Gomera the birds spent the sunset/early night outside in their cages before transferred to the funnels during night. Experiments were carried out until early December – most on starry nights and all in the local magnetic field.

The ten juvenile Pied Flycatchers were bimodally oriented in September with a peak in about SW (17) and another almost as big peak in N (12). In October a few bird/nights were still northerly but otherwise the orientation was very significant SW. In November the orientation was more scattered SW-WSW but still very significant. Finally, in December the rather few bird/nights oriented significantly SW. There was no late autumn shift towards SSE as predicted by the vector orientation hypothesis. Perhaps the initial N-peak was a navigational response back towards the migratory route through Europe.

The ten adult Pied Flycatchers showed a bimodal SSW/NW (6/5) response in early September. In late September until November the orientation was significantly SW(WSW) but more scattered than in the juveniles. In December the birds were disoriented. Again, there was no shift in late autumn towards SSE. As in the juveniles the rather westerly orientation in November could perhaps be perceived – partly – as a navigational response towards the wintering area in Ghana/Nigeria.

In the Garden Warblers there was no difference between juveniles and adults, and no initial northerly peak as in the flycatchers. The orientation was rather scattered though significant. The grand mean vector of the 15 birds showing consistent orientation was 201° – 0.656 ($P < 0.01$). As the wintering area is mostly SSW of Naivasha both vector orientation and/or navigation towards the wintering area could be responsible for the orientation.

In the juvenile Lesser Whitethroats three birds were responsible for almost all migratory activity. In September the orientation was bimodally SW/N, in October the northerly peak was the most prominent, and in November/December the orientation was significant NNE-NE. If anything, the orientation looks mostly as navigation towards the wintering area in Sudan.

Conclusion

Clearly, the data of the juvenile sparrows presented by Thorup *et al.* (2007) is indicative of some sort of compensation for the displacement across US. For me it looks like a gradual shift from an initial uncontrolled wind drift towards an active more westerly heading. Perhaps it takes some time before a navigation system takes over and works properly when a bird is far outside the normal range of the population.

Acknowledgements

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Resumé

Kompensation for V/Ø-forflytning i USA af unge Hvidkronede Spurve

Thorup *et al.* (2007) fangede unge og voksne Hvidkronede Spurve på efterårstrækket i det nordvestlige USA og forflyttede dem til New Jersey tæt ved den amerikanske østkyst. Her blev de sluppet fri udstyret med radiosendere, så man kunne følge deres fortsatte træk indenfor de første op til 40 km (hos ungfuglene).

De voksne fugle kompenserede meget klart for forflytningen. De var V-orienterede, hvad der svarer mere til en kurs tilbage mod fangststedet i Washington State end en VSV-rettet navigation mod bestandens vinterkvarter i det SV-lige USA/NV-lige Mexico (Fig. 1).

De unge fugle var S-SSV-orienterede, hvad der blev fortolket som ukompenseret orientering i bestandens normaltrækretning, der blev sat til at være S.

Udfaldet af forsøget mindede således om orienteringen af de voksne og unge Stære i Perdecks (1958) ikoniske forflytning fra Holland til Schweiz. Konklusionen af de Hvidkronede Spurves orienteringssystem blev derfor den klassiske: Unge fugle kompasorienterer i normaltrækretningen, medens de voksne fugle navigerer mod det område, hvor de har tilbragt mindst en tidligere vinter. Kompasorienteringen ligger i generne; navigationen er noget tillært.

Problemet er bare, at hvis man indregner vinddrift i spurvenes træk, så (a) ændrer de unge fugles orientering sig til lidt V for SSV, hvad der i forbindelse med (b) en – mere rimelig antaget – normaltrækretning mellem SØ og S må fortolkes som en klart kompensatorisk respons (i følge definitionen af Thorup & Rabøl 2007), dog en mindre en af slagsen sammenlignet med de voksne fugles meget klare kompensation.

Konklusionen er derfor, at de unge fugle også viser (islæt af) navigation (mod trækrute/vinterkvarter) og ikke bare kompasorienterer i normaltrækretningen.

Denne konklusion vil provokere mange: Opfattelsen på bjerget er nemlig, at unge fugle på deres første efterårstræk 1) kompasorienterer i normaltrækretningen (trækket er genetisk programmeret som vektororientering; se nedenfor); 2) ikke er i stand til at navigere mod et sted, hvor de ikke har været før. 1) er en generalisering af fortolkningen af Perdecks forsøg, og opfattelsen understøttes af nogle, men ikke flertallet af andre forsøg (se senere). Den er altså ikke generel. 2) er et ikke-underbygget postulat.

De voksne fugles navigation mod vinterkvarteret forestiller man sig opstået på den måde, at de indprentede sig positionen af det sted, hvor de endte det første år og med succes klarede at overvintre. Det er altså et godt sted at vende tilbage til. Andre steder er (ofte) ikke så gode, og de unge fugle, der forsøgte at overvintre i disse mindre gode steder, klarede ikke overvintringen så godt og fik ikke så mange efterkommere i de følgende år (dødeligheden var større). Spørgsmålet er så, om de gode steder ligger spredt indenfor hele det område, hvor de unge fugle overvintrede eller forsøgte på det, eller om de ligger koncentreret centralt eller excentrisk indenfor området. Med andre ord: Er bestanden af de voksne fugles overvintringsområde af en mindre udstrækning end de unge fugles. Det ved man ikke, men det antager de fleste nok implicit, at det er.

Når de unge fugle antages at vektororientere, betyder det, at de er genetisk udstyret med kendskabet til en normaltrækretning, fx SW fastlagt i forhold til magnetisk N og/eller stjerne N. Desuden med et starttidspunkt for trækket og et samlet antal flyvetimer (fx 100), der med den for arten normale flyvehastighed (fx 30 km i timen) vil medføre, at fuglene – i eksempelvis 20 træktrin à 150 km – bevæger sig 3000 km mod SW til vinterkvarteret – forudsat selvfølgelig at der ikke er for meget variation på fastlæggelse og fastholdelse af trækretningen, antallet af træktimer og forstyrrelser (drift) fra vinden.

Kompasorientering er en et-trins proces, medens koordinatnavigation normalt (og noget gammeldagst) opfattes som en to-trins-proces: 1) først bestemmer fuglen, hvor den er i forhold til målet, så 2) lægger den en kompaskurs ind rettet mod målet. Med hensyn til 1): Fuglens mål er bestemt af et sæt i fuglen indeholdte koordinat/gradientværdier. Det kan fx være en bestemt kombination af bredde- og længdegrader såsom 10ºN/10ºV. Hvis fuglen nu kan måle/estimere sig frem til, at den i sin aktuelle position befinder sig på positionen 50ºN, 30ºØ, så ligger målet 40º mod S og 40º mod V, hvilket efterfølgende kan omsættes til en kompaskurs på lidt S for SV (det bliver ikke 225º, fordi fuglen befinder sig på en kugleflade med større afstand mellem breddegraderne end længdegraderne). I dette eksempel kan man beregne den konstante kompaskurs (loxodromen) mellem de to positioner til 223,9º og afstanden til 6171,2 km.

Det er let at vise, at en kæde af kompasstyrede træktrin spreder meget mere fra fugl til fugl end et træk, der er baseret på navigation mod et mål (Fig. 1 og 2 i hovedartiklen). Hvis vi forestiller os en bestand af fugle, der yngler omkring 50ºN/30ºØ (Kyiv, Ukraine) og overvintrer omkring 10ºN/10ºV (Guinea i Vestafrika), kan trækforløbet tænkes at være programmeret som kompasorientering mod 223,9º og 25 træktrin hver af en længde på 246,8 km (hvad der – fx – kan omsættes til 8,23 timers træk pr. nat med 30 km/timen hver tredie nat i en periode på to en halv måned). Hvis vi antager nogle rimelige usikkerheder på at bestemme kompaskurser og positioner, hvortil kommer effekten af vinddrift under trækket, når vi frem til, at – lad os sige 70 % af endepunkterne i et trækforløb i en bestand af trækfugle baseret på kompasorientering ender i et vinterkvarter med en udstrækning på i størrelsesordenen 1000 × 1000 km, medens et navigationsbaseret system er meget mere nøjagtigt, og måske ender indenfor et område på ca. 300 × 300 km.

Det korte af den lange er altså, at givet nogle områder er bedre at overvintre i end andre (giver større overlevelse/flere efterkommere), så er et navigationssystem meget mere præcist og må antages at medføre større overlevelse end et system baseret alene på kompasorientering. Derfor er det en fordel for de unge fugle (hvis de ikke er genetisk udstyret med et navigationssystem) at skifte system fra kompasorientering til navigation, hvor de lærer og indprenter sig vinterkvarterets position i et navigationssystem, efter at de er nået frem til det efter det første mere usikre forløb baseret på kompasorientering. Men er der evidens for, at de voksne fugles overvintrings-/rasteområder er mindre end de unge fugles? Jeg har kigget i Bønlykke *et al.* (2006) for danske ringmærkede fugle, men der er ikke noget at komme efter. Det virker rimeligt, at fuglene indprenter sig koordinaterne af deres første vinterposition, hvor de overlevede, og at de vender tilbage hertil de følgende år. Men det sker måske i lokale duftgradientfelter a la brevduer, der ikke kan give anledning til et kompensatorisk, navigatorisk respons virkende over lange afstande.

Jeg har vel en tro på, at koordinatnavigationen ikke udvikler sig således, men at den er med – måske i svækket/uudviklet form – allerede fra begyndelsen hos de unge fugle, når de starter på efterårstrækket. Jeg tror specielt på, at de indprenter sig gradientværdier som startpositionen, fordi det (formentlig) er genetisk vigtigt for bestandens sammenhæng, at fuglene næste forår vender tilbage til et område med en genpøl, der matcher deres egen og er tilpasset området og det øvrige trækforløb).

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