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Orientation in pied flycatchers: the relative importance of magnetic and visual information at dusk

SUSANNE ÅKESSON* & JOHAN BÄCKMANT†

*†Department of Animal Ecology, Lund University

†Department of Zoology, Zürich University, Switzerland

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We investigated the orientation of juvenile pied flycatchers, *Ficedula hypoleuca*, during autumn migration in south Sweden using orientation cage experiments, to study the relative importance of visual and magnetic information at sunset. We performed cage tests under 12 experimental conditions that manipulated the geomagnetic and visual sunset cues available for orientation: natural clear skies in the local or a vertical magnetic field; simulated total overcast in the local or a vertical magnetic field; natural pattern of skylight polarization and directional information from stars screened off, with the sun's position as normal or shifted 120° anticlockwise with mirrors; reduced polarization in the local or a vertical magnetic field; directions of polarization (e-vector) NE/SW and NW/SE, respectively, in the local or a vertical magnetic field. The pied flycatchers were significantly oriented towards slightly south of west when they could use a combination of skylight and geomagnetic cues. The mean orientation was significantly shifted along with the deflection of the sunset position by mirrors. Reduced polarization had no significant effect on orientation either in the local, or in a vertical, magnetic field. The birds tended to orient parallel with the axis of polarization, but only when the artificial e-vector was aligned NW/SE. The mean orientation under simulated total overcast in a vertical, and in the local, magnetic field was not significantly different from random. It is difficult to rank either cue as dominant over the other and we conclude that both visual and magnetic cues seem to be important for the birds' orientation when caught and tested during active migration.

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Nocturnal passerine migrants depart on migration flights mostly during or shortly after sunset (reviewed by Moore 1987). However, the time of departure probably differs between species, latitude and time of season (Åkesson et al. 1996a). Nocturnal passerine migrants possess at least two different compass systems for orientation based on the geomagnetic field and celestial cues (stars, sun and the related pattern of skylight polarization; for reviews see, for example, Emlen 1975; Able 1980; Moore 1987; Wiltschko & Wiltschko 1995). During twilight, visual information from the sun, the skylight polarization pattern and, later on, the stars become particularly prominent (cf. Figure 1 in Åkesson et al. 1996a). The pattern of partially linearly polarized skylight arises from the scattering of light within the earth's atmosphere. The directions of polarization (e-vector directions) form a regular pattern across the entire celestial hemisphere, with a symmetry plane at the solar and antisolar

meridian (cf. Brines 1980; Brines & Gould 1982; Wehner 1989). At sunset, as much as 70–80% of the incoming overhead light is linearly polarized (Rozenberg 1966). Nocturnal passerine migrants departing during twilight tend to make use of visual sunset cues for orientation (e.g. Bingman & Able 1979; Moore 1987; Able 1989; Helbig & Wiltschko 1989; Helbig 1990, 1991; Sandberg 1991; Phillips & Moore 1992). However, it is not completely understood how visual cues at sunset are related to geomagnetic information for orientation.

Several research methods have been applied to study the birds' orientation at dusk: (1) shifting the position of the setting sun by mirrors (Moore 1982; Sandberg 1991); (2) deflecting the e-vector axis or reducing the degree of skylight polarization by filters (Able 1982; Moore 1986; Helbig & Wiltschko 1989; Helbig 1991); (3) clock shifting the birds' internal clock relative to the natural photoperiod (Moore 1980; Able & Cherry 1986; Helbig 1991); and (4) deflecting geomagnetic north clockwise or anticlockwise relative to geographical north with magnetic coils (e.g. Wiltschko & Wiltschko 1975a, b; Sandberg et al. 1988a, 1991; Åkesson 1994 and references

Correspondence and present address: S. Åkesson, Department of Animal Ecology, Lund University, Ecology Building, SE-223 62 Lund, Sweden (email: susanne.akesson@zoekol.lu.se).

Table 1. Number of young pied flycatchers captured at Falsterbo Bird Observatory and tested in orientation cage experiments in south Sweden under different visual and magnetic conditions in autumn

Experimental condition					
Visual	Magnetic	Inactive	Disoriented	Included	Total
Natural clear skies*	Local	0	0	67	67
Natural clear skies*	Vertical	0	2	49	51
Simulated total overcast*	Local	7	6	39	52
Simulated total overcast*	Vertical	2	10	34	46
SS control	Local	0	2	23	25
SS shifted 120° ACW	Local	2	2	21	25
Depolarization	Local	2	3	35	40
Depolarization	Vertical	0	2	15	17
e-vector NE/SW	Local	0	0	18	18
e-vector NE/SW	Vertical	0	0	4	4
e-vector NW/SE	Local	0	0	15	15
e-vector NW/SE	Vertical	0	0	11	11
		13 (3.5%)	27 (7.3%)	331 (89.2%)	371 (100%)

For details of experimental conditions see Methods and Table 2.

*Experiments conducted partly with the same birds as presented in Åkesson (1994).

given therein). The majority of these studies have shown the primary importance of visual cues while others have shown a dominance of magnetic over visual cues (Wiltschko & Wiltschko 1975a, b; Bingman & Wiltschko 1988; Munro & Wiltschko 1995), or failed to show responses to manipulations of the axis of skylight polarization pattern at twilight (Sandberg 1988). The variable responses to visual and magnetic cue manipulations observed in these studies suggest differences between species in their responses to the experimental treatments (cf. Helbig 1990; but see also Åkesson 1994), and that the test procedure, repeated tests versus single tests with individual birds, might affect the birds' responses (cf. Wiltschko et al. 1997) or that the birds' migratory experience prior to the test might influence orientation (Sandberg 1994; Åkesson 1993; Bäckman et al. 1997).

In this study we carried out experiments with autumn-migrating, young pied flycatchers, *Ficedula hypoleuca*, in order to investigate the relative importance of geomagnetic and visual sunset cues (i.e. sun position and skylight polarization pattern) for orientation at dusk. We conducted circular orientation cage experiments under 12 experimental conditions with natural and manipulated visual cues by: (1) screening off visual cues by opaque Plexiglas sheets; (2) shifting the sun's position 120° anticlockwise by mirrors; (3) decreasing the degree of polarization by using pseudodepolarizers; and (4) deflecting the axis of the e-vector of polarized skylight (+45° and -45°). The experiments under natural clear skies and under filters manipulating the skylight polarization pattern were performed in the local geomagnetic field as well as in a vertical magnetic field (details are given below). Our aim was to restrict the birds to a limited set of cues and to put different cues in conflict in order to find out which ones birds predominantly use for orientation at sunset during their first migration.

METHODS

Study Site and Experimental Birds

Juvenile pied flycatchers, aged according to Svensson (1984), were captured during the autumn migration period at a stopover site in southern Sweden (Falsterbo Bird Observatory, 55°23'N, 12°50'E) during 1990–1993, 1995 and 1996. We performed the following numbers of experiments: 1990: 60; 1991: 5; 1992: 157; 1993: 22; 1995: 29; 1996: 58 (Table 1). We transported the experimental birds by car to the experimental site at Stensoffa Ecological Field Station (55°42'N, 13°25'E), ca. 55 km northeast of Falsterbo Bird Observatory. At the test site we housed the birds indoors in a room with windows, under the natural photoperiod and local geomagnetic conditions (total intensity of approximately 49 000 nT and angle of inclination +70°; measured by a fluxgate magnetometer). The birds were kept individually in spacious cages (350 × 350 × 450 mm), with unlimited water with vitamins and food (mealworms). Each bird was held in captivity for between 10 and 25 days and was tested only once in each of the experimental conditions. Out of a sample of 55 pied flycatchers for which mass was measured during captivity all birds remained healthy and increased in weight (mean mass increase 2.8 g, range 0.4–8.9 g, mean mass at capture 12.9 g). Therefore, the enforced delay in migration most probably had negligible adverse effects on the birds. After the experiments were finished the birds were released at Stensoffa Ecological Field Station. Permission to conduct orientation cage experiments with passerine birds was given by the Regional Ethical Committee for Animal Experiments, the Ministry of Agriculture and the Swedish Environmental Protection Agency.

Experimental Equipment and Treatments

We used two similar types of circular orientation cages (modified Emlen cages; Emlen & Emlen 1966), with a top

diameter of 300 mm (310 mm) and an inner height of 150 mm (125 mm), allowing the birds to see approximately 160° of the sky above. The orientation cages were all constructed in nonmagnetic materials and the tops of the cages were covered with fine-mesh plastic net allowing the birds to see the natural sky. In the first type of cage the activity of the birds was registered from their claw marks in the pigment of typewriter correction paper (Tipp-Ex) which was attached to the sloping walls (see e.g. Rabøl 1979). After the experiment, the paper was subdivided into 24 sectors and the claw marks across a selected line above the cage floor were counted in each sector. In addition we used a second type of cage with automatic registration. In these cages the sloping walls were subdivided into eight 45° sectors, under each of which a microswitch was placed and connected to a counter or a computer. When the bird jumped on the sectors it closed the microswitch and the jump was recorded by the specific counter or the computer. Later we calculated individual mean vectors on the basis of the registrations in either the 24 or eight sectors (Batschelet 1981). We found no difference in the birds' orientation that could be explained by the cage type (cf. Åkesson 1994), and therefore the data sets were pooled.

In tests performed under clear sky conditions, the birds could see the natural sky from the zenith down to approximately 10° above the horizon. We simulated total overcast conditions by placing opaque diffusing Plexiglas sheets (3 mm) on top of the circular cages under clear or partly cloudy skies (0–7/8). Under natural total overcast (8/8) the birds were exposed to the natural overcast skies instead.

We used an experimental set-up with mirrors to deflect the visual cues in the lower part of the sunset sky about 120° anticlockwise. The circular orientation cage was placed inside a circular plastic tube (500 mm diameter, 400 mm height). Four symmetrically arranged windows (200 × 240 mm, permitting a view of the lower part of the sunset sky between ca. 10° and 45° above the horizon) allowed the birds a view towards the cardinal compass directions. On top of the circular plastic tube a sheet of 3-mm opaque diffusing Plexiglas was arranged preventing visibility of directional cues from the sky above (for details on set-up see Sandberg 1991). Control birds were allowed an unmanipulated view of the sunset sky through the windows. In the experimental condition we attached mirrors (back-coated glass, 250 × 300 mm) to each of the four windows, thereby deflecting the visual cues above the horizon about 120° to the left of their normal position.

To manipulate the degree of polarization, we used a double layer of a commercially available pseudodepolarizer (Hostaphan polyethylene terephthalate; Hoechst AG, Wiesbaden, Germany) to cover the top of the orientation cages. Two sheets of Hostaphan (each 0.18 mm thick) were taped together with their fast axes positioned 45° relative to each other (for details on the function of pseudodepolarizers consisting of linear wave retarders, see Shurcliff 1962). Polarized light passing through this arrangement of linear wave retarders was depolarized by over 90% (91.8% at 625 nm), while they caused a 10–15%

reduction in light intensity between 400 and 800 nm (Moore & Phillips 1988). The optically clear and colourless pseudodepolarizers did not alter the light intensity distribution of the sky and allowed the birds an unobstructed view of the natural sky above.

Sheets of linear dichroic polarizer (Plexiglas laminated HN-38; Polaroid) were placed on top of the cages to alter the axis of the e-vector of incident plane-polarized light. Light passing through these filters is almost 100% linearly polarized in a uniform direction, having a total light transmittance of 38%. We altered the orientation of the e-vector by shifting the axes of the polarizers by 45° either clockwise (e-vector NE/SW) or anticlockwise (e-vector NW/SE) relative to geographical north.

We used electromagnetic coils (modified Helmholtz coils, 800 × 800 mm), powered by car batteries (12 V), arranged in pairs around the orientation cages to manipulate the horizontal component of the geomagnetic field. The coils were constructed to produce a homogeneous field in the centre, where the orientation cages were placed (for technical specification of the coils see Sandberg et al. 1988a).

Experimental Procedure

We performed the orientation cage experiments outdoors in an open test field during the autumn migration period in August and September. Tests were initiated 10 min after local sunset and lasted for 60 min. During the experiments the birds were able to see the natural sunset sky glow and the first visible stars at the end of the test period. Individual birds were tested only once in each test category and the experiments were performed in a random order. If the weather permitted, we tested the birds on successive nights. Not all birds were tested in all experimental categories.

The experiments were performed in the following conditions: (1) natural clear skies (160° of sky vision, control) in the local geomagnetic field (inclination +70°); (2) natural clear skies in a vertical magnetic field (inclination +90°); (3) simulated total overcast in the local geomagnetic field; (4) simulated total overcast in a vertical magnetic field; (5) SS control: ca. 10–45° of the sunset sky above the horizon was visible through four windows in the cardinal compass directions, but the natural pattern of skylight polarization and directional information from stars above was screened off with diffusing opaque Plexiglas sheets arranged on top of the cages (local geomagnetic field); (6) SS 120° ACW: with a similar amount of view of the sky visible above the horizon as in SS control, but with the position of the sun shifted 120° anticlockwise with mirrors (local geomagnetic field); (7) depolarization of the skylight with pseudodepolarizers in the local geomagnetic field; (8) depolarization in a vertical magnetic field; (9) direction of polarization (e-vector) changed to NE/SW by polarization filters in the local geomagnetic field; (10) direction of polarization changed to NE/SW in a vertical magnetic field; (11) direction of polarization changed to NW/SE in the local geomagnetic field; and (12) direction of polarization changed to NW/SE in a vertical magnetic field. In four of the test

Table 2. Mean angles of orientation (unimodal distributions: α ; bimodal distributions: V_a/V_b) vector lengths (r , r_2 ; range between 0 and 1, being inversely related to the angular scatter) and numbers (N) of pied flycatchers included in orientation cage experiments under different visual and magnetic conditions

Experimental condition		N	α	r	V_a/V_b	r_2	SS	95% CI
Visual	Magnetic							
Natural clear skies‡	Local	67	267°	0.56***	110°/290°	0.33***	292°	±17°
Natural clear skies‡	Vertical	49	222°	0.24	—	—	288°	—
Simulated total overcast‡	Local	40	293°	0.25†	145°/325°	0.25†	—	—
Simulated total overcast‡	Vertical	34	222°	0.09	—	—	—	—
SS control	Local	23	273°	0.52**	92°/272°	0.87	288°	±34°
SS 120° ACW	Local	21	141°	0.50**	132°/312°	0.22	169°§	±36°
Depolarization	Local	35	269°	0.38**	97°/277°	0.13	288°	±37°
Depolarization	Vertical	15	253°	0.30	125°/305°	0.40†	287°	—
e-vector NE/SW	Local	18	272°	0.51**	104°/284°	0.24	281°	±39°
e-vector NE/SW	Vertical	4	245°	0.37	57°/237°	0.51	282°	—
e-vector NW/SE	Local	15	296°	0.84***	122°/302°	0.74***	290°	±18°
e-vector NW/SE	Vertical	11	282°	0.72**	112°/292°	0.51†	288°	±32°
e-vector NE/SW all	Local & vertical	22	268°	0.48**	92°/272°	0.22	282°	±35°
e-vector NW/SE all	Local & vertical	26	290°	0.79***	118°/298°	0.64***	289°	±16°

Experimental conditions: SS (sunset) control: sunset sky was visible but the natural pattern of skylight polarization was screened off with Plexiglas sheets on top of the cage; SS 120° ACW: as for SS control but with the sunset position shifted 120° anticlockwise with mirrors; depolarization: skylight depolarized with pseudodepolarizers; e-vector: direction of skylight polarization changed by $\pm 45^\circ$ to NE/SW or NW/SE.

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Rayleigh test.

‡Experiments conducted partly with the same birds as in Åkesson (1994).

§Natural position of sun: 289°.

conditions (natural clear skies and total overcast in both vertical and local magnetic fields) some of the birds tested were the same as in Åkesson (1994; Table 2).

Statistics

We registered the activity of the birds either as claw scrapes or as counter registrations and used tests with at least 40 registrations during 1 h in further analyses. We calculated the mean heading of individual birds during each test by using vector addition, and excluded tests when birds failed to show a reasonably well-defined orientation (the limit was arbitrarily set to $P > 0.05$ according to the Rayleigh test; cf. Batschelet 1981). Based on these criteria only 3.5 and 7.3% of the tests were excluded because of low activity or disorientation, respectively (see Table 1 for number of birds included in the experiments). Mean headings for individual birds were used to calculate sample mean vectors, axes of orientation and degree of scatter (r , r_2) according to standard procedures given in Batschelet (1981). The Rayleigh test was applied to test for significant directional preferences (Batschelet 1981). Differences in scatter of individual mean headings (indicated by †) and mean orientation ($F_{1,df}$) between groups were analysed with Mardia's 'test for homogeneity of concentration parameters' and 'one-way classification test', respectively (Mardia 1972). Watson's U^2 test was used to test whether two circular distributions ($P > 0.05$ according to Rayleigh test) differed from each other (Batschelet 1981). We used 95% confidence intervals to analyse whether the mean orientation differed from the direction of the sunset point in the middle of the test hour or from

the orientation of the artificial e-vector axis (Batschelet 1981).

RESULTS

Orientation in Relation to Sunset Position

Pied flycatchers tested under natural clear sky conditions and in the local geomagnetic field (control) showed a significant mean orientation towards slightly south of west (Table 2, Fig. 1). The mean orientation was significantly different from the average sunset position in the middle of the test hour (SS: 292°, 95% confidence interval: $\pm 17^\circ$, $P < 0.05$) and coincided rather well with the expected southwesterly migratory direction of this species (Zink 1973; Roos 1984), and fairly well with a westerly mean orientation in autumn reported for hand-reared pied flycatchers from south Sweden (Alerstam & Högstedt 1983).

Experiments performed in the local geomagnetic field, with a visual sky field of ca. 10–45° above the horizon and with the pattern of skylight polarization around zenith screened off by opaque diffusing Plexiglas (SS control) resulted in a mean orientation towards the west, not significantly different from the sunset point (SS: 288°, 95% confidence interval: $\pm 34^\circ$, NS; Table 2, Fig. 2). The mean orientation of the SS control was not significantly different from the unscreened control condition ($F_{1,88} = 0.12$, NS). Birds exposed to a 120° anticlockwise rotation of visual sunset cues in the lower part of the sky (SS 120° ACW) were clearly affected by this treatment and their mean orientation was significantly different from

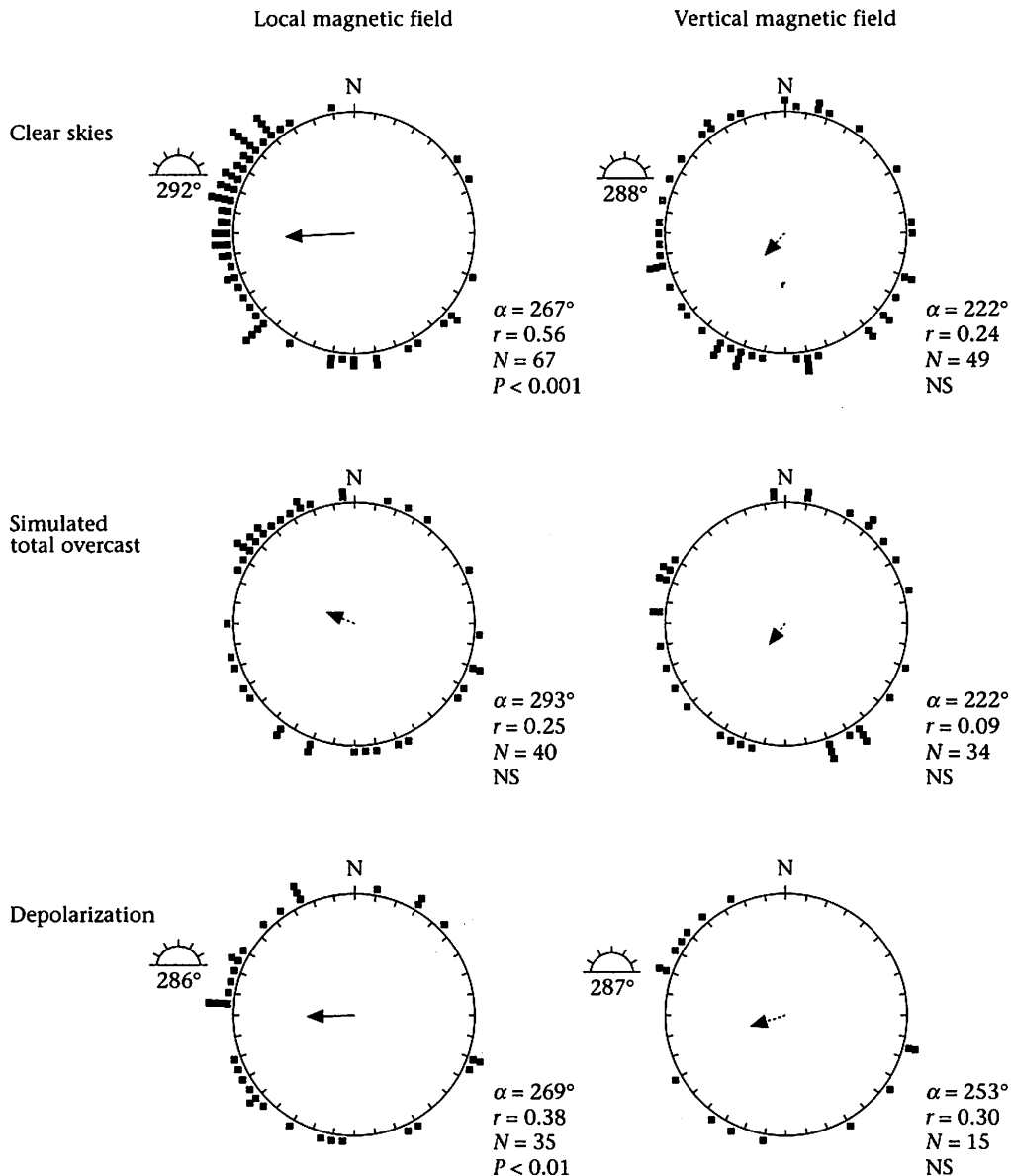


Figure 1. Results of orientation cage experiments under natural clear sky conditions with young pied flycatchers during autumn migration in south Sweden. The experiments were performed in the local and a vertical magnetic field, respectively, under natural clear skies and with 160° of the natural sky visible (control), under opaque Plexiglas sheets simulating total overcast, and under pseudodepolarizers reducing the degree of polarization (Depolarization). Squares indicate the mean orientation of individual birds and the arrow indicates the mean of the group. For each test condition the mean angle of orientation and the mean direction towards the position of the sun in the middle of the test hour are given. Broken lines indicate vectors for distributions that were not significantly different from random. For information about mean vector lengths, number of birds and significance levels, see Table 2.

the SS control group with a similar restricted sky view above the horizon ($F_{1,42}=25.4$, $P<0.001$). The mean orientation of the SS 120° ACW group was not significantly different from the deflected sunset position (SS: 169°; 95% confidence interval: $\pm 36^\circ$, NS), but was directed slightly to the left of the sun's position as was observed in the control condition (Fig. 2).

Simulated total overcast in the local geomagnetic field resulted in increased scatter in individual mean headings relative to tests under natural clear sky conditions ($t=2.5$, $P<0.05$; degree of scatter; r , see Table 2).

Orientation under Depolarized Skylight and Shifted e-vectors

Birds tested under depolarized skylight showed a significant mean orientation towards the west which did not differ significantly from the sunset position, in the local geomagnetic field (SS: 288°, 95% confidence interval: $\pm 37^\circ$, NS; Fig. 1). The mean orientation under depolarized skylight in a vertical magnetic field was not significantly different from random; however, fewer birds were tested in this group (Fig. 1). However, the mean

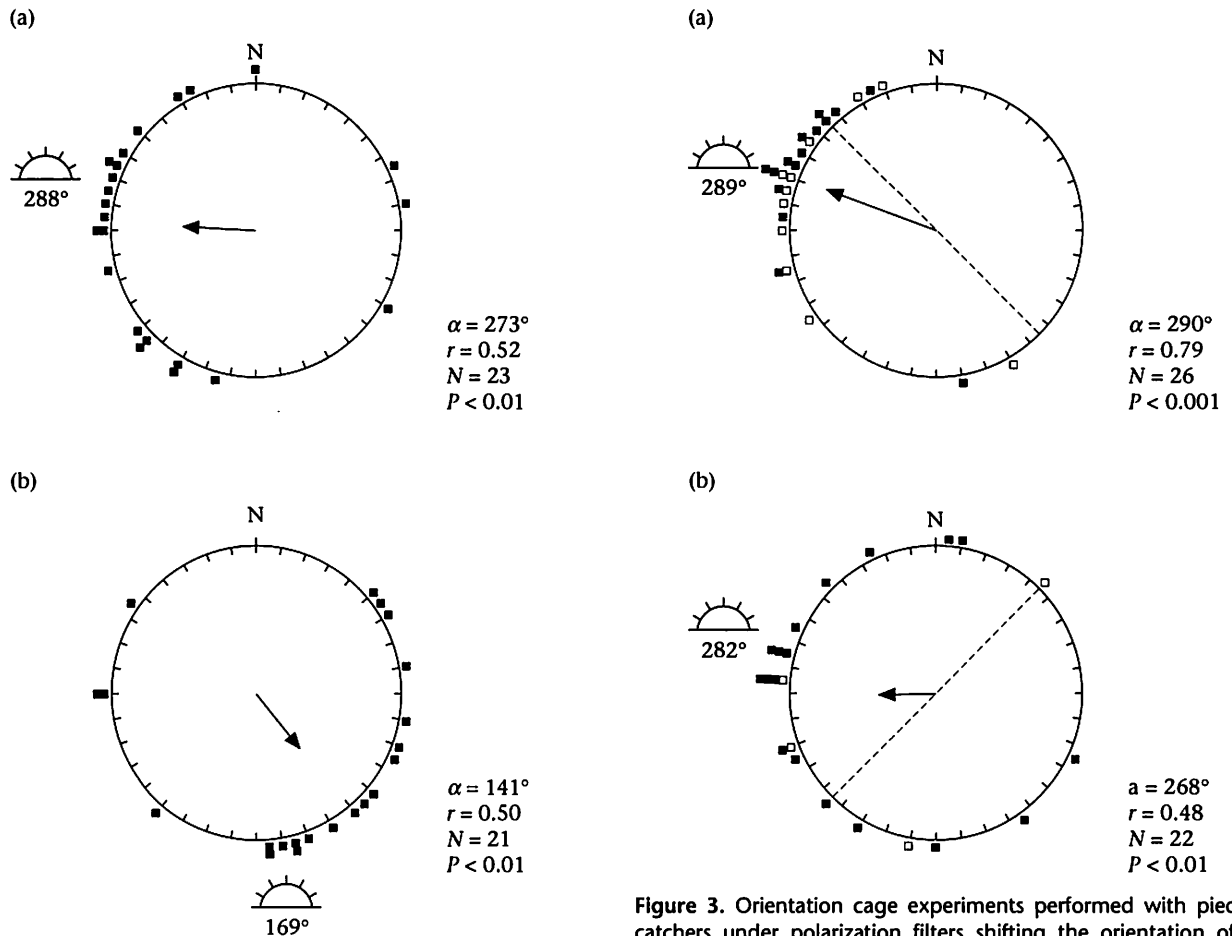


Figure 2. Results of autumn orientation cage experiments in the local geomagnetic field with young pied flycatchers in south Sweden. (a) The natural skylight polarization above was screened off by opaque Plexiglas sheets permitting only 10–45° of the natural sky above the horizon to be visible to the experimental birds (SS control). (b) The birds had the same restricted view of 10–45° of the sky above the horizon but the position of the sun was shifted 120° anticlockwise with mirrors (SS 120° ACW). For further information see Fig. 1 and Table 2.

orientation under depolarized skylight in a vertical magnetic field did not differ significantly from that in the local geomagnetic field ($U^2=0.059$, NS), nor did control clear sky tests differ from those under depolarized light in the local geomagnetic field ($U^2=0.090$, NS).

When the direction of polarization (e-vector) was shifted 45° anticlockwise or clockwise, the pied flycatchers showed a significant mean orientation approximately towards the west of northwest and west, respectively (Fig. 3, Table 2). The mean orientations for tests performed under different directions of polarization for which tests in natural and vertical magnetic fields were pooled differed by 22°. The mean orientation for clear sky tests in the local geomagnetic field was significantly more scattered compared with experiments under e-vector NW/SE in the local geomagnetic field ($t = -2.17$, $P < 0.05$) and the difference in mean angle of orientation was 23° (Table 2). We found no difference in mean orientation between control clear sky tests in the local geomagnetic field and

Figure 3. Orientation cage experiments performed with pied flycatchers under polarization filters shifting the orientation of the e-vector (a) 45° anticlockwise (e-vector NW/SE) or (b) 45° clockwise (e-vector NE/SW) relative to geographical north. ■: The mean orientation of individual birds for tests in the local geomagnetic field; □: vertical magnetic field. For further information see Fig. 1 and Table 2.

experiments with the e-vector axis deflected NE/SW in the local geomagnetic field ($F_{1,83}=0.061$, NS). There were only four tests with the e-vector deflected NE/SW in a vertical magnetic field and the mean orientation did not differ from random (Table 2). We found no significant difference between the mean orientation and the position of the sunset in the middle of the test hour for experiments in the local geomagnetic field and under e-vector NW/SE (SS: 290°, 95% confidence interval: $\pm 18^\circ$, NS) or e-vector NE/SW (SS: 281°, 95% confidence interval: $\pm 39^\circ$, NS). The mean orientation in these groups did not differ from the end of the artificial e-vector axes closest to the sun's position during the test (included in the 95% confidence intervals given above). The mean orientation of pied flycatchers under e-vector NW/SE in a vertical magnetic field was not significantly different from the sun's position, but was just significantly different from the end of the e-vector closest to the sun (SS: 288°, 95% confidence interval: $\pm 32^\circ$, $P < 0.05$). However, the mean orientations were directed slightly to the right (e-vector NW/SE) and to the left (e-vector NE/SW) of the sun, respectively (Fig. 3). There was a significant difference in scatter between the two e-vector groups in the local

geomagnetic field (i.e. e-vector NE/SW versus to NW/SE: $t=2.0$, $P<0.05$). This difference in scatter was also observed when the mean orientation for all tests performed with the e-vector shifted to NE/SW (i.e. tests in natural and vertical magnetic fields pooled) was compared with the corresponding tests with e-vector NW/SE ($t=2.5$, $P<0.05$). There was no difference in mean angle of orientation between tests under e-vector NW/SE in the local geomagnetic field and tests in a vertical magnetic field ($F_{1,24}=0.63$, NS), and therefore the tests could be pooled. For pooled tests under e-vector NW/SE there was a significant difference between the mean angle of orientation and the direction of the e-vector axis pointing towards the northwest (SS: 289° , 95% confidence interval: $\pm 16^\circ$, $P<0.05$). This difference was also statistically significant for all experiments performed under e-vector NE/SW (SS: 282° , 95% confidence interval: $\pm 35^\circ$, $P<0.05$).

Effects of Magnetic Field Manipulations

We found a significant difference in scatter between clear sky tests in the local and in a vertical magnetic field ($t=2.69$, $P<0.05$; Table 2). Under simulated overcast skies, however, there was no significant difference in orientation in the local and the vertical magnetic field ($U^2=0.081$, NS). Further statistical comparisons of magnetic field effects on orientation relative to visual sunset cues have been given above.

DISCUSSION

Orientation in Relation to the Sunset Azimuth

Our results provide information on the role of visual sunset cues at dusk relative to geomagnetic information for orientation in young pied flycatchers. They clearly show the importance of the sun's position at dusk in the selection of a migratory direction (Figs 1, 2). The mean orientation under unrestricted sky vision was significantly different from the sunset direction and the birds showed a fixed angle of orientation in relation to the shifted sun's position, obviously ignoring the conflicting directional information from the geomagnetic field in this condition. The position of the sun at sunset and the importance of information from the lower part of the natural sunset sky for orientation have earlier been demonstrated for nocturnally migrating robins, *Erithacus rubecula* (Sandberg 1991). In these experiments the robins demonstrated meaningful migratory orientation only when given full view of the natural sunset sky (160° as in our experiments). Furthermore, they responded to a shift of the sunset position by mirrors in a similar way to our pied flycatchers (Fig. 1).

Previous experiments with nocturnal passerine migrants captured at Falsterbo Bird Observatory and tested shortly after sunset at dusk have indicated strong effects of the position of the sun on the birds' orientation in circular orientation cages (Sandberg et al. 1988b; Åkesson 1994; Åkesson & Sandberg 1994, cf. mean

orientation towards the west in hand-reared birds from southern Sweden, Alerstam & Högstedt 1983). The birds' directional choices were in several cases oriented between the expected migratory direction for the species and the sun's position during the test. This orientation behaviour seems to be caused partly by an attraction to the sun, perhaps because of a temporarily reduced urge to migrate or a reverse migration (cf. Åkesson et al. 1996b), and partly by selection of the proper migratory direction (Åkesson 1994). Such mixed behaviours seem to be common among nocturnal migrants captured at Falsterbo Bird Observatory in autumn (i.e. Sandberg et al. 1988b; Åkesson 1994; Åkesson & Sandberg 1994) and are presumably a result of the birds' migration experiences prior to capture and the particular location of this capture site (i.e. at the outermost coast of a peninsula pointing towards the southwest and coinciding with the dominating expected migratory direction in this area; cf. map given in Figure 1 in Åkesson et al. 1996b). Birds captured here in autumn arrive at the coast mainly after flying over land and are prone to fly back towards the north to northeast to stopover sites further inland, before they resume migration and continue in the expected migratory direction towards the southwest (Lindström & Alerstam 1986; Sandberg et al. 1988b; Åkesson et al. 1996b). At Falsterbo, it is mainly lean birds that make reverse flights (Åkesson et al. 1996b). At Ottenby, located on the island of Öland in the Baltic Sea ($56^\circ 12'N$, $16^\circ 24'E$), birds use geomagnetic information to choose their directions (i.e. fat birds: in the expected migratory direction; lean birds: in reverse directions; robins; Sandberg 1994; chaffinches, *Fringilla coelebs*: Bäckman et al. 1997). Thus, the preferred direction of movement of a bird in a particular environmental and physiological condition can be changed temporarily and is actively selected based on available compass information.

Autumn-migrating pied flycatchers captured at Falsterbo do shift their preferred orientation in relation to shifts of the sun's position (this study), but in cue-conflict experiments where the horizontal component of the magnetic north was shifted 90° anticlockwise relative to geographical north, the birds at least partly (43°) followed the magnetic shift ignoring the natural sunset sky information (Åkesson 1994). Based on both these findings it is difficult to tell which of the two cues dominates in this species when tested during migration in this particular environmental condition. Both visual and magnetic information seem to be important for the pied flycatchers' orientation. Furthermore, when the birds were deprived of visual clear sky cues (simulated overcast) and the birds had access only to magnetic field information, the birds' orientation became random, indicating an inability to orient when the visual cues were not available.

Previous studies indicate that species might differ in the hierarchical dominance of different cues, related to geographical area, migratory situation or even experimental paradigm. Perhaps the conflicting orientation behaviours are a result of an interaction between the inherited migratory direction as set mainly by magnetic compass information (e.g. Weindler et al. 1996) and the compass

system used during migratory flight. The latter might be based on visual sunset cues and later transferred to stars at night (cf. Moore 1980; Alerstam & Pettersson 1991). In this respect the calibration between compass systems seem to be particularly important during this transition period between day and night, when within a relatively short period, the birds have access to a number of compass cues for orientation (cf. Rozenberg 1966; Åkesson et al. 1996a). The importance of compass calibration within the twilight period has already been demonstrated for some nocturnal passerine migrants (Phillips & Moore 1992; Able & Able 1995) but further experiments in this field are needed.

Visual versus Magnetic Cues at Dusk

We found no significant effect of depolarized skylight on the pied flycatchers' orientation. The birds' mean orientation remained more or less the same as in the natural clear sky condition. The mean orientation in depolarization tests in a vertical magnetic field, without meaningful directional magnetic information, did not differ from random but there was no increase in scatter of individual mean headings compared with depolarization tests in the local geomagnetic field or control clear sky tests. Increased scatter of individual mean orientations under depolarization filters have been reported for nocturnally migrating robins and blackcaps, *Sylvia atricapilla* (Helbig 1990, 1991), as well as for diurnally migrating yellow-faced honeyeaters, *Lichenostomus chrysops* (Munro & Wiltschko 1995). In the latter species an increase in scatter under depolarized light in a vertical magnetic field was observed only when the sky was partly covered by clouds, and especially when the sun itself was hidden behind clouds. As in the present study, experiments under depolarized light and with directional information from the local magnetic field resulted in orientation more or less in the expected migratory direction in yellow-faced honeyeaters (Munro & Wiltschko 1995) and in white-throated sparrows, *Zonotrichia albicollis* (Able 1989). Given access to directional information from the local magnetic field, the birds seem to use predominantly this information for selecting the migratory direction.

Helbig (1990, 1991), in contrast to other experimenters, performed orientation cage experiments (on blackcaps and robins) in a location (on top of a roof), where the local magnetic field was largely disturbed by fluctuations in intensity and direction. Presumably these magnetic fluctuations caused the migrants to ignore geomagnetic information for orientation. Strangely the birds seemed also to ignore the directional information from the light intensity gradient of the sky (i.e. their orientation was random under depolarized light). It is unclear why some migratory species seem to ignore the light intensity and colour gradients of the sky (Helbig 1990, 1991), while others seem to use this information to locate the sun when denied meaningful information from the skylight polarization pattern and the geomagnetic field (i.e. yellow-faced honey eaters, Munro & Wiltschko 1995, and perhaps also white-throated sparrows, Able 1989). It should be noted that the pseudodepolarizers did not

cancel out the pattern of skylight polarization completely (probably 9–10% remained), and perhaps this is enough for the birds to orient based on information from the e-vector. Our experimental treatment of visual cues, however, did not differ from other studies with pseudo-depolarizers, where clear effects on the birds' orientation have been observed (e.g. Helbig 1990, 1991; Munro & Wiltschko 1995).

The experiments with the natural axis of polarized skylight (e-vector) deflected 45° clockwise or 45° anticlockwise suggested that the birds aligned their orientation with that of the imposed e-vector when the artificial e-vector was aligned NW/SE. The responses differed between the two groups depending on the orientation of the e-vector. The mean orientation was largely scattered when the e-vector was shifted 45° clockwise (NE/SW), and the birds did not seem to align with the e-vector axis. In the anticlockwise shift of the e-vector (NW/SE) the mean orientation was highly significant and the birds tended to orient between the sun's position and the closest side of the e-vector axis. We conclude that the directional choices of the birds in this experimental configuration varied between conditions and therefore seem to be partly affected by the sun's position, the imposed orientation of the artificial e-vector and the direction of migration towards west of southwest. The presence or absence of meaningful directional information from the local magnetic field did not seem to have any effect on the birds' orientation when the e-vector was changed to NW/SE.

Experiments performed with North American as well as European nocturnal passerine migrants have demonstrated clear responses to imposed artificial e-vectors of different alignments, in which the birds oriented more or less bimodally along the axis of the e-vector (Moore 1980; Able 1989, 1989; Helbig & Wiltschko 1989; Helbig 1991; Phillips & Moore 1992), and in most cases ignoring the conflicting directional information from the sun or the local magnetic field (i.e. Able 1989; Phillips & Moore 1992). Other studies have demonstrated little or no effect on the birds' orientation relative to the shifted e-vectors (Sandberg 1988; Munro & Wiltschko 1995; this study), suggesting a primary importance of local magnetic cues relative to skylight polarization patterns. However, when making hierarchical considerations between different cues one must keep in mind the highly artificial character of the e-vector stimuli (cf. Able 1989) relative to, for example, the magnetic field. The majority of responses to imposed e-vectors demonstrate alignment of the birds' bimodal directional choices with the artificial e-vector rather than the predicted unimodal orientation shifted in relation to natural migratory directions (e.g. Able 1989; Helbig & Wiltschko 1989; Helbig 1991). We cannot rule out that the artificial e-vector pattern might act as a superstimulus to the bird rather than cause a natural orientation response.

Taken together, our experiments manipulating the degree of polarization and the direction of the e-vector (NW/SE) show no clear effect relative to the visual cue manipulations. In contrast to these findings, experiments that shifted the sun's position by mirrors resulted in clear

shifts of migratory orientation in the pied flycatchers, pointing towards a dominating effect of visual information relative to geomagnetic field information. However, at the same time we found an increase in scatter of individual mean headings when visual clear sky cues were excluded, indicating an inability to orient by the geomagnetic field alone. We must conclude that young pied flycatchers caught on migration seem to use both visual and geomagnetic cues for orientation at dusk (cf. Åkesson 1994) and that the interaction between the different compass systems in birds on migration is clearly complex and not yet fully understood. We cannot exclude that this behaviour is related to the site of capture (i.e. coastal), such that birds caught at an ecological barrier show a flexible orientation caused by different urges to continue in the expected forward direction or to move in reverse directions. We tested direct responses of birds in relation to different orientation cues set in conflict and not the calibration of different compass systems relative to each other. For the future it is important to study the interrelationship between different compasses by performing experiments to test how these are calibrated during migration in different species and under different migratory conditions, as has initially been considered in some studies (Phillips & Moore 1992; Able & Able 1995; Wiltschko et al. 1997).

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