MIGRATING YOUNG PIED FLYCATCHERS *FICEDULA HYPOLEUCA* DO NOT COMPENSATE FOR GEOGRAPHICAL DISPLACEMENTS

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Summary

The present study tested whether young Scandinavian pied flycatchers, *Ficedula hypoleuca*, would direct their orientation back towards their southwest-directed migratory route in autumn if displaced by the maximal biologically realistic distance due south or due west. The aim was to clarify the nature of their inherited spatiotemporal orientation programme. Forty-eight young pied flycatchers were caught and tested at Christiansø, Denmark. They were then divided into three groups of equal size and orientation, of which one group was displaced due south and another due west, while the third remained as a control at Christiansø. Three different experimenters then simultaneously tested their orientation. The birds oriented in the same direction at all localities, showing no signs of compensatory orientation. This result suggests that young pied flycatchers on their first autumn migration use a simple clock-and-compass strategy to reach their wintering area. If this suggestion holds, then all the prerequisites (a compass and an internal clock) for orientation during the autumn migration seem to be known at present, at least at the behavioural level. In addition, the present study provides further evidence supporting the assumption that observations in an orientation funnel reflect the orientation of actual migration.

Key words: *Ficedula hypoleuca*, pied flycatcher, migration, bird, orientation, navigation, clock-and-compass, funnel experiment, displacement.

Introduction

What are the spatiotemporal orientation programmes (see e.g. Berthold, 1991; Mouritsen, 1998*b*, 1999) and reaction patterns of young night-migrating passerines over the course of their first migratory season? This question has been the subject of controversy, since conflicting results have emerged from both real and simulated displacement experiments. Two alternative hypotheses have been proposed: the clock-and-compass hypothesis and the navigation hypothesis. The clock-and-compass model (a 'vector navigation hypothesis', see Berthold, 1991, pp. 97–99) describes the migratory programme as a series of unrelated migratory steps oriented in an almost constant direction (the compass) under a predetermined time schedule (the circannual clock). The 'coordinate' or goal area navigation hypothesis (see Rabøl, 1969, 1978, 1994) suggests that the orientation programme of night-migrating passerines is a navigational process in which the birds continuously orient towards a moving goal area or the wintering area. For more detailed descriptions of these hypotheses, see Rabøl (1978), Berthold (1991) and Mouritsen (1998*b*, 1999).

Perdeck's (1958) impressive displacement experiment using European starlings *Sturnus vulgaris* is the classic textbook experiment, which provides convincing evidence that young European starlings use a simple clock-and-compass strategy, whereas adult European starlings seem to have acquired navigational abilities through associative learning and experience. Can Perdeck's (1958) conclusions be generalised to all types of birds, including night-migrating passerines? European starlings migrate relatively short distances during the day and, most importantly, they migrate in large flocks. This means that all a young European starling theoretically needs to do on its first migration is to stick close to its parents or other adults and learn where to go *en route*. In comparison, young night-migrating passerines have to migrate much longer distances at night and, most importantly, they do so alone without guidance from adults. Therefore, selection may have forced them to use a more sophisticated orientation mechanism. Consequently, Perdeck's (1958) demonstration that young European starlings use a simple clock-and-compass mechanism cannot be generalised to night-migrating passerines (or any other type of birds) until experiments on such birds have confirmed its probable use.

Rabøl (1969, 1978) proposed that the directions of birds recorded in orientation funnels following a geographical displacement could reveal the nature of the inherited orientation programme (in reality, such results reveal only the compass/directional component of such a programme) of

night-migrating passerines on their first migration. If the birds were to compensate for geographical displacements (i.e. turn towards their normal migratory route), some kind of 'coordinate' navigation directed towards a goal area somewhere (normally ahead) on the original migration route would be suggested, whereas a 'clock-and-compass' programme (see Berthold, 1991; Mouritsen, 1998b) would be suggested if the birds failed to compensate.

The general pattern emerging from several displacement studies is one of directional shifts towards the migration route in accordance with compensatory orientation – especially in the case of long-distance migrants displaced by less than 9° (geographically) in autumn under test conditions of a starry sky (Rabøl, 1969, 1970, 1972, 1975, 1994, 1995). However, other displacement studies have revealed no compensatory orientation (e.g. Rabøl, 1970, 1975, 1981, 1993), and the only study in the literature testing birds that were, without question, naturally displaced by wind (blackcaps, *Sylvia atricapilla*, tested on the Faeroe Isles) also found no compensatory reactions (Rabøl, 1985).

Some simulated displacements under the autumn starry sky of a planetarium have resulted in directional shifts, suggesting compensatory orientation (Rabøl, 1992; J. Rabøl, unpublished data). Emlen (1967), in contrast, found no compensation in similar planetarium experiments with indigo buntings *Passerina cyanea* performed in spring. The same result was obtained in clock-shifted redstarts *Phoenicurus phoenicurus* and garden warblers *Sylvia borin* observed in autumn (Rabøl, 1970).

Mouritsen (1998b) approached the basic question of compensation *versus* no compensation from a different angle. He performed a computer simulation of migration assuming that the birds utilised the compass component of the clock-and-compass mechanism in the simplest possible way. The calculated directional concentration as a function of distance correlated strongly with the actual concentration of ringing recoveries of pied flycatchers ringed in Scandinavia and recovered the same autumn. This strong correlation suggests that young pied flycatchers do not need compensatory abilities. However, the result does not exclude the possibility that young pied flycatchers may compensate if they make very large mistakes or drift very far. Still, the results strongly suggest that the vast majority of the pied flycatchers do not compensate during their first autumn migration (i.e. if compensatory abilities exist, then the vast majority of the birds did not make mistakes large enough or drift far enough to trigger such a system).

The aim of the present study was to displace young pied flycatchers caught in Scandinavia to investigate whether they show compensatory orientation on their first migration when displaced by approximately the maximum biologically realistic distance (based on indications from ringing recoveries). The results of such displacement experiments may suggest whether young night-migrating passerines are equipped with both compasses and a map or with compasses alone and can be compared directly with the predictions of Mouritsen (1998b). Second, the present study aimed at collecting further evidence as to whether the patterns observed in an orientation funnel reflect what the bird would do if it were actually migrating.

The study was designed to maximise changes of direction if compensatory orientation existed and to control for local variations. This was achieved by displacing birds symmetrically from a population of southwest-migrating pied flycatchers towards the west and the south and measuring their orientation relative to a control group that remained at the site of capture. If they showed non-compensatory behaviour, the birds would choose the same migration direction at all three sites. If they showed compensatory behaviour, however, the birds displaced to the west and to the south should show the same (large) change in direction towards the normal migration route while birds kept at the site of capture should keep their original southwest orientation.

Materials and methods

Experimental birds

Forty-eight first calendar year pied flycatchers *Ficedula hypoleuca* caught in mistnets during migration at Christiansø Bird Observatory (55°19′N, 15°12′E), off Bornholm, Denmark, were used for the experiments. At the site of capture, they were kept outdoors in small circular plastic cages (top diameter 44 cm, bottom diameter 29 cm, height 30 cm) in the natural magnetic field with food (mealworms) and water *ad libitum*. At noon and during some nights, the cages were placed in a large tent. Every evening from approximately 1 h before to 2 h after sunset, the birds were placed in their cages on a hill, which provided them with an open view of the sky and sunset. This facilitated a potentially important transfer of directional information from sunset cues to the magnetic compass and/or the star compass (see Fig. 10 in Wiltschko and Wiltschko, 1991).

To maximise the numbers of migration-motivated birds, the pied flycatchers were caught when large numbers of migrating birds were grounded. Large numbers of grounded birds are thought to represent 'emergency landings' of actively migrating birds. In addition, a group of birds caught on the same day usually shows more homogeneous orientation behaviour than a group of birds caught over several days or weeks. The birds used for experiments had a fat index (on a scale of 0–8, according to Kaiser, 1993) of 4 (the intestine invisible owing to fat coverage) or greater except for a few birds, which had a fat index of 3 (the intestine just visible through the fat). On the day of capture, however, the birds had fat indices between 1 and 5. Fat birds were used in experiments to avoid reverse orientation (Sandberg *et al.* 1988; Sandberg, 1994; Åkesson *et al.* 1996; Sandberg and Moore, 1996).

Forty-nine individuals were caught on 27 August 1997. Because four of these birds escaped, three birds caught 5 days previously were also used. These 48 individuals were tested in orientation funnels on 27 August at Christiansø. On 28 August, they were separated into three matched groups of 16 birds. The groups were matched such that the sample mean vectors of the

orientations of the three groups on 27 August were as similar as possible. The birds were allowed to see the sunset and the stars on the evening of 28 August.

On 29 August, one group was transferred by car and aeroplane in dark paper boxes to Klelund Plantation (55°35′N, 8°54′E), South Central Jutland west of Christiansø. The birds were kept outdoors in cages identical to those used by Mouritsen (1998a) in the natural magnetic field with food (mealworms) and water *ad libitum*. The cages enabled the birds to see the sky and sunset. This group was tested in orientation funnels under overcast conditions on 30 August and under starry conditions on 31 August and 1 September. Release experiments were performed under completely calm (wind speed $0.3\,\mathrm{m\,s^{-1}}$ measured 2.5 m above ground level with a wind probe; Testo, type 452) and starry conditions on 1 September.

The second group of birds was transferred to Pec in the Czech Republic (50°19′N, 15°34′E) by aeroplane and car in dark paper boxes on 29 August. They were kept in a car (with windows) in small circular plastic cages, identical to those used on Christiansø, in the natural magnetic field with food (mealworms) and water *ad libitum*. In the evening, from approximately 1 h before to 2 h after sunset, the birds were provided with an open view of the sky and sunset. This group was tested in orientation funnels under starry conditions on 31 August and 1 September. Veterinary restrictions prohibited release experiments, and the birds were returned to Denmark for release.

The third group of 16 birds was retained at Christiansø as a control. This group was tested in orientation funnels under starry conditions on 30 and 31 August. Release experiments were carried out on 1 September under starry conditions, but with a light wind from the southeast (135°, wind speed 4.8–$5.2\,\mathrm{m\,s^{-1}}$ measured 10 m above ground level at the local weather station).

Experimental sites

The orientation funnel experiments at Christiansø were carried out on the eastern side of the island on a broad path. A stone wall screened direct light from a lighthouse, which was situated northwest of the experimental site, but the beam was clearly visible passing overhead. To the east was the shoreline. The release experiments were carried out from the highest hill on the island.

At Klelund Plantation, the funnel experiments were performed in a large forest clearing (approximately 300 m×400 m). The surrounding forest shielded all artificial light sources on the ground by effectively raising the horizon by 5–10°. The birds were released from an open field 1.7 km north of the forest clearing.

In the Czech Republic, the funnel experiments were carried out at two neighbouring sites. A site near Holovousy was used on 31 August. This village is situated a few hundred metres to the south of the experimental site, and some street lights from the village were visible low on the horizon. Towards the southeast or south-southeast, the town of Hradec-Kralove

produced an obvious strip of artificial light. Towards the north was the edge of a forest, which effectively raised the horizon by 5–10°. Under perfectly starry conditions, the artificial light sources should have been barely visible from the funnels (the visual range is approximately 160° upwards), but during approximately 30 min of the experimental time, a diffuse cloud towards the southeast constituted a clearly lighter portion of the sky. To exclude the effects of phototactic responses, the 1 September experiments were carried out in the hills south of Pec. At this site, very few artificial light sources were visible and the only artificial light that could have been visible from the funnels was a very weak glow towards northeast to northwest.

Equipment

Modified Emlen funnels (Emlen and Emlen, 1966) identical to those used by Mouritsen (1998a) and similar to those used by Rabøl (1979, 1992) and Åkesson (1993, 1994) were used. Emlen funnels are circular orientation cages (top diameter 300 mm, bottom diameter 130 mm, slope 45°) with the top opening covered by a fine-meshed plastic net, allowing the birds to see the sky. The directionality of the birds' activity was recorded as scratches in the pigment of typewriter correction paper (first used by Rabøl, 1979) glued to the inclined walls of the funnels. The entire wall of the funnels was covered with typewriter correction paper (see Åkesson, 1993; Mouritsen, 1998a).

To make the experimental condition 'overcast' as constant as possible, an overcast sky was simulated by covering the funnels with translucent plastic sheets (a detailed description can be found in Mouritsen, 1998a), even when the sky seemed totally overcast.

Test procedure

Prior to experiments, the test birds were allowed to view the sunset and the appearance of the first stars. Approximately 2 h after sunset, each experimental bird was transferred from its cage to a numbered textile bag or plastic bucket. When it was completely dark, i.e. when the glow from the setting sun had vanished and the stars were the only visible celestial cue, the birds were transported to the experimental site and transferred to the funnels. The experiments lasted for 1.5–2 h, commencing 3–4 h after sunset. The experimenters left the experimental site as fast and quietly as possible after the experiments had been initiated.

After the last funnel experiments, the Klelund and Christiansø birds were released with small light capsules glued to their tails using the method described by Mouritsen (1998a; see also Ottosson *et al.* 1990). Briefly, the birds were handled and released individually at intervals of 7–10 min. A Cyalume lightstick 2.9 mm×24 mm (type yellow 95281-16, mass 0.14 g) was attached to the two central tail feathers using Scotch tape. Since the mass of the lightstick is only approximately 1 % of the body mass of the bird, this procedure does not harm the birds or impair their flight (Kenward, 1987). All light was switched off and the bird to be released was

allowed to see the sky for approximately 30 s before being thrown vertically into the air. The bird was then tracked through a pair of binoculars (Leica 10×42) for as long as possible, and the vanishing bearing was noted to the nearest 5 ° using a conventional compass (Saura HB-65G). If the bird landed or flew very close to ground, the vanishing bearing was not regarded as being related to the migratory direction and was therefore excluded.

Data analysis and statistics

In the funnel experiments, the mean direction was estimated visually to the nearest 5 ° while the correction paper was still glued to the funnel walls. This visual estimation, although subjective, is very easy and accurate. Several preliminary tests were performed (H. Mouritsen and O. N. Larsen, unpublished observations) in which both experienced and inexperienced scientists visually estimated the mean directions of the same correction papers. Estimates by experienced and inexperienced observers differed by ±5 °, with deviations of more than 10 ° occurring very rarely (<10 %). The result of a given experiment was included only if at least 30 scratches were visible on the funnel paper and an easily identifiable and unimodal mean direction was apparent. This ensured that disoriented and unreliable orientation results were excluded (7 out of 48 recordings were excluded on the day of capture and only 3 out of 112 recordings during the following days as a result of these exclusion rules).

The mean direction of each bird that satisfied the exclusion rules was depicted as a single dot in Fig. 1. From the mean directions of each individual, a sample mean direction α and vector length $\mathbf{r}$ were calculated using vector addition (Batschelet, 1981).

The graphical representations and calculations of the circular data were made using a custom-designed computer program. Differences in mean direction between experimental groups were analysed using the Watson–Williams test (Batschelet, 1981). If $\mathbf{r}$ was smaller than 0.75 for one of the samples involved, confidence intervals were calculated instead. Results for which $P \geqslant 0.05$ were regarded as non-significant.

Analysis of ringing recovery data

To estimate the normal migratory direction, all same-autumn ringing recoveries of pied flycatchers ringed in Scandinavia (Finland, Norway, Sweden and Denmark) and recovered within Europe or North Africa until 1996 were analysed (N=1138). A 'same-autumn recovery' was defined as a bird ringed after 14 June (birds ringed as nestlings between 1 and 14 June were also included) and recovered before 1 March the following year. For each recovery, we calculated the direction between the ringing and the recovery sites using the formulae describing loxodrome routes (loxodrome routes are described by constant compass courses; see also H. Mouritsen, unpublished results and manuscript in preparation). Finally, the mean direction of all the recoveries was calculated.

Results

The pied flycatchers oriented in the same direction at all three localities and showed no sign of compensation for the displacements. The main results are summarised in Fig. 1.

On the day of capture and under starry conditions, the 48 pied flycatchers oriented significantly in a southwesterly direction (Fig. 1F, Rayleigh test, α=221 °, $\mathbf{r}$=0.31, N=39, P<0.05), which coincides well with the normal migratory direction. The latter direction was estimated from an analysis of all same-autumn recoveries of pied flycatchers from Scandinavia, which showed a mean direction of 212±19 ° (mean ± S.D.; 95 % confidence interval 211–213 °; N=1138). The 16 control birds on Christiansø showed a highly significant orientation towards south-southwest on both 30 and 31 August under starry conditions (Fig. 1E,G; Rayleigh test; 30 August, α=200 °, $\mathbf{r}$=0.85, N=16, P<0.001; 31 August, α=188 °, $\mathbf{r}$=0.84, N=15, P<0.001).

The 16 birds displaced to Klelund Plantation showed a significant orientation towards south-southwest on both 31 August and 1 September under starry conditions (Fig. 1B,C; Rayleigh test; 31 August, α=214 °, $\mathbf{r}$=0.52, N=15, P<0.02; 1 September, α=199 °, $\mathbf{r}$=0.63, N=16, P<0.01). On 30 August, the Klelund birds also showed a significant orientation towards southwest when tested under simulated overcast (Fig. 1A; Rayleigh test; α=222 °, $\mathbf{r}$=0.49, N=15, P<0.05). The 16 birds displaced to the Czech Republic showed a significant orientation towards the south on both 31 August and 1 September under starry conditions (Fig. 1H,I; Rayleigh test; 31 August, α=170 °, $\mathbf{r}$=0.82, N=16, P<0.001; 1 September, α=183 °, $\mathbf{r}$=0.73, N=16, P<0.002).

The mean directions of birds displaced to Klelund or the Czech Republic did not differ significantly from each other in any case (Fig. 2; all 95 % confidence intervals overlap; Christiansø, 221±100 ° (day of capture), 200±18 ° and 188±18 °; Klelund, 222±47 °, 214±43 ° and 199±30 °; the Czech Republic, 170±20 ° and 183±24 °, respectively). A slight tendency towards more southerly headings over time was observed.

The birds released at Klelund on the very calm (wind speed <0.5 m s^{-1}) and starry night (Fig. 1D) migrated in a clear southwesterly direction (Rayleigh test; α=223 °, $\mathbf{r}$=0.61, N=13, P<0.01). This direction coincided well with, and was not significantly different from, the direction indicated by the birds in the orientation funnels during the same night (compare Fig. 1D with Fig. 1C; 95 % confidence intervals overlap: release, 223±37 °, N=13; funnel, 199±30 °, N=16). During the release experiments, the same behavioural pattern as described by Mouritsen (1998a) was observed. Thirteen birds showed the typical migratory departure behaviour, two showed landing behaviour and one lost its lightstick when released. A direct comparison at the individual level (Fig. 3) showed that the vanishing bearings under completely calm conditions (see Fig. 1D) and the directions shown in prior orientation funnel experiments on the same night under starry skies in the natural magnetic field (see Fig. 1C) did not differ significantly from each other
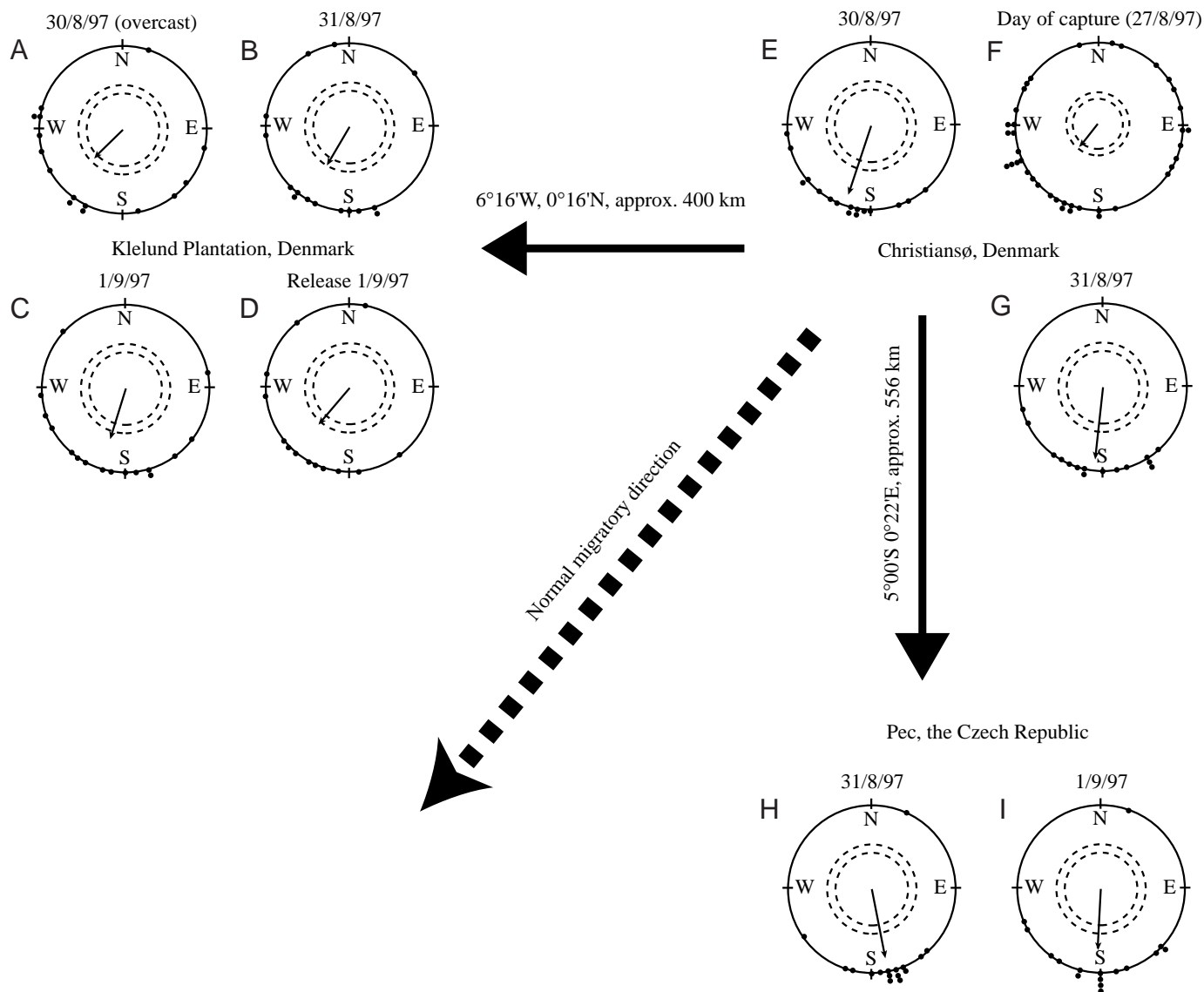
Fig. 1. Results of funnel (A–C, E–I) and release (D) experiments with first-year pied flycatchers during the autumn migration before and after displacement from the site of capture at Christiansø, Denmark. The dots at the edges of the circles indicate the mean orientation of migratory restlessness in orientation funnels or the vanishing bearings (release experiments) exhibited by the individuals that passed the exclusion rules. The sample mean vector is depicted as an arrow originating from the centre of the circle. The length of the sample mean vector is proportional to the angular concentration. The inner and outer dashed circles indicate radii with significance levels of $P=0.05$ and $P=0.01$, respectively, according to the Rayleigh test (Batschelet, 1981). The large bold arrows show the directions of the displacements (actual direction and distance are also shown). The bold dashed arrow indicates the normal migratory direction of Scandinavian pied flycatchers. Release experiments from Christiansø were strongly affected by the prevailing wind and are not shown.

(95 % confidence interval: expected direction $0°$, mean direction $37±39°$; $N=13$).

The birds released at Christiansø in light southeasterly wind ($135°$, wind speed $5\,\mathrm{m\,s^{-1}}$) migrated in a highly significant westerly direction (results not shown; Rayleigh test; $\alpha=270°$, $r=0.94$, $N=14$, $P<0.001$), i.e. between the wind direction and the normal migration direction. The vanishing bearings consequently differed significantly from the orientations shown by the same birds in the funnels (Watson–Williams test: 30 September, $F_{1,28}=40.47$, $P<0.001$; 31 September,

$F_{1,27}=51.85$, $P<0.001$). Fourteen of the experimental birds showed the typical departure behaviour and two birds showed landing behaviour.

Discussion

Correlation between orientation in funnels and migratory direction

Orientation funnels are widely used in studies of bird migration. Therefore, it is important to evaluate the validity of

the critical assumption that the directional preference we observe in an orientation funnel reflects the directional preference of the bird if it had actually been migrating. Unfortunately, this has not been tested routinely in the past. Support for this assumption was provided by Ottosson *et al.* (1990) for wheatears *Oenanthe oenanthe* caught and tested in Scandinavia in autumn but not for wheatears caught and tested in Greenland in autumn. Able (1990), in his study on white-throated sparrows *Zonotrichia albicollis* tested in spring, also found no clear support for the assumption. In contrast, Sandberg and Moore (1996) studying red-eyed vireos *Vireo olivaceus* found a close correlation between the vanishing bearings of released birds and the results of funnel directionality in autumn and also a fairly good correlation in spring. However, different individuals were used for funnel and release experiments. Finally, Mouritsen (1998*a*) found a clear correlation between funnel directionality and vanishing bearings of the same individual redstarts *Phoenicurus phoenicurus* tested in autumn.

In the studies of Able (1990), Ottosson *et al.* (1990) and Sandberg and Moore (1996), funnel experiments were performed around sunset, and the birds could potentially see the sunset and/or polarised light patterns from the sun, while the stars were invisible. As in almost all other sunset experiments, the funnel orientations observed in these studies seem to have been influenced by positive phototaxis towards the setting sun. In contrast, by the time that the birds were released after the funnel experiments, the glow from the setting

Fig. 3. Comparisons between vanishing bearings and orientation funnel experiments on the same night under starry skies in the natural magnetic field. The directions did not differ significantly from each other (95 % confidence interval: expected direction 0°; mean direction 37±39°; N=13, P>0.05). A dot in the north of this figure indicates that the mean direction recorded in the orientation funnel (see Fig. 1C) was identical to the vanishing bearing under completely calm conditions (see Fig. 1D). The dashed line indicates the expected mean direction on the assumption that the directional preference shown in an orientation funnel reflects the actual migratory directional preference of the bird. See Fig. 1 for further details.
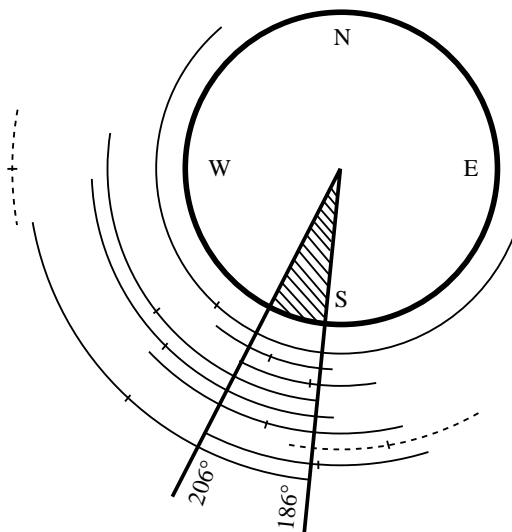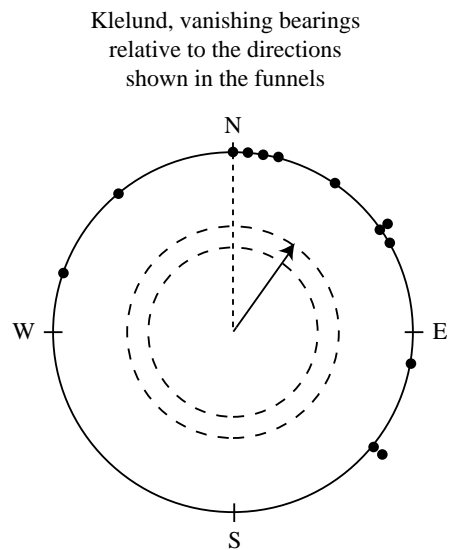

Fig. 2. Graphical representation of the 95 % confidence intervals for all mean directions. All 95 % confidence intervals overlap the interval 186–206° except for the 31 August experiment in the Czech Republic, which may have been affected by phototactic responses, and the releases on Christiansø, which were strongly affected by wind. The confidence intervals of the latter two experiments are shown as broken lines. From the inside out, the confidence intervals are for the experimental groups depicted in Fig. 1F, Fig. 1E, Fig. 1G, Fig. 1A, Fig. 1B, Fig. 1C, Fig. 1H, Fig. 1I, Fig. 1D, Fig. 1E and (outermost) the wind-biased release on Christiansø, respectively.

sun had vanished and the stars were the only celestial cue. This experimental design may have reduced the correlation between funnel orientation and vanishing bearing after release. Only in the present study and in that of Mouritsen (1998*a*) were both funnel and release experiments performed on the same individuals in the dark under starry skies, and both studies support the assumption.

When discussing the validity of orientation experiments in funnels, it is important to realise that comparisons between funnel orientation and bearings derived from long-distance ringing recoveries are not appropriate as rigorous tests of correlation between funnel orientation and actual migration. The reason for this is that orientation on the small geographical scale of funnel experiments is not necessarily the same as that on the large geographical scale of ringing recoveries. The directional concentration on a large geographical scale is necessarily much greater than that on a small geographical scale, irrespective of the orientation mechanism (clock-and-compass or navigation) used, as can be predicted mathematically (Rabøl, 1978; Mouritsen, 1998*b*). The same reasoning has been used by Wallraff (1978) in his discussion of the possible effects of flocking on orientation. Detailed studies of short-distance (approximately 50–150 km) ringing recoveries, however, could be used to test the correlation between funnel orientation and actual migration direction.

Unfortunately, a sufficient number (more than 20) of such recoveries probably only exists for few, if any, localities.

Wind effects

A strong wind effect was observed when birds were released on Christiansø in a light wind (5.0±0.5 m s^{-1}; mean ± S.D.) from the southeast (135°). The birds showed a westerly orientation (270±20°), i.e. a compromise direction between that of the wind vector (315°) and the funnel direction (188±32°) of the same individuals (Fig. 1G). This suggests that the migratory direction of pied flycatchers, and probably of small passerines in general, is strongly affected by even low wind velocities. Observations of the behaviour of the birds after their release support this suggestion. The pied flycatchers typically climbed steeply, as under calm conditions, but soon started circling or hovering. First, they tried to fly in the usual south-southwesterly migratory direction, but they progressed very slowly. They soon appeared to give up and changed to a westerly course, climbing slowly but steadily. This behaviour and compromise course for pied flycatchers in the present study are almost identical to those observed previously in redstarts (Mouritsen, 1998*a*).

Orientation

The present study shows that two groups of displaced young pied flycatchers oriented in the same direction as controls remaining at the site of capture. Had the birds compensated for displacement, both groups would have made similar but opposite changes in orientation, both directed towards the normal migratory route. However, even small non-significant tendencies in the directional preferences of the displaced groups actually pointed away from the normal migratory route.

In the present study, all orientations (except for the light-biased experiment in the Czech Republic on 31 August) are judged to be equal, because they do not deviate significantly from the interval 186–206° (Fig. 2, overlap zone for all 95% confidence intervals). A migratory direction between 186° and 206° is slightly more southerly than expected from the ringing recoveries (212°). In comparison, a mean migratory direction of 203° was found in an analysis of all European autumn-banding recoveries north of the Sahara of garden warblers *Sylvia borin*, which have a migration route similar to that of pied flycatchers (Klein *et al.* 1973). A possible explanation is that Scandinavian pied flycatchers tend to start out on a southerly course before turning southwest somewhere south of Denmark. Ringing data (Rabøl, 1969, 1995; Mouritsen, 1998*b*, unpublished results) support this suggestion. The autumn route of pied flycatchers migrating from Scandinavia may therefore include three legs rather than the two suggested for birds from other parts of Europe (southwest to southern Spain and then south (or south-southeast) through Africa; see e.g. Gwinner and Wiltschko, 1978).

It may seem peculiar that the orientation of 48 pied flycatchers on the day of capture is much more scattered than that shown by the same birds on all following test nights regardless of location. The sample mean vector based on 48

birds barely reaches the 5% significance level (Fig. 1F), whereas those of the test groups are highly significant, despite each one being based on only 16 samples (Fig. 1A–E,G,I). This phenomenon, however, is commonly observed in newly caught birds (Muheim, 1996; H. Mouritsen, unpublished data). Usually, on the first day or two after capture, their activity is rather low and their orientation rather scattered. After 2-3 days with food and water *ad libitum*, they increase their activity and seem to fix their orientation. Probably, their motivation to continue migration is low on the day of capture (they would rather settle to forage for a day or two) but after 2–3 days it increases to a relatively constant level. Consequently, experimenters should avoid using data from wild-caught birds during the first couple of days after capture.

Unchanged orientations following displacements were to be expected if the test birds used simple compass orientation only. This result is in accordance with predictions from a modelling study of autumn-migrating young Scandinavian pied flycatchers (Mouritsen, 1998*b*) and with the results of several displacement studies. However, it contrasts with the findings of other studies. A short review of the previous literature on night-migrating passerines in support of and in contradiction to the clock-and-compass and navigation hypotheses is given by Mouritsen (1999). In addition, three simulated displacements performed in planetariums should be considered. Emlen (1967) supported the clock-and-compass hypothesis, whereas Rabøl (1992, unpublished results) suggested that navigational responses were more important. However, planetarium experiments often involve simulated displacements much larger than the 5° (geographically) of the present study (Emlen, 1967; Rabøl, 1992, unpublished results). One possibility is that birds compensate only for geographical displacements larger than 5°. However, birds are not likely to make directional mistakes that result in deviations of 45° or more from their normal migratory direction at distances of 500 km (corresponding to approximately 5° geographically) (Mouritsen, 1998*b*; Fig. 2). Therefore, a navigational system that comes into operation only if the mistakes exceed 10 or 15° (geographically) would have little if any biological significance. Catching birds at Christiansø and dividing them into four equal groups, of which three were displaced for orientation experiments to, for instance, Klelund in Jutland (+5°), Newcastle in England (+15°) and Londonderry in Northern Ireland (+20°), could probably test this hypothesis.

If the finding that young pied flycatchers do not use navigational abilities during migration can be generalised to all night-migrating passerines, then a coherent description of the first autumn migration of young night-migrating passerines seems possible: in autumn, these birds set out on their journey equipped with a genetically encoded compass, a time schedule and a couple of emergency plans only (see Mouritsen, 1999). At present, we know that night-migrating passerines have an inherent time schedule (for a review, see Gwinner, 1996) and that they possess at least two compasses (e.g. Wiltschko and Wiltschko, 1991, 1996; Mouritsen, 1998*a*), a magnetic compass and a celestial compass. An elusive map sense and/or

any presently unknown east–west navigational cue are not required (see Wiltschko and Wiltschko, 1996). In conclusion, the present study supports the clock-and-compass hypothesis.

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