

Compensatory orientation in Pied Flycatchers *Ficedula hypoleuca* following a geographical displacement

JØRGEN RABØL



(Med et dansk resumé: Kompensatorisk orientering af Broget Fluesnapper *Ficedula hypoleuca* efter forflytning fra Christiansø til Skallingen)

Introduction

Rabøl (1969) proposed that the orientation following a geographical displacement could reveal the nature of the inherited orientational programme of a juvenile migrant bird. If no compensation was carried out a vector-orientation/clock-and-compass programme (Fig. 1A) would be inferred, whereas a compensatory orientation would be indicative of some sort of coordinate navigation directed towards a goal area further ahead along the migratory route (Fig. 1B).

However, this proposal was a little naive and premature as several other systems in principle could be responsible for compensatory orientation (Fig. 1C, D, and E). D was proposed by W. Wiltschko in Rabøl (1972), and C by Wiltschko & Wiltschko (1976). Rabøl (1978, 1980) discussed the kind of displacement experiments (B, C, or D) which might reveal the nature of the compensatory orientation, and later (Rabøl 1981) displaced Robins *Erithacus rubecula* to the Canary Islands in order to test whether B or D offered the best description of the results. Finally, Rabøl (1983, 1985) proposed the cross-axis hypothesis which provides a further system which may lead to compensatory orientation (Fig. 1E, and Rabøl 1993, in press).

Within the related field of pigeon homing two systems for the establishment of the departure direction, basically similar to C and D, have been much discussed: (1) Orientation based solely on en

route information. The directions during transport are registered in relation to a compass, and some sort of path integration (Wallraff 1990) is carried out. When released the pigeons orient opposite to the resultant vector direction of the outward transport. (2) Orientation based solely on information gathered at the site of release, i.e. the process of navigational site localization (Wallraff 1990). A set of home values is compared with the set of values registered at the site of release, and a departure direction is established. Since pigeons deprived of all useful compass information during transport are still homeward oriented when released and show no difference from the untreated controls (Wallraff 1980), system (1) can be ruled out.

The research hypothesis of this paper is C of Fig. 1 – much in the same way as model (1) in the pigeon experiments by Wallraff (1980) mentioned above. We consider whether the compensatory orientation following a displacement could be the resultant between the standard direction (perceived as a vector and established through a clock-and-compass process) and a vector back in the direction of the displacement established by a compass.

In recent years there has been a tendency to expand the original, simple clock-and-compass hypothesis into a strategic model in the sense of Arthur (1987), or even into a law of nature. This is not surprising, because the clock-and-compass

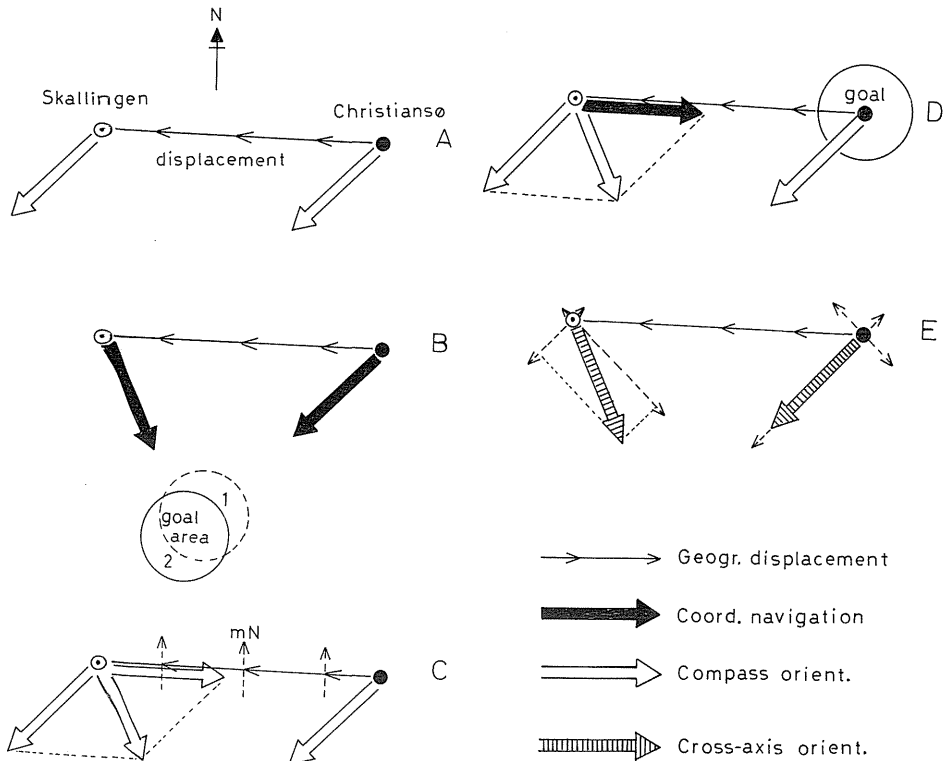


Fig. 1. Five possible systems responsible for the orientational reactions following a displacement from Christiansø to Skallingen. The birds are trapped as migrants on Christiansø and first tested here. Soon afterwards they are displaced to Skallingen and tested again. A thick white arrow shows compass orientation, and a thick black arrow coordinate navigation. A) Simple compass orientation, no compensation. B) Orientation at both sites based on coordinate navigation towards a (moving) goal area along the migratory route (at positions 1 and 2 at the time of testing on Christiansø and Skallingen, respectively). C) Reverse path integration, i.e. the birds detect the westerly displacement during transport and establish a reverse vector by means of a compass. A resultant SSE-vector arises. D) Coordinate navigation, where the birds establish the position of Skallingen relative to the experienced position of Christiansø. From the compensatory vector and the SW standard vector a resultant SSE-vector arises. E) Cross-axis orientation, where a dominant SW-vector on Christiansø is shifted towards a dominant right angle vector towards SE because of some simple sort of sign-navigation (e.g. a delayed sunset).

A til E viser orienteringen på Skallingen efter et forudgående forsøg på og en forflytning fra Christiansø. Hvis der alene er indflydelse fra det simple kalender- og kompas-system (A) sker der ingen ændring i orienteringen. Hvis orienteringen er under indflydelse af et af de fire andre systemer ses en kompenserende SSØ orientering på Skallingen. I B er orienteringen begge steder baseret på koordinat-navigation (fed sort pil) mod et målområde fremme i trækruten. I C er der kun retnings-orientering indblandet (fed hvid pil), og den Ø-rettede kompensations-vektor er resultatet af, at fuglene under forflytningen har mærket, at de er blevet bevæget mod vest i forhold til en retnings-reference, f.eks. magnetisk nord. I D er kompensations-vektoren fastlagt på forsøgsstedet ved hjælp af en koordinat-navigatorisk sammenligning af Christiansø og Skallingen. Endelig er kompensations-vektoren i E resultatet af styrke-ændringer i de fire vinkelrette vektorer i et retningskors system.

hypothesis is virtually self-evident and describes the migratory progress in simple language, so in some sense it seems unnecessary (or even provocative) to test it.

Nevertheless, at least some expansions of the clock-and-compass hypothesis – such as Fig. 1C – are testable: if the birds when transported are de-

prived of the necessary stimuli for establishment of a compensatory vector, the orientation after the transport should be the same as before. On the other hand, if such deprived birds do compensate for the displacement this is a strong indication that coordinate navigation or cross-axis orientation plays a role in the process (Fig. 1B, D, or E).

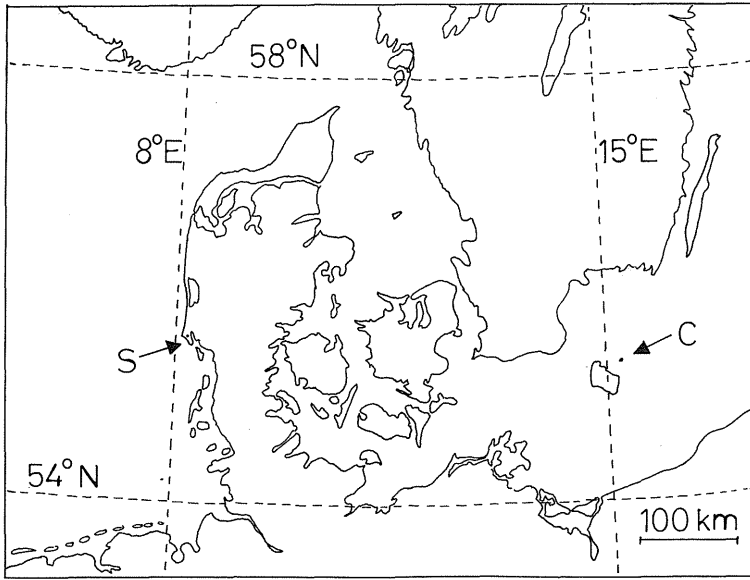


Fig. 2. Southern Scandinavia with positions of Christiansø (C) and Skallingen (S) indicated. The distance between the two sites is about 450 km or 7° .

Beliggenheden af de to forsøgsteder Christiansø og Skallingen.

Materials and methods

On four occasions in August Pied Flycatchers *Ficedula hypoleuca* (most of them juveniles, 1Y) were trapped on Christiansø in the Baltic Sea and transported 450 km (7°) W to Skallingen (Fig. 2). The birds were resting migrants on the first, straight part of their autumn migration from Finland towards the Iberian Peninsula.

The Pied Flycatcher was considered an appropriate species for the experiment because the migratory orientation for all the birds in the population should be close to SW, with little inter-individual variation in orientation. Furthermore, displacement to western Denmark should result in a compensatory orientation towards S or SE, significantly counterclockwise to and clearly distinguishable from the standard direction towards SW.

On all four occasions the flycatchers in the sample were trapped on a morning where a distinct wave of immigration to the island was recognized. Such birds are well suited for orientation experiments: the funnel activities are significant, and the concentration of the sample mean vector (based on individual mean directions) is high. The weather at arrival should also meet certain conditions before a sample of birds was accepted for the experi-

ments: the wind should be in the southwestern sector, between SSE and NW, and not too strong. According to common experience, birds arriving in such winds display a SW-orientation on Christiansø.

The birds were kept two by two in cans or baskets and fed mealworms. All samples except one were displaced from the island on the same or next day, following arrival and trapping.



Emlen funnels still covered with plastic sheets before the orientation experiments. Photo: Mads Jensen Bunch.
Fire orienteringstragte dækket til før nattens forsøg.

On each occasion a sample of birds in good condition was divided into two equal groups, controls and experimentals. The latter were transported in a very strong and heterogeneous magnetic field produced by bar-magnets attached horizontally on or close to the transportation boxes. The horizontal magnetic field intensity as experienced by the birds was at least 5-10 times stronger than that of the Earth. The experienced magnetic north shifted several times when the boxes were moved. Under such circumstances the experimentals should not be able to establish a compensatory vector in relation to the geomagnetic field. The controls were kept at a safe distance from any magnets during displacement.

During the transports by boat, car, and aeroplane, all birds were caged singly within small cardboard-boxes which were placed four by four within larger transportation boxes, permitting no view of the sun or stars. Very probably this way of transport also excludes any use of olfactory stimuli for establishing the direction of displacement.

Soon after the arrival to Skallingen the fly-catchers were transferred two by two to big plastic baskets covered by a cloth net. From that moment, the controls and experimentals were treated in exactly the same way, without bar magnets. Well before sunset the birds were placed outdoors in the baskets with visibility to the horizon in all directions. Here the birds experienced the geomagnetic field, the path and setting of the sun, and for at least 30 minutes the emergence of the stars, before transfer to the funnels.

The birds were tested singly in Emlen funnels with an about 160° vision of the sky. Orientation was registered by means of the correction-paper method (Rabøl 1979). The experiments lasted 90-120 minutes and were finished about midnight.

The orientation and amount of activity of the individual birds were estimated almost exactly in the same way as described by Rabøl (1979), by carefully inspecting the pattern of scratches in order to locate maxima and minima of activity.

The mean direction was estimated to the nearest 5° . In case of a clear bimodal pattern the directions of both peaks were estimated. Normally, a major and a minor peak could be distinguished.

The concentration of scratches around the mean direction was estimated as high, medium, low, or zero.

The amount of activity was labelled on a scale from 0 through 4: zero (0), low (1), medium (2), high (3), and very high (4). We also used intermediate values, such as "low to medium" (1.5), or



Photo: John Larsen.

"low (medium)" (1.25). The number of scratches is known to increase by a factor of 4-5 with each step on the activity scale (Rabøl unpublished), but was normally not counted in the present experiments.

The symbols in the figures (cf. Fig. 3) translate as follows: each dot denotes the mean direction (of a unimodal activity pattern) of a single bird on a single night. The big dots refer to an activity ≥ 1.5 , with white, dotted, and black dots used for low, medium, and high concentration, respectively. A small white dot refers to a mean direction with an activity ≤ 1.25 . The asterisks refer to the two peaks in a bimodal activity pattern. Sometimes the two peaks are based on approximately the same amount of activity and then the orientation is denoted by two medium-sized asterisks (as in Fig. 6). Normally, however, a bimodal activity pattern contains one large and one small peak. In such cases the large activity peak is denoted by a large asterisk, and the small peak by a small asterisk. Two kinds of sample mean vectors are calculated and shown in the figures: one based on big dots only (fully drawn), and another (hatched) based on both big and small dots and the large asterisks in the bimodal patterns.

The significance of the sample mean vector was tested by means of the Rayleigh test, and the probability of coincidence of two sample distribu-

- high concentration, \geq medium activity
- ⊙ medium concentration, \geq medium activity
- low concentration, \geq medium activity
- high/medium/low concentration, low activity
- ✱ ✱ bimodal orientation, large and small mode
- ✱ ✱ bimodal orientation, two equal modes

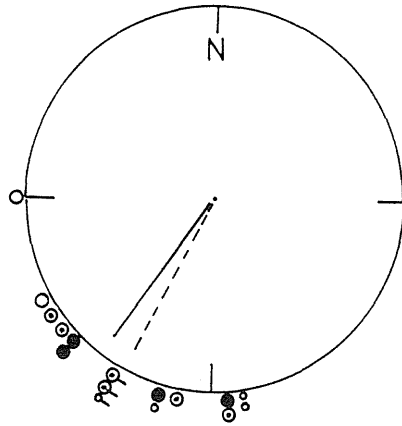


Fig. 3. The orientation on Christiansø on 21 August 1990 of 16 Pied Flycatchers, 3 adults (marked with a bar) and 13 juveniles. The sample mean vectors are 215° (fully drawn vector, $r=0.894$, $n=12$, $P<0.001$) and 207° (hatched vector, $r=0.888$, $n=16$, $P<0.001$).

Forsøg på Christiansø den 21. august 1990. Hver prik står for den gennemsnitlige opspringsretning hos én fugl. Stregene i midten af cirklen viser retningen og koncentrationen (længden) af gruppe-gennemsnitsvektoren, beregnet på to lidt forskellige måder. Der ses orientering mod SSV-SV, hvilket svarer meget godt til trækruteforløbet fra Finland mod Spanien.

tions by means of the Watson-Williams test or the Mardia-Wheeler-Watson test (Batschelet 1981).

During 1986 through 1990 displacements were carried out on four occasions. On the first three occasions no preceding orientation experiments were made on the trapping site; in those cases we have no proof of a prior SW orientation. In 1990, however, the same birds were tested first on Christiansø and then at Skallingen.

1) Eleven juveniles were trapped on Christiansø on 8 August 1986, and transported to Skallingen on the same day. Overcast and rain prevented funnel experiments that day, but in the evening of 9 August the birds were exposed to a clear sunset and tested under a clear, starry sky.

2) Fourteen juveniles were trapped on Christiansø on 27 August 1989. However, transport to Skallingen was not possible before 30 August. The birds were kept outdoors at Skallingen on 30 August from before sunset until 10 p.m., but total overcast and showers prevented funnel experiments to be carried out that night. On 31 August the birds experienced a clear sunset and were tested under a clear, starry sky.

3) Fourteen juveniles were trapped on Christiansø on 31 August 1989 and transported to Skallingen on the same day. The birds were outdoors from before sunset to midnight, and experienced a clear sunset and a starry sky. On 1 September the birds likewise experienced a clear sunset and starry sky from within the baskets. However, during the subsequent 2-hour exposure in the fun-

nels the sky was almost totally overcast (7-8/8) and no star patterns were visible, only occasional stars. Therefore the birds were retained for one more experiment, which took place on 2 September under a starry sky, after a sunny afternoon and clear evening sky.

4) Eighteen birds (15 juveniles and 3 adults) were trapped on Christiansø on 20 August 1990 where the birds experienced a clear sunset, but overcast and rain prevented funnel experiments. On 21 August the birds experienced a clear sunset and the start of a starry night from within the baskets. The funnel experiments started and ended under an almost clear sky with an intervening spell of overcast. Two adults displayed very low and disoriented activity and were released. The remaining birds were divided into two groups (8 controls and 8 experimentals) whose sample mean vectors were almost identical. On 22 August these 16 birds were brought to Skallingen where they arrived the following morning. The birds experienced a clear sunset and were tested under a clear, starry sky.

5) Eighteen birds (15 juveniles and 3 adults) were trapped on Christiansø on 23 August 1990, having arrived in a weak NW wind. They experienced a clear sunset and were tested under a starry sky during the following night (some of them were also tested on 26 August). These birds were not displaced to Skallingen but serve as a reference, typifying the orientation on Christiansø of Pied Flycatchers arriving under weak and/or westerly winds.

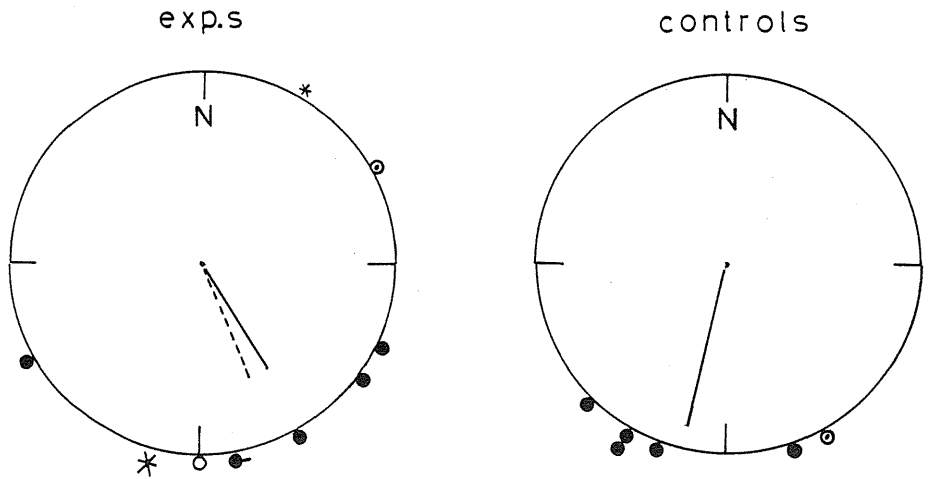


Fig. 4. The orientation at Skallingen on 23 August 1990 of 15 of the same birds as in Fig. 3 (7 controls and 8 experimentals; the only adult tested is marked with a bar). The fully drawn sample mean vectors of controls and experimentals are 193° ($r=0.887$, $n=6$, $0.001 < P < 0.01$) and 148° ($r=0.648$, $n=7$, $0.01 < P < 0.05$), respectively; the corresponding hatched vector of experimentals is 156° ($r=0.658$, $n=8$, $0.01 < P < 0.05$).

Forsøg på Skallingen den 23. August 1990 med de samme fugle som vist på Fig. 3. Fuglene er delt i to grupper efter betingelserne under transporten: "exp.s" er blevet flyttet i et kraftigt og forstyrret magnetfelt, "controls" i det normale uforstyrrede magnetfelt. De to gruppe-gennemsnitsvektorer peger mod henholdsvis SØ-SSØ og S-SSV, men de afviger ikke statistisk signifikant fra hinanden. Slås de to grupper sammen fås en gennemsnitsretning mod SSØ-S, der er forskudt ca 40° til venstre for gennemsnitsretningen af de samme fugle på Christiansø (Fig. 3).

Results

Figs 3, 4, and 5 show the orientation of the birds tested in 1990.

Compared with the orientation on Christiansø on 21 August (Fig. 3) the orientation shifted to the left (counterclockwise), especially in the experimentals (Fig. 4). The sample mean vectors of the controls and experimentals seem different, but according to the Watson-Williams test the difference is not statistically significant ($0.10 < P < 0.20$) and has the opposite direction of the expected, assuming a compensatory reaction based on a reverse vector and a clock-and-compass system (Fig. 1C). Therefore it makes sense to combine the controls and experimentals; the combined sample mean vector is 172° (fully drawn vector, $r=0.701$, $n=13$, $0.001 < P < 0.01$), or 175° (hatched vector, $r=0.717$, $n=14$, $P < 0.001$).

This is significantly different from the sample mean vector on Christiansø on 21 August (Watson-Williams test, $0.02 < P < 0.05$). However, as the two samples consist of (almost) the same individuals the application of the Watson-Williams test is conservative, so we also made a pairwise comparison (Fig. 5) and applied the confidence interval test (Batschelet 1972). According to this pro-

cedure the counterclockwise shift was significant (fully drawn vector: $0.01 < P < 0.05$, $n=11$; hatched vector: $P < 0.01$, $n=13$).

Fig. 6 shows the orientation on Christiansø of the 18 birds that arrived on 23 August 1990. The difference between the mean vector of this sample and that from 21 August 1990 (Fig. 3) was not significant ($0.20 < P < 0.30$).

Fig. 7 shows the orientation of the birds displaced in 1986 and 1989, tested on three starry nights at Skallingen. The small difference between the samples justifies their combination. No difference is found between the sample mean directions of the experimentals and the controls.

If the experimentals and the controls of Fig. 7 are combined, the sample mean vector based on the unimodal activities ≥ 1.5 was 172° ($r=0.583$, $n=29$, $P < 0.001$). Compared to the sample mean vector of Fig. 6 (223° ; $r=0.721$, $n=17$), the angular difference of 51° counterclockwise is statistically significant ($0.01 < P < 0.025$, Mardia-Wheeler-Watson).

If the two Christiansø-distributions (Figs 3 and 6) are combined and compared with the combined Skallingen distributions (Figs 4 and 7) the angular difference is 47° (fully drawn vector, $n=(29,42)$),

or 40° (hatched vector, $n=(33,48)$), which are both statistically significant ($0.001 < P < 0.01$).

Fig. 8 shows the orientation at Skallingen on the overcast night of 1 September 1989. The mean vector is the reverse of the expected SW orientation on Christiansø (Figs 3 and 6), and is statistically significant. However the distribution looks bimodal with modes at N and E. Applying the method of Holmquist & Sandberg (1991) two modes of 80° and 357° are found ($r_{1,3}=0.907$, $n=13$, $P < 0.001$, cf. Tab. 2 in Holmquist & Sandberg (1991)). The N mode is most prominent in the experimentals, the E mode in the controls. However, according to the Watson-Williams test the difference between the controls and experimentals is not significant ($0.30 < P < 0.40$).

Discussion

Is the orientation compensatory?

A significant counterclockwise shift in orientation is found following the displacements. This observation is in good accordance with earlier displacement experiments, both spring and autumn, carried out on starry nights (Rabøl 1969, 1970, 1972, 1975, 1981, 1985, 1988, 1992, 1993, in press).

An important question is whether the counterclockwise shift is caused by the displaced birds' internal clock still being in phase with the time on Christiansø. If so, and if the birds make use of simple compass orientation in relation to the afternoon sky, the sunset, or a star or star-pattern on the southern sky, a counterclockwise shift of no more than 7° is to be expected. If the birds make use of compass orientation in relation to a circumpolar star or star-pattern, or the geomagnetic field, no discernible change is to be expected. A compass-based shift between 0° and 7° can only explain a minor part of the observed shift of about 40° .

The NE-orientation on the overcast night of 1 September 1989 could be termed reverse standard orientation. Rabøl (1972, 1975, in press) describes other experiments where displaced birds tested under overcast conditions displayed reverse standard orientation.

The orientation system involved

The lacking difference between the mean directions of the displaced controls and experimentals clearly indicates that a simple clock-and-compass system in combination with a compensatory vector based on information collected en route (Fig. 1C) did not cause the counter-clockwise shift.

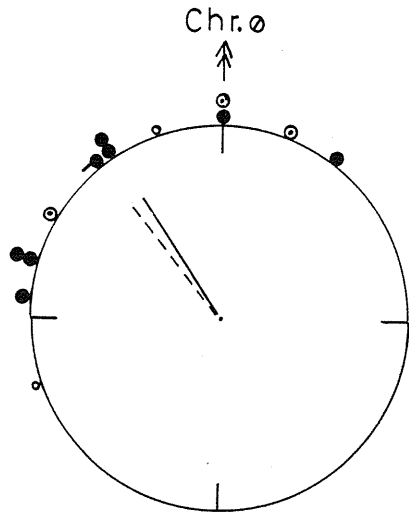


Fig. 5. The orientation at Skallingen on 23 August 1990 relative to the orientation on Christiansø on 21 August 1990. 13 out of 15 birds showed orientation on both occasions (the single adult marked with a bar). Sample mean vectors are -33° (fully drawn, $r=0.785$, $n=11$, $0.001 < P < 0.01$) and -37° (hatched, $r=0.759$, $n=13$, $P < 0.001$).

Orienteringen på Skallingen 23. august 1990 afbildet relativt til orienteringen på Christiansø 21. august 1990.

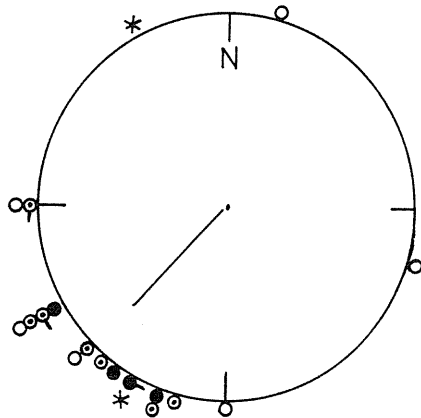


Fig. 6. The orientation on Christiansø of 18 Pied Flycatchers (15 juveniles and 3 adults, the latter marked with a bar) on 23 or 26 August 1990. The birds, trapped on Christiansø on 23 August, arrived in a weak NW wind and were tested under a starry sky. In 5 birds the activity on 23 August was low (< 1.5), and a subsequent experiment was carried out on 26 August where all activities were ≥ 1.5 . The sample mean vector is 223° ($r = 0.721$, $n = 17$, $P < 0.001$).

Orienteringen af en anden gruppe Brogede Fluesnapperer fanget og testet på Christiansø den 23. august 1990.

However, the compensatory orientation of the experimentals does not prove that the migratory process is due to an inherited programme based on coordinate navigation towards a goal area moving along the migratory route (Fig. 1B). The response can be explained by at least two other models: a) a cross-axis system (Fig. 1E, Rabøl 1983, 1985), or b) a system where simple clock-and-compass orientation combines with a compensatory vector established by means of coordinate navigation towards the position of Christiansø (or some other experienced position on the autumn migratory route, Fig. 1D).

a) The cross-axis hypothesis basically rests on compass-orientation, but the outcome is not necessarily an orientational response in the standard direction. It could be one of four: orientation in the standard direction, orientation in the reverse standard direction, or orientation in one of the two directions at right angles to the standard direction. Reverse standard orientation is believed to be triggered by an overshoot of the goal area, by unfavourable conditions (such as food-stress or captivity), or by an inferior stimulus-situation (e.g., an overcast sky), whereas right-angle orientation could be a reaction to a preceding wind drift or elicited by a low motivational state (Rabøl 1983, 1985). If a wind drift is recognized by the birds through an advanced or delayed sunset or rotational phase of the starry sky, then a system based on cross-axis orientation approaches a true navigational system (Rabøl 1985, 1988).

b) involves coordinate navigation in some form without assuming "inherited" coordinate navigation towards a position where the bird has never been before (as presumed in the goal area navigation hypothesis). In fact, reluctance to accept "inherited" coordinate navigation reflects a pseudo-problem: what is the real difference between 1) navigating towards a position where some set of coordinate values has been experienced, and 2) navigating by extrapolation from an experienced position towards a position where the bird has never been before (following the model of Fig. 1 in Rabøl 1980)? Recall that the migratory progress always starts in an experienced position, the breeding ground or some other pre-migratory area.

The navigatory system or navigatory component responsible for the compensatory orientation in the present and earlier experiments is presumably based on the stars. Simulated W/E-displacements under a planetarium sky elicited a clear compensatory orientation (Sauer & Sauer 1960, Rabøl 1992).

Displacement by the wind

Migrants are displaced by the wind and therefore must be able to cope with displacements and return to their normal migratory route.

Rabøl (e.g. 1975) has shown that the orientation of newly arrived long-distance migrants and Robins on Christiansø is directed more or less into the wind at arrival, thus compensating for recent wind drift. Among others, Baird & Nisbet (1960), Evans (1968), and Moore (1990) give similar evidence of compensatory orientation following wind drift.

Three further examples of such compensatory orientation of birds trapped and tested on Christiansø can be given: 1) Twenty Pied Flycatchers (almost all juveniles) trapped in the period 19-23 August 1976, in and after a period of steady northerly and easterly winds, and tested on the night following arrival, displayed southeasterly orientation (sample mean vector 123° , $r=0.75$). The birds may have originated in the Baltic states or Russia and drifted too far W, and the easterly component could be compensation for a preceding drift (Rabøl unpubl.). 2) Six out of eight Pied Flycatchers trapped in the period 5-9 September 1991, with strong NNW-winds were oriented between 265° and 345° ; the sample mean vector of the 8 birds was 304° , with $r=0.40$ (Rabøl unpubl.). 3) Redstarts *Phoenicurus phoenicurus* and Garden Warblers *Sylvia borin* trapped at Blåvand (westernmost Jutland) in a period with steady (north)easterly winds showed E-ESE orientation at nearby Skallingen on 16 September 1993, significantly counter-clockwise to the presumed standard direction of SSE-S (Rabøl in press).

It has been claimed (unknown referee) that the first case mentioned above invalidate the interpretation of the pattern shown in Fig. 7, i.e. that the orientation at Skallingen should not be considered as compensatory but only reflects the orientation as it would have been if the birds in advance had been tested on Christiansø. This, however, is very improbable. Fig. 7 is a composite of the very similar results of three different displacements which were all carried out after arrivals to Christiansø under light wind conditions likely to produce southwesterly orientation. Anyway, one should bear in mind that significant deviations from the standard direction are never compatible with the predictions of the simple clock-and-compass hypothesis, whereas the observed deviations mentioned above are all compatible with the expectations of a cross-axis or goal area navigation system.

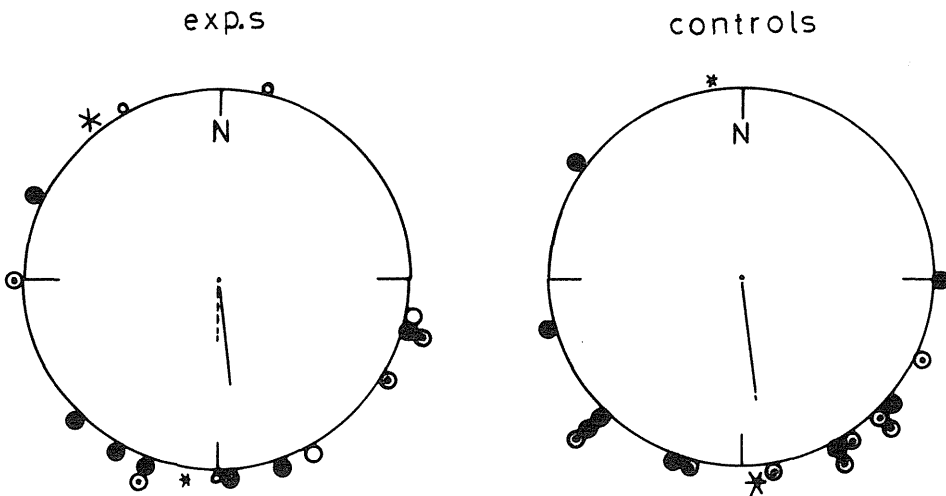


Fig. 7. The orientation at Skallingen on 3 starry nights (9 August 1986, 31 August 1989, and 2 September 1989) of birds displaced from Christiansø. Fully drawn sample mean vectors of controls and experimentals are 172° ($r=0.614$, $n=16$, $0.001 < P < 0.01$) and 173° ($r=0.545$, $n=13$, $0.01 < P < 0.05$), respectively; corresponding hatched vectors are 172° ($r=0.636$, $n=17$, $0.001 < P < 0.01$) and 180° ($r=0.319$, $n=17$, $P > 0.05$).

Orienteringen på Skallingen af tre grupper fluesnapperer fanget på Christiansø i efterårene 1986 og 1989. I gennemsnit er både "exp.s" og "controls" (se Fig. 4) orienteret lidt øst for S. Som Fig. 3-4 viser Fig. 6-7 den typiske orientering på henholdsvis Christiansø og Skallingen i forbindelse med svage "vestlige" vinde (mellem SSØ og NV).

The expansion of the clock-and-compass hypothesis

The expansion of the clock-and-compass hypothesis is evident in two ways.

1) A tendency to ignore significant deviations of the sample mean vector from the standard direction and the predictions of the clock-and-compass hypothesis (e.g. Gwinner & Wiltschko 1978 (see also the critique by Rabøl 1985), Beck & Wiltschko 1982, and Bingman 1984). It seems not to be appreciated that the simple clock-and-compass hypothesis is invalidated by such results which cannot be explained by stochastic processes or spurious deflections caused by the experimental conditions.

2) Inclusion of compensatory orientation of unknown origin within the capacity of the simple clock-and-compass system (Helbig pers. comm. 1989, Wallraff 1991). Wallraff (1991) writes "... external signals might well influence the intended direction. For instance, some positional information as derived from the starry sky, the geomagnetic field, or something else may inform the birds that they have reached a critical site or line (e.g. latitude) at which they should change their compass". Wallraff may well be right in this statement but, as already discussed by Rabøl (1985), we have then moved outside the domain of

a simple clock-and-compass system and into something else and more, such as one of the systems B, C, D or E (Fig. 1).

As mentioned in the Introduction, the simple clock-and-compass hypothesis could be considered a strategic model – like, e.g., the basic Lotka-Volterra equations of competition and predation, or the simple optimal foraging models (Begon et al. 1990). Such models are almost impossible to test and reject under natural (not controlled) conditions. The clock-and-compass "hypothesis" could be considered a summary of the migratory progress in directional and temporal terms, and has been confirmed – not too convincingly – in experiments with non-displaced cage-birds removed far from their natural migratory context and progress, and analyzed crudely by second or third order statistics. Obviously, such treatment will reduce complex patterns, produced by coordinate navigation or cross-axis orientation, into simple patterns which look like the outcome of simple one-direction orientation.

In conclusion, I consider the simple clock-and-compass hypothesis an appropriate description of the reaction of a deprived cage-bird tested without the possibilities of performing a navigatory act. Probably, under the natural migratory progress, the clock-and-compass system should be regarded as

an auto-pilot which may be switched on in case of an uncomplicated routine flight, or if all the complicated steering systems break down. Such a simple system could probably never in itself guide the bird safely through a long and complicated migratory progress.

Outlook

In recent reviews on the orientational mechanisms of migrant birds the migratory progress has been described exclusively in terms of the clock-and-compass system (e.g. Able & Bingman 1985, Wiltschko & Wiltschko 1988a, 1988b, Berthold 1990, Helbig 1990, Wallraff 1990).

Emlen (1975), though, seriously considered the possibility of coordinate navigation in juvenile birds and also regarded geographical displacements as a method capable of throwing light on the innate orientational programme. However, geographical displacements with migrant birds are no longer performed (except by me), presumably because the view has settled that birds only navigate towards an earlier experienced position, as revealed by ringing recoveries of geographically displaced Sparrowhawks *Accipiter nisus* (Drost 1938), Starlings *Sturnus vulgaris* (Perdeck 1958, 1967), and Teals *Anas crecca* (Wolff 1970). Only the adult birds showed more or less clear signs of orientation towards their normal wintering area, whereas juvenile birds did not change their normal (standard) migratory direction. Very reasonably it was concluded that these species have no inherited knowledge of the position of their wintering area, but only of the standard direction.

However, all these species are short- or medium-distance migrants, and one should be cautious in generalizing to other species, especially long-distance migrants. Juveniles of long-distance migrants tested in funnels by Evans (1968) and Rabøl (e.g., this study) clearly compensated a displacement mediated by wind or man.

Displacement experiments – both real and simulated – with migrant birds (Rabøl 1985, 1992, 1993, in press) ought to be given a comeback as a basic procedure when investigating orientation mechanisms and systems.

Summary and conclusion

Pied Flycatchers displaced in autumn from Christiansø to Skallingen compensated the displacement, i.e. the course shifted significantly counterclockwise from about SW to SSE-S. No difference was found between experimentals (displaced in a disturbed and meaningless magnetic

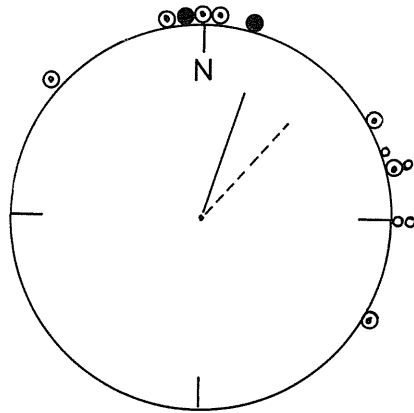


Fig. 8. The orientation on the overcast night of 1 September 1989 at Skallingen, controls and experimentals combined. The birds were displaced from Christiansø. Sample mean vectors are 19° (fully drawn, $r=0.687$, $n=9$, $0.01 < P < 0.05$) and 43° (hatched, $r=0.674$, $n=13$, $0.001 < P < 0.01$).

Orienteringen på Skallingen den 1. september 1990 på en overskyet nat. På alle de andre nætter var det helt eller næsten helt skjult.

field) and controls (displaced without magnetic disturbances). Both groups were displaced without access to visual celestial cues, and olfactory cues must also have been screened away.

Obviously, path integration based on magnetic, celestial, or olfactory cues is not a necessary component in compensatory orientation. The compensatory orientation must be based on site localization in some way.

Acknowledgments

Jette Andersen and Søren Hansen carried out some of the experiments, and John Faldborg, Jens Bagger and Mikkel Lausten trapped the birds on Christiansø. MS Ertholm, Ringbilen and Danair transported the birds.

Resumé

Kompensatorisk orientering af Broget Fluesnapper *Ficedula hypoleuca* efter forflytning fra Christiansø til Skallingen

I efterårene 1986, 1989 (2 gange) og 1990 lavede jeg orienteringsforsøg på Skallingen med unge Brogede Fluesnapperne fanget få dage forinden som trækgæster på Christiansø.

Tidligere tragt-forsøg (se Rabøl 1988) havde vist, at trækfugle oftest vil kompensere for en forflytning. I det aktuelle forsøg, med en normal orientering mod sydvest på Christiansø, skulle en forflytning til Vestjylland resultere i en venstre-drejet orientering mod syd eller sydøst.

Specielt 1990-forsøget (Fig. 3-5) bekræfter da også forventningen om en kompensatorisk respons.

Meningen med forsøget gik imidlertid videre end til at få bekræftet tidligere erfaringer. Det basale formål var at få belyst, om det medfødte trækprogram alene bundet i et kalender- og kompas system (se pp. 99-102 i Rabøl 1988) med tilhørende kompas-baserede kompensationer efter princippet vist på Fig. 1C. Næsten alle tidens træk- og orienterings-forskere hælder til denne anskuelse – hvis de overhovedet anerkender, at unge trækfugle kan kompensere for en geografisk forflytning på deres første efterårstræk. Det gør unge trækfugle nemlig ikke altid, ihvertfald ikke undersøges kort- og mellem-distance-trækkere som Krikand *Anas crecca* (Wolff 1970), Spurvehøg *Accipiter nisus* (Drost 1938), og Stær *Sturnus vulgaris* (Perdeck 1958, 1967). Også mine egne tragt-forsøg på Færøerne med Munk *Sylvia atricapilla* viser ukompenseret orientering i normaltrækretningen hos fugle, der er kommet til Færøerne efter en fejlflyvning eller en vind-assisteret drift fra Norge. Men i mange andre tilfælde ser man klar kompensatorisk orientering. Det gælder således for langdistancetrækkere testet i tragte under en stjerneklar himmel (Evans 1968, Rabøl 1988, 1993), og der er også mange eksempler på synligt dag-træk og radar-observationer, der viser klart islet af kompensation efter en forudgående eller pågående vinddrift (Rabøl 1988). Så kompensatorisk orientering er et almindeligt forekommende fænomen. I det hele taget er der ofte så store variationer og afvigelser fra den forventede normaltrækretning i orienteringsforsøg og observerede trækbevægelser, at disse ikke lader sig forstå og beskrive alene ud fra et medfødt kalender- og kompassystem. Et sådant rummer kun mulighed for simple og fastlåste beskeder såsom: "august/september træk SV, oktober/november træk SSØ, december stop" (gældende for en finsk Broget Fluensnapper, der trækker over Spanien til et vinterkvarter i Nigeria). Der er overhovedet ingen frihedsgrader i et sådant system, og de store observerede afvigelser og variationer kan ikke alle (bort)forklares som pseudodrift (pp. 159-164 i Rabøl 1988), støj i systemet, forsøgs-artefakter, eller hvad man nu ellers kan finde på.

Som allerede nævnt har jeg her været ude efter at teste hypotese C på Fig. 1, men C er ikke den eneste mulige forklaring bag en kompensatorisk orientering. Der er i hvert fald tre andre muligheder, vist som B, D, og E på Fig. 1, så der skal en speciel forsøgsprocedure til at afgøre, om C er af betydning. Denne procedure består i, at fuglene under forflytningen fra Christiansø til Skallingen har været delt over i to lige store grupper: forsøgs- hhv. kontrol-fugle. De første blev transporteret i et meget kraftigt og uensartet magnetfelt, hvor de ikke havde nogen mulighed for at fastlægge den vestlige forflytningsvej vha. deres magnetkompas. Denne mulighed havde kontrolfuglene, som blev transporteret i det normale, uforstyrrede jordiske magnetfelt. Som i mine tidligere forflytningsforsøg havde ingen af grupperne mulighed for at fastlægge forflytningsvejen i forhold til deres sol- eller stjernekompas. Under en transportform som den anvendte kan man også tillade sig at se bort fra dufte som

kilde til en kompas-baseret erkendelse af transportvejens forløb.

Hvis C på Fig. 1 er forklaringen på en kompenserende orientering, så skal forsøgs-fuglene på Skallingen vise ukompenseret sydvest-orientering, medens kontrol-fuglene skal være sydøst- til sydorienteede. Det er jo kun kontrol-fuglene, der har haft mulighed for at erkende forløbet af forflytningen ud fra magnet-kompasset. Hvis der derimod er navigation indblandet i kompensations-processen – som der er i B, D og E på Fig. 1 – så bør både forsøgs- og kontrol-fugle være sydøst- til sydorienteede på Skallingen.

Hvad viser resultaterne så? For det første, at der ingen forskel er på orienteringen af kontrol- og forsøgs-fugle. Begge grupper viser SSØ-S orientering. For det andet, at orienteringen på Skallingen er venstredrejet i forhold til sydvestorienteringen på Christiansø, og at denne drejning er statistisk signifikant. Se Fig. 3-5 og 7.

C er altså ikke nogen god forklaring på den kompensatoriske orientering efter forflytningen, men om den rigtige forklaring så er B, D eller E (Fig. 1), kan ikke afgøres med en forsøgsprocedure som den her anvendte. Rabøl (1978) giver nogle anvisninger på, hvordan man kan teste B mod D. Et forflytningsforsøg til de Kanariske øer (Rabøl 1981) var et forsøg herpå, men det faldt noget uklart ud, måske fordi der blev brugt Rødhals *Erithacus rubecula*, der er en mellemdistancetrækker. Også en forflytning af langdistancetrækkere til Kenya i 1987 (Rabøl 1993) gav i princippet mulighed for at skelne mellem B og D, og faldt mest ud til fordel for B. Men ovenover alting svæver E (retningskors-orientering, se pp. 117-118 i Rabøl 1988), der (næsten) altid kan forklare (næsten) alting, så det ender jo nok med, at kalender- og kompass-folket hen ad vejen skifter hypotese fra C til E. Specielt B – koordinat navigation mod et vandrende målområde (se pp. 102-104 i Rabøl 1988) – betragtes af de fleste som helt usandsynlig, og det kan da også være, at den nu til dags bør betragtes som et historisk kuriosum, der i sin tid fremtrådte som det eneste logiske alternativ til den helt simple og "stive" kalender- og kompasshypotese (A på Fig. 1). Men hvad enten det nu er B, D eller E, der kommer nærmest virkeligheden, så rummer de alle i sig en større eller mindre grad af "medfødt" navigation. Tiden og verden er blevet for kompleks at færdes i for dem der kun er udstyret med et kompas.

References

- Able, K.P. & V.P. Bingman 1985: The development of orientation and navigation behavior in birds. – *Quart. Rev. Biol.* 62: 1-29.
- Arthur, W. 1987: The niche in competition and evolution. – John Wiley and Sons, Chichester.
- Baird, J. & I.C.T. Nisbet 1960: Northward fall immigration on the Atlantic coast and its relation to off-shore drift. – *Auk* 77: 119-149.
- Batschelet, E. 1972: Recent statistical methods for orientation data. Pp. 61-91 in: Galler, S.R., K. Schmidt-Koenig, G.J. Jacobs & R.E. Belleville (eds):

- Animal orientation and navigation. – U.S. Gvmt Printing Office, Washington, D.C.
- Batschelet, E. 1981: Circular statistics in biology. – Academic Press, New York.
- Beck, W. & W. Wiltschko 1982: The magnetic field as a reference system for genetically encoded migratory direction in Pied Flycatcher (*Ficedula hypoleuca* Pallas). – *Z. Tierpsychol.* 60: 41-46.
- Begon, M., J.L. Harper & C.R. Townsend 1990: Ecology. Individuals, populations, and communities. – Blackwell, Boston.
- Berthold, P. 1990: Orientation in birds: Concluding remarks. A brief definition of the research field's position. – *Experientia* 46: 426-428.
- Bingman, V.P. 1984: Night sky orientation of migrating Pied Flycatchers raised in different magnetic fields. – *Behav. Ecol. Sociobiol.* 15: 77-80.
- Drost, R. 1938: Über den Einfluss von Verfrachtungen zur Herbstzugzeit auf den Sperber, *Accipiter nisus*. – *Proc. 9 Int. Orn. Congr.*: 503-521.
- Emlen, S.T. 1975: Migration: Orientation and navigation. Pp. 129-219 in: Farner, D.S. & J.K. King (eds): *Avian Biology*, Vol. V. – Academic Press, New York.
- Evans, P.R. 1968: Reorientation of passerine night migrants after displacement by the wind. – *Brit. Birds* 61: 281-303.
- Gwinner, E. & W. Wiltschko 1978: Endogenous controlled changes in migratory direction of the Garden Warbler, *Sylvia borin*. – *J. comp. Physiol.* 125: 267-273.
- Helbig, A. 1990: Are orientation mechanisms among migratory birds species-specific? – *Trends in Ecology and Evolution* 5: 365-367.
- Holmquist, B. & R. Sandberg 1991: The broken axis approach – a new way to analyze bi-directional circular data. – *Experientia* 47: 845-851.
- Moore, F.R. 1990: Evidence for redetermination of migratory direction following wind displacement. – *Auk* 107: 425-428.
- Perdeck, A.C. 1958: Two types of orientation in migratory Starlings, *Sturnus vulgaris* L., and Chaffinches, *Fringilla coelebs* L., as revealed by displacement experiments. – *Ardea* 46: 1-37.
- Perdeck, A.C. 1967: Orientation of Starlings after displacement to Spain. – *Ardea* 55: 194-202.
- Rabøl, J. 1969: Orientation of autumn migrating Garden Warblers (*Sylvia borin*) after displacement from western Denmark (Blåvand) to eastern Sweden (Ostenby). A preliminary experiment. – *Dansk Orn. Foren. Tidsskr.* 63: 93-104.
- Rabøl, J. 1970: Displacement and phaseshift experiments with night-migrating passerines. – *Ornis Scand.* 1: 27-43.
- Rabøl, J. 1972: Displacement experiments with night-migrating passerines (1970). – *Z. Tierpsychol.* 30: 14-25.
- Rabøl, J. 1975: The orientation of nightmigrating passerines without the directional influence of the starry sky and/or the Earth magnetic field. – *Z. Tierpsychol.* 38: 251-266.
- Rabøl, J. 1978: One-direction orientation versus goal area navigation in migratory birds. – *Oikos* 30: 216-223.
- Rabøl, J. 1979: Magnetic orientation in night migrating passerines. – *Ornis Scand.* 10: 69-75.
- Rabøl, J. 1980: Is bicoordinate navigation included in the inherited programme of the migratory route? – *Proc. 17 Int. Orn. Congr.*: 535-539.
- Rabøl, J. 1981: The orientation of Robins *Erithacus rubecula* after displacement from Denmark to Canary Islands, autumn 1978. – *Ornis Scand.* 12: 89-98.
- Rabøl, J. 1983: Evolution of orientation in migratory birds. – *Ornis Fenn. Suppl.* 3: 17-19.
- Rabøl, J. 1985: The moving goal area and the orientation system of migrant birds. – *Dansk Orn. Foren. Tidsskr.* 79: 29-42.
- Rabøl, J. 1988: Fuglenes træk og orientering – Bogan, Copenhagen.
- Rabøl, J. 1992: Star-navigation in night-migrating passerines. – *Dansk Orn. Foren. Tidsskr.* 86: 177-181.
- Rabøl, J. 1993: The orientation system of longdistance passerine migrants displaced in autumn from Denmark to Kenya. – *Ornis Scand.* 24: 183-196.
- Rabøl, J. in press: Compensatory orientation in Garden Warblers *Sylvia borin* and Redstarts *Phoenicurus phoenicurus* following a geographical displacement. – *Dansk Orn. Foren. Tidsskr.*
- Rüppell, W. 1944: Versuche über Heimfinden ziehender Nebelkrähen nach Verfrachtung. – *J. Orn.* 92: 106-132.
- Sauer, E.F.G. & E.M. Sauer 1960: Star navigation of nocturnal migrating birds. The 1958 planetarium experiment. – *Cold Spring Harb. Symp. Quant. Biol.* 25: 463-473.
- Wallraff, H.G. 1980: Does pigeon homing depend on stimuli perceived during displacement? I. Experiments in Germany. – *J. comp. Physiol.* 139: 193-201.
- Wallraff, H.G. 1990: Navigation by homing pigeons. – *Ethology Ecology & Evolution* 2: 81-115.
- Wallraff, H.G. 1991: Conceptual approaches to avian navigation systems. Pp. 128-165 in: Berthold, P. (ed.): *Orientation in Birds*. – Birkhauser, Basel.
- Wiltschko, W. & R. Wiltschko 1976: Die Bedeutung des Magnetkompasses für die Orientierung der Vögel. – *J. Orn.* 117: 362-387.
- Wiltschko, W. & R. Wiltschko 1988a: Magnetic orientation in birds. – *Current Ornithology* 5: 67-121.
- Wiltschko, W. & R. Wiltschko 1988b: Magnetic versus celestial orientation in migrating birds. – *Trends in Ecology and Evolution* 3: 13-15.
- Wolff, W.J. 1970: Goal orientation versus one-direction orientation in Teal, *Anas c. crecca*, during autumn migration. – *Ardea* 58: 131-141.

Accepted 5 April 1994

Jørgen Rabøl
Department of Population Biology,
Universitetsparken 15,
2100 Copenhagen Ø, Denmark