

Comparative orientation experiments with different species of passerine long-distance migrants: effect of magnetic field manipulation

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Abstract. The orientation of four species of passerine long-distance migrants was studied in spring and autumn by orientation cage experiments during the twilight period after sunset in Sweden. Two groups of migrants from the Palaearctic–African migration system were used: migrants wintering mainly north of the magnetic equator in west Africa (pied flycatcher, *Ficedula hypoleuca*, and redstart, *Phoenicurus phoenicurus*) and migrants wintering south of the magnetic equator in southeast Africa (thrush nightingale, *Luscinia luscinia*, and marsh warbler, *Acrocephalus palustris*). Orientation experiments were conducted in three magnetic conditions, in the local geomagnetic field and in a deflected and in a vertical magnetic field, under clear and simulated total overcast conditions, respectively. The results did not provide any convincing indications about differences in the orientation system between the two groups of migrants. The responses of all species seemed to be affected in a similarly complex way by celestial as well as magnetic cues, involving conflicting elements of a possible attraction towards the brightest part of the twilight sky as well as orientation in the migratory direction. Shifting the horizontal component of the magnetic field neither shifted nor disrupted orientation. Abolishing the horizontal component of the magnetic field increased the orientational scatter in three species in spring and one in autumn. Simulated total overcast largely abolished orientation, except in two species (in the local geomagnetic field only) that do not migrate across the geomagnetic equator.

Nocturnal bird migrants have been demonstrated to use celestial and magnetic cues for orientation (for reviews see, for example, Able 1980; Moore 1987; Wiltschko & Wiltschko 1988, 1991; Alerstam 1990); however, the inter-relationships between the different cues used in the orientation mechanism are poorly understood. Suggested species-specific differences in the orientation mechanism (Able & Bingman 1987; Helbig 1990) have been indicated in comparable orientation cage experiments between a temperate migrant (the robin, *Erithacus rubecula*) and three species of tropical migrants (*Sylvia* warblers; Wiltschko & Wiltschko 1975a, b, 1978) and between two long-distance migrants, the wheatear, *Oenanthe oenanthe* (Sandberg et al. 1991) and the marsh warbler, *Acrocephalus palustris* (Åkesson 1993). The differences in orientation, for example in calibration time, between short- and long-distance migrants have been suggested to be an ecological adaptation to the different distances and speeds of the migration in temperate and long-distance migrants (Wiltschko & Wiltschko 1975a, b).

The magnetic compass of robins is based on the inclination and not on the polarity of the magnetic field (Wiltschko & Wiltschko 1972). An inclination compass mechanism reveals no directional information in a horizontal magnetic field and it is therefore in theory impossible to use at the geomagnetic equator. Several migratory bird species breed at northerly latitudes and winter in the Southern Hemisphere (e.g. Moreau 1972), passing the area of the magnetic equator on migration. Two species of trans-equatorial migrants have been demonstrated to possess an inclination compass (the garden warbler, *Sylvia borin*; Wiltschko 1974; and the bobolink, *Dolichonyx oryzivorus*; Beason 1989; but see also Beason & Nichols 1984) and have been shown to respond to shifts of the inclination after a simulated equator crossing (Beason 1992; Wiltschko & Wiltschko 1992). However, to what extent birds rely on magnetic information when travelling along different migration routes, crossing or not crossing the magnetic equator, is poorly known.

To investigate whether the orientation mechanism used by different long-distance migrants is

species-specific and adapted to the situations the birds are expected to encounter on migration, I conducted comparative orientation experiments in manipulated magnetic fields with species from two groups of migrants within the Palaearctic-African migration system. The two groups were selected on the basis of the autumn migration direction and whether the birds during their migration are expected to pass the magnetic equator (southeast migrants in autumn: thrush nightingale, *Luscinia luscinia*, and marsh warbler; cf. Zink 1973) or to stay mainly in tropical winter quarters north of the magnetic equator (southwest migrants; pied flycatcher, *Ficedula hypoleuca*, and redstart, *Phoenicurus phoenicurus*). The experiments were designed to reveal whether the birds use the magnetic field or whether they rely mainly on visual cues for orientation at the sunset period, during both spring and autumn migration in Sweden.

Orientation experiments were performed under clear as well as under simulated overcast skies in three magnetic conditions: in the local geomagnetic field, in a deflected magnetic field (where magnetic north was shifted to geographical west) and in a vertical magnetic field. In the local geomagnetic field under clear skies I expected the birds to orient in their preferred migratory direction. If the birds rely mainly on magnetic information, they should show this migratory direction under total overcast in the control condition and change their orientation in the deflected magnetic field. In a vertical magnetic field, birds relying on magnetic information will be disoriented and show a non-significant or scattered orientation under clear as well as under overcast skies. Birds that use visual cues for orientation may still be oriented in a vertical magnetic field under clear sky, but will become disoriented under overcast conditions. The birds' fat content was recorded to allow any effect of body condition on orientation responses (Åkesson 1993; Sandberg 1994) to be taken into account.

METHODS

Study Site and Experimental Equipment

The experimental birds were captured during the migration periods (April-May; August-October) at stop-over sites in southern Sweden mainly at Falsterbo Bird Observatory (55°23'N, 12°50'E), but also at Ottenby Bird Observatory

(56°12'N, 16°24'E; 31 thrush nightingales in spring and eight redstarts in autumn). After capture the birds were transported by car to the experimental site at Stensoffa Ecological Field Station (55°42'N, 13°25'E), approximately 55 km northeast of Falsterbo Bird Observatory and 200 km west-southwest of Ottenby Bird Observatory. The birds were housed in rooms with windows under the natural photoperiod and in the local geomagnetic field (inclination +70°). The birds were kept individually in spacious cages (350 × 350 × 450 mm) and fed with an unlimited amount of mealworms and water with vitamins. Each bird was held in captivity approximately 10 days and was used in orientation experiments up to six times.

The birds were aged according to criteria used in Svensson (1984), and in autumn only juvenile birds were included in the experiments. To investigate whether body condition had an effect on the orientation, the birds were weighed with a pesola spring-balance (50 g) and the fat deposits on the birds' bellies and in the tracheal pits were classified according to a scale for visual fat classification (Pettersson & Hasselquist 1985), at capture and each evening before the experiments were initiated.

I performed orientation experiments with two similar types of circular orientation cages (modified Emlen-cages; see 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. The cages were constructed in non-magnetic materials and the tops of the cages were covered with fine-meshed plastic net allowing the birds to see the natural sky. In the first type of cage with automatic registration, the sloping walls were subdivided into eight 45° sectors and under each sector microswitches were placed and connected to a counter. The activity was registered at the specific counters when the birds were jumping on the sectors. A second type of cage was used for complementary tests alongside the cages with automatic registration. The sloping walls of this cage were covered with typewriter correction paper (Tipp-Ex), and the birds' activity was registered as claw marks in the paper (Rabøl 1979; Beck & Wiltchko 1981). After the experiments the paper was subdivided into 24 sectors and the claw marks across a certain line, passing through the majority of the registrations between 20 and 100 mm above the orientation cage floor,

were counted in each sector. Vector addition (Batschelet 1981) was used to calculate the mean orientation of individual birds on the basis of the registrations in the eight and 24 sectors, respectively. I found no significant differences in the birds' orientation depending on cage-type, and therefore the data sets were pooled.

Electromagnetic coils (modified Helmholtz coils, 800×800 mm), powered by car batteries (12 V), were 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 cage was placed (for technical specification see Sandberg et al. 1988b). Total overcast conditions were simulated by placing opaque diffusing Plexiglas sheets on top of the orientation cages under clear or partly covered sky conditions (0–7/8). Under natural total overcast (8/8; 7% of the tests), the birds were exposed to the natural sky instead.

Experimental Procedure

The experiments started 10 min after local sunset and lasted 60 min. During the experimental period the birds were able to see sky glow from the sunset, and during the last part of the test-hour the first stars were visible. In the spring, I tested thrush nightingales, pied flycatchers and redstarts, while in the autumn I tested only juvenile marsh warblers, pied flycatchers and redstarts, as it is difficult to catch sufficient numbers of adults at this time.

Orientation experiments were performed in the following three magnetic conditions (under clear as well as overcast conditions): in the local geomagnetic field (inclination $+70^\circ$; control), in a deflected magnetic field (magnetic north was shifted 90° to geographical west, inclination $+70^\circ$; deflected) and in a vertical magnetic field (inclination $+90^\circ$; vertical). Each bird was tested only once under each of the six experimental conditions.

Statistics

The birds' activity was recorded as counter registrations or claw marks in the orientation cages, and tests were included in the analysis if there were at least 40 registrations during 1 test-hour. The mean orientation of individual birds during each test was calculated by vector addition,

and tests when birds failed to show a reasonably well-defined orientation (the limit was set to $P > 0.05$ according to the Rayleigh test; cf. Batschelet 1981) were excluded. The limit was used simply as a criterion to exclude highly disoriented and unreliable results from the analysis and relatively few tests were excluded on these grounds (see Table I for the number of birds included in the experiments). Differences in scatter of individual mean headings (indicated by ϵ) and mean orientation (F_1) between groups were analysed with Mardia's 'test for homogeneity of concentration parameters' and 'one-way classification test', respectively (Mardia 1972). I used 95% confidence intervals to see whether the mean orientation differed significantly from the direction of the sunset point (Batschelet 1981).

Body Condition, Level of Activity and Test Order

Table II shows fat content and mean mass recorded at capture of birds used in the orientation experiments. In autumn marsh warblers put on large amounts of fat before migration flights towards the southeast, while thrush nightingales carried the smallest fat reserves when arriving on spring migration (Table II). To investigate whether fat content had any effect on the orientation responses within each species in each test condition, the birds were divided into two similar-sized groups, based on the fat class recorded each evening before the experiments were initiated (Table II). Birds with small fat reserves (fat classes 0–4) were distinguished from birds in high fat classes (≥ 5). Mardia's one-way classification test (Mardia 1972) was used to investigate whether there was any significant difference in the orientation between the two groups with respect to concentration as well as mean direction of the orientation. In only four out of 36 test conditions did the two groups differ significantly with respect to either scatter or mean direction, which is almost what could be expected by chance. Consequently, there were no important indications that variation in fat reserves showed any significant relationship with the pattern of orientation within species.

I investigated whether the birds' activity had an effect on the orientation in the same way as for the fat content described above. For each test condition the birds were divided into two groups with approximately half the sample each. One group included birds exhibiting low activity in the

Table I. Number of birds tested in orientation experiments in Sweden under different experimental conditions in spring (S) and autumn (A), respectively

			Inactive	Disoriented	Included	Total
Thrush nightingale (S)						
Clear sky	Control		9	2	62	73
	Deflected		5	2	59	66
	Vertical		1	3	57	61
Overcast	Control		10	12	49	71
	Deflected		12	8	51	71
	Vertical		16	7	46	69
Pied flycatcher (S)						
Clear sky	Control		0	1	26	27
	Deflected		0	0	22	22
	Vertical		0	1	19	20
Overcast	Control		9	4	11	24
	Deflected		3	0	18	21
	Vertical		1	6	15	22
Redstart (S)						
Clear sky	Control		3	6	43	52
	Deflected		4	4	39	47
	Vertical		4	3	36	43
Overcast	Control		31	8	32	71
	Deflected		8	3	26	37
	Vertical		3	5	25	33
Marsh warbler (A)						
Clear sky	Control		17	6	41	64
	Deflected		3	2	45	50
	Vertical		12	4	36	52
Overcast	Control		23	12	25	60
	Deflected		17	7	31	55
	Vertical		15	8	31	54
Pied flycatcher (A)						
Clear sky	Control		1	0	71	72
	Deflected		0	2	51	53
	Vertical		0	2	49	51
Overcast	Control		8	7	40	55
	Deflected		2	7	40	49
	Vertical		2	10	34	46
Redstart (A)						
Clear sky	Control		1	3	28	32
	Deflected		2	4	22	28
	Vertical		1	1	20	22
Overcast	Control		5	11	24	40
	Deflected		4	6	22	32
	Vertical		8	9	20	37
			14%	11%	75%	

Experiments were conducted under clear skies and under simulated total overcast conditions in the following magnetic conditions: in the local geomagnetic field (control), in a deflected magnetic field and in a vertical magnetic field. Inactive birds (14%; ≤ 40 registrations per test-hour) or disoriented birds (11%; see text) were excluded from the analysis.

orientation cages (40–499 registrations per test-hour) and the other group represented highly active birds (≥ 500). Again the orientation of the two groups was significantly different with respect to either concentration or mean direction in only

four out of the 36 test-condition comparisons, which is close to what could be expected by chance. Hence, there were no consistent differences in orientation between birds demonstrating low or high activity in the orientation cages.

Table II. The distribution of birds in different fat classes recorded at capture (visual scale for fat classification; Pettersson & Hasselquist 1985), mean fat class and mean mass (g), of birds used in orientation experiments in spring (S) and autumn (A), respectively

	Fat class									<i>N</i>	$\bar{X} \pm \text{SD}$	Mass $\bar{X} \pm \text{SD}$
	0	1	2	3	4	5	6	7	8			
Thrush nightingale (S)	2	3	19	25	19	5	2	0	0	75	3.0 ± 1.2	23.3 ± 1.9
Pied flycatcher (S)	0	1	2	6	9	8	2	0	0	28	4.0 ± 1.2	12.6 ± 0.8
Redstart (S)	0	3	4	11	15	28	5	0	0	66	4.2 ± 1.2	15.0 ± 1.1
Marsh warbler (A)	0	0	6	9	18	14	14	5	1	67	4.6 ± 1.5	14.1 ± 1.4
Pied flycatcher (A)	1	0	2	29	15	25	7	0	0	79	4.0 ± 1.2	12.8 ± 0.7
Redstart (A)	0	0	3	16	9	9	0	0	0	37	3.6 ± 0.9	14.7 ± 1.0

Table III. Vector length (r) and number of birds included in orientation cage experiments with different species of passerine long-distance migrants in Sweden

	Control		Deflected		Vertical	
	r	(N)	r	(N)	r	(N)
Clear sky						
Thrush nightingale (S)	0.55***	(62)	0.36***	(59)	0.31**	(57)
Pied flycatcher (S)	0.69***	(26)	0.40*	(22)	0.17	(19)
Redstart (S)	0.63***	(43)	0.48***	(39)	0.36**	(36)
Marsh warbler (A)	0.28*	(41)	0.22	(45)	0.31*	(36)
Pied flycatcher (A)	0.51***	(71)	0.31**	(51)	0.24	(49)
Redstart (A)	0.43**	(28)	0.37*	(22)	0.30	(20)
Overcast conditions						
Thrush nightingale (S)	0.21	(49)	0.13	(51)	0.14	(46)
Pied flycatcher (S)	0.74***	(11)	0.12	(18)	0.36	(15)
Redstart (S)	0.37*	(32)	0.16	(26)	0.12	(25)
Marsh warbler (A)	0.19	(25)	0.22	(31)	0.24	(31)
Pied flycatcher (A)	0.28*	(40)	0.06	(40)	0.09	(34)
Redstart (A)	0.21	(24)	0.25	(22)	0.17	(20)

For further information see Table I.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Rayleigh test (Batschelet 1981).

For individual birds the experiments in different test conditions were performed in random order. I analysed whether test order had any influence on the birds' orientation by comparing tests where the birds had been exposed to conflicting magnetic and visual information in the immediately preceding experiment with tests that were not preceded by such cue-conflict experiments (cf. Wiltshko & Wiltshko 1975b); I failed to find a statistically significant difference, and conclude that the orientation patterns demonstrated in this study (Figs 1 and 2) have not been affected by test order to any important degree.

RESULTS

Orientation under Clear Skies

Table III gives the mean vector lengths and significance levels (according to the Rayleigh test; Batschelet 1981). The vector length (r) describes the scatter of the circular distribution (ranges between 0 and 1, the scatter being inversely related to the vector length).

In spring the birds generally showed orientation tendencies towards the northwest in all experimental categories under clear skies (Fig. 1). The orientation was highly significant in the local geomagnetic field, while the scatter in mean

orientation increased in the other two conditions with a manipulated magnetic field (Fig. 1, Table III). There was a significant difference in scatter between the tests under control conditions and in a vertical magnetic field in the thrush nightingale ($t = 2.1$), the pied flycatcher ($t = 2.6$) and the redstart ($t = 2.0$, $P < 0.05$ in all three cases). The mean orientation in the control situation corresponded well with the expected migratory direction towards north in spring, but was not significantly different from the sunset point in the thrush nightingale ($P > 0.05$, 95% confidence interval $\pm 18^\circ$; Batschelet 1981), the pied flycatcher ($P > 0.05$, $\pm 21^\circ$) or the redstart ($P > 0.05$, $\pm 18^\circ$).

In autumn the mean orientation in the local geomagnetic field under clear skies was significant in all three species (Fig. 2, Table III). In the marsh warbler the mean orientation corresponded well with the expected migratory direction towards southeast to south, and was significantly different from the sunset point ($P < 0.05$, 95% confidence interval $\pm 48^\circ$). Pied flycatchers and redstarts showed westerly orientation in autumn, not significantly different from the sunset point ($P > 0.05$, 95% confidence interval, pied flycatcher $\pm 17^\circ$, redstart $P > 0.05$, $\pm 36^\circ$), but slightly different from the expected southwesterly to southerly migratory direction. The scatter in mean orientation increased in a vertical compared with a

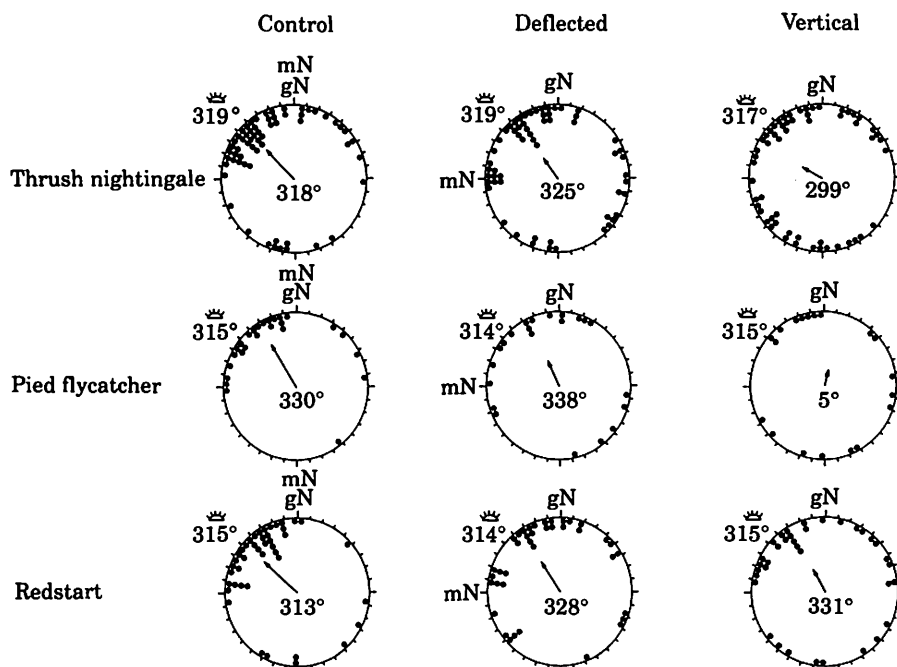


Figure 1. Results of orientation experiments under clear skies with three species of passerines during spring migration in Sweden. The experiments were performed in the local geomagnetic field (control, inclination $+70^\circ$), in a deflected magnetic field (mN towards gW, inclination $+70^\circ$) and in a vertical magnetic field (inclination $+90^\circ$), respectively. ●: The mean orientation of individual birds. The mean angle of orientation of the group is indicated by the arrow. Absence of arrow-head indicates that the circular distribution is not significantly different from random. For each test condition the directions towards magnetic north (mN) and geographical north (gN) and the mean direction towards the position of the sun in the middle of the test-hour are indicated. In spring, pied flycatchers and redstarts return from winter quarters in west Africa on expected migratory courses towards north to northeast, while thrush nightingales, returning from southeast Africa, are expected to migrate towards northwest to north. For information about mean vector lengths, number of birds and significance levels, see Table III.

normal magnetic field under clear skies, significantly in pied flycatchers ($t=2.3$, $P<0.01$), but not significantly in redstarts ($t=0.6$, $P>0.05$) and marsh warblers ($t=0.2$, $P>0.05$).

The birds did not respond to the declination of the magnetic field with a corresponding shift in mean orientation (90°), as expected if they relied on magnetic information for their orientation, either in spring or in autumn (Figs 1 and 2). There was a tendency for a magnetic response in the pied flycatcher in autumn (shift in orientation between control and deflected magnetic condition), where an anticlockwise shift of 40° in the mean orientation was observed in the deflected magnetic field compared with the control situation ($F_{1,120}=4.5$, $P<0.05$).

Orientation under Total Overcast Conditions

Generally, the birds' orientation under overcast conditions was highly scattered and not significantly different from random except in a few cases with a normal geomagnetic field (pied flycatcher, spring and autumn; redstart, spring; Table III, Figs 3 and 4). The spring orientation of pied flycatchers and redstarts under control conditions was in good agreement with the expected migratory direction towards north to northeast (Fig. 3). Generally the scatter was larger under total overcast compared with clear sky conditions, but the difference in concentration was significant for the thrush nightingale only ($t=2.8$, $P<0.01$, spring, control experiments).

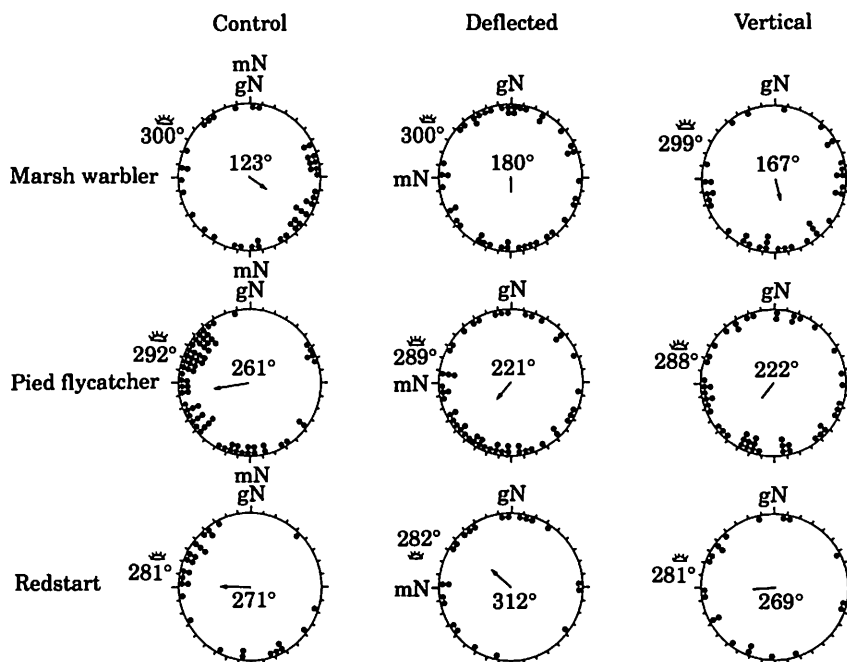


Figure 2. Results of autumn orientation experiments under clear skies with three species of juvenile bird migrants in Sweden. Pied flycatchers and redstarts migrate towards southwest to south in autumn to wintering areas in west Africa. Marsh warblers migrate towards southeast to south in autumn to wintering areas in southeast Africa. For further information see Fig. 1 and Table III.

DISCUSSION

Orientation under Total Overcast Conditions

The distribution of individual mean headings was normally more scattered under simulated total overcast than under clear skies, and no directional changes could be demonstrated as a result of deflected magnetic fields, indicating a general importance of visual cues for the birds' orientation (see Figs 3 and 4, and Table III). The pied flycatcher and the redstart were significantly oriented in their spring migratory direction towards north to northeast under overcast (pied flycatcher significantly oriented also in autumn), indicating successful use of the magnetic compass sense (Figs 3 and 4). I conclude that simulated total overcast largely abolishes orientation, except in the two species that do not migrate across the geomagnetic equator.

Effects of Magnetic Manipulation on Direction

In this study the experimental birds under clear skies failed to show a consistent change in their

orientation according to the shift of the magnetic field (see Figs 1 and 2). Only in the case of juvenile pied flycatchers in autumn was there a suggestion of a possible incomplete directional response to the magnetic field. Under overcast the orientation was normally highly scattered and no directional changes could be demonstrated as a result of deflected magnetic fields.

Orientation experiments under natural clear skies with conflicting visual and magnetic information (deflected magnetic fields) have given orientation tendencies in agreement with the magnetic shifts (Wiltschko et al. 1971; Wiltschko & Wiltschko 1975a, b; Bingman 1987; Bingman & Wiltschko 1988), but have also failed to demonstrate clear magnetic responses (Wiltschko & Höck 1972; Moore 1985; Sandberg et al. 1988b, 1991; Åkesson 1993). Out of 32 experiments under clear skies with shifted magnetic fields, a significant change in the birds' orientation in accordance with the magnetic deflection was demonstrated in only 11 cases (Table IV). This is interesting because it indicates that when the birds have access to visual information from the natural

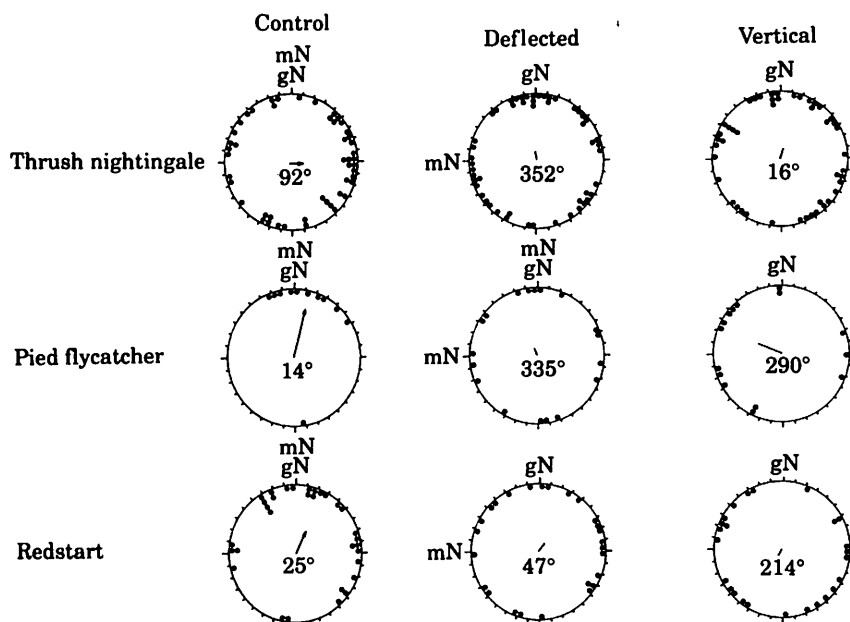


Figure 3. Results of orientation experiments with three species of passerine migrants under total overcast conditions during spring migration. For further information see Fig. 1 and Table III.

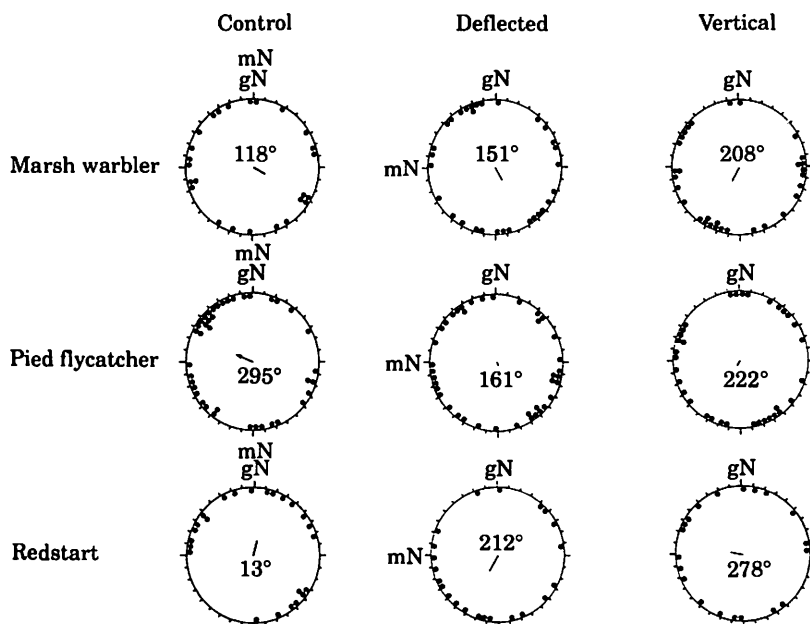


Figure 4. Results of orientation experiments with three species of juvenile passerine migrants in autumn under total overcast conditions. For further information see Fig. 1 and Table III.

Table IV. Orientation experiments performed in deflected magnetic fields under natural clear skies in spring (S) and in autumn (A)

Species	Season	Magnetic deflection	Directional response of birds	Time of test	References
Dunnoch	S	+120°	+144°(***)	Twilight	Bingman & Wiltchko 1988, Germany
Dunnoch	S	+120°	+122°(***)	Twilight	Bingman & Wiltchko 1988, Italy
Robin	S, A	+115°, +115°	+12° (NS), +4° (NS)	Morning	Wiltchko & Höck 1972, Germany
Robin	S, A	+115°, +115°	-23° (NS), -16° (NS)	Afternoon	Wiltchko & Höck 1972, Germany
Robin	S	+90°, -90°	-33° (*), +9° (NS)	Twilight	Sandberg et al. 1988a, b, Falsterbo, Sweden
Robin	A	+90°, -90°	+6° (NS), +16° (NS)	Twilight	Sandberg et al. 1988a, b, Falsterbo, Sweden
Robin	S	+90°, -90°	Bimodal (NS), -51° (NS)	Twilight	Sandberg et al. 1988a, b, Ottenby, Sweden
Robin	A	+90°, -90°	Bimodal†, bimodal†	Twilight	Sandberg et al. 1988a, b, Ottenby, Sweden
Robin	S, A	+115°, +115°	+116° (***), +146° (?)	Night	Wiltchko et al. 1971, Germany
Robin	S	+120°	+86° (***)§	Night	Wiltchko & Wiltchko 1975b, Spain
Robin	S	+120°	+58° (*)	Night	Bingman 1987, Italy
Thrush nightingale	S	-90°	+7° (NS)	Twilight	This study
Redstart	S, A	-90°, -90°	+15° (NS), +41° (NS)	Twilight	This study
Wheatear	A	-90°	-38° (NS)	Twilight	Sandberg et al. 1991, Sweden
Wheatear	A	-90°	-8° (NS)	Twilight	Sandberg et al. 1991, Greenland
Marsh warbler	A	-90°	+24° (NS)	Twilight	Åkesson 1993, Kenya
Marsh warbler	A	-90°	+57° (NS)	Twilight	This study, Sweden
Subalpine warbler	A	+120°	+145° (***)	Night	Wiltchko & Wiltchko 1975a, Spain
Lesser whitethroat	A	+120°	+117° (***)	Night	Wiltchko & Wiltchko 1975a, Spain
Garden warbler	A, A	+120°, +120°	+152° (**), +122° (***)	Night	Wiltchko & Wiltchko 1975a, Spain††
Pied flycatcher	S, A	-90°, -90°	+8° (NS), -40° (*)	Twilight	This study
Savannah sparrow	S	-90°†	+54° (NS)	Twilight	Moore 1985, North America

The magnetic deflections and the directional responses of the birds are given. Significance levels are according to the Mardia's one-way classification test (Mardia 1972) and Watson & Williams test (Batschelet 1981) and indicate whether the directional responses of the experimental birds are significantly different from the mean orientation in the control condition.

†Sunset direction shifted +90°.

‡The orientation in the deflected magnetic field was bimodal, and clearly different (not tested statistically) from the unimodal control direction.

§Control compared with late tests in the deflected magnetic field; the directional response of all birds in a deflected magnetic field was +30° (*, $t=2.7$; difference in concentration, Mardia's test for homogeneity of concentration parameters).

††Corresponds to tests in autumns 1972; and 1971 and 1973 (see Wiltchko & Wiltchko 1975a).

* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

clear sky the magnetic information may not always be used as a primary orientation cue. In one study the time of day when the experiments were performed may explain why the birds did not respond to the magnetic shifts (Wiltschko & Höck 1972). In other studies body condition and migration strategy have been suggested to affect the orientation responses in nocturnally migrating birds (Sandberg et al. 1988a, b; Åkesson 1993; Sandberg 1994).

Why did the birds in this study not respond to deflections of the magnetic field? There may be at least three possible explanations. First, the intensity of the magnetic field may have been disturbed in the experimental situation, caused by incorrect orientation of the electromagnetic coils, so that the birds were unable to use the magnetic information for orientation (cf. Wiltschko 1978). However, the orientation of the magnetic coils was carefully checked before each night's experiments and it is unlikely that the field intensity was affected more than a few per cent. Although I cannot completely rule out this possibility, it seems highly improbable that this small variation in field intensity would have completely destroyed the birds' ability to orient magnetically.

Second, the birds may have tried to escape from the orientation cages, perhaps showing positive photo-taxis towards the brightest part of the twilight sky, rather than true migratory orientation. Indeed, the mean orientation of many birds under clear skies did not deviate significantly from the sunset point, and the adjoining part of bright sky may have exerted some kind of attraction on the birds. Photo-taxis alone, however, cannot explain the results because the scatter in the birds' orientation increased significantly when the magnetic field was manipulated (cf. below). There was probably a distinct element of migratory orientation involved in the birds' response, because in most control tests under clear skies the birds did not deviate much from the expected migratory direction. In the marsh warbler, the control orientation was clearly separated from the sunset point and in agreement with the southeasterly direction of the migration route (Fig. 2).

Third, the birds may have predominantly used visual sunset cues for orientation and not paid much attention to the magnetic field under clear skies. This has been experimentally demonstrated for savannah sparrows, *Passerculus sandwichensis*, in a conflict experiment at sunset, in which both

the sunset direction and the magnetic field were shifted at the same time. The birds responded to the sunset deflection and obviously ignored the magnetic field (Moore 1985; cf. Table IV). In my study there was generally an increase in scatter when the magnetic conditions were manipulated compared with the control situation, except for marsh warblers in autumn (Table III). This may indicate that some individuals take notice of the magnetic field, while others do not (cf. below).

Experiments on the interaction of stellar and magnetic information during ontogeny in pied flycatchers suggest that there may be an asymmetry in how easily information is transferred from the magnetic field to stellar cues, depending on whether the magnetic north was shifted clockwise or anticlockwise compared with stellar north (see Prinz & Wiltschko 1992). Relatively few studies under clear skies have demonstrated responses in relation to anticlockwise shifts of the horizontal component of the magnetic field (responses observed in 21% of the anticlockwise experiments), compared with tests in clockwise magnetic shifts (61%; cf. Table IV). Whether this reflects a true asymmetry in the orientation system, as indicated by Prinz & Wiltschko (1992), or whether it reflects a greater tendency to rely on magnetic information under starry skies than in twilight conditions (eight out of 11 clockwise tests demonstrating a successful shift in the birds' orientation were performed under clear starry skies, while all anticlockwise tests were done in the twilight period after sunset; cf. Table IV) is unclear. It remains to be shown if an asymmetry in the orientation system might explain the lack of a clear magnetic response to anticlockwise magnetic shifts under clear sunset skies.

In conclusion, shifting the horizontal component of the magnetic field under clear skies did not shift or disrupt the orientation of the birds, except for a possible response to the magnetic field in the pied flycatcher in autumn.

Effects of Magnetic Manipulation on Scatter

The scatter in mean orientation increased not only under total overcast conditions but also when the magnetic field was manipulated under clear sky conditions and especially in a vertical magnetic field (except for juvenile marsh warblers in autumn). This tendency for orientation to be scattered in a vertical magnetic field under clear

skies is interesting, and has also been reported for dunnocks, *Prunella modularis*, robins, garden warblers and savannah sparrows (for references see Table V). In 13 out of 15 studies (binomial test, $P < 0.01$), the concentration in mean orientation decreased in a vertical magnetic field compared with the control condition (Table V).

It seems mysterious why the responses of birds in this study, orienting in a well-defined way under clear skies, and apparently being at least partly attracted towards the brightest part of the twilight sky, became scattered when the magnetic field was changed from normal to vertical. One possible interpretation is that information from both celestial and magnetic cues somehow act in concert to determine directional choice. Existing hypotheses about successive inter-calibration between different orientation cues (cf. Wiltschko & Wiltschko 1988) seem unable to accommodate the present results. Rather they suggest the existence of a more complex simultaneous integration of visual and magnetic cues in the birds' orientation mechanism.

Another possible interpretation is that some of the birds rely mainly on visual cues for their orientation while others rely on magnetic cues, or that each individual bird uses these different types of cue during part of the time of each test period. As a consequence, the orientation will deteriorate (leading to increased scatter) both when celestial cues and when magnetic cues are missing. I found no indication that the individuals differed in responses depending on their fat reserves or level of activity in the orientation cages.

I conclude that abolishing the horizontal component of the magnetic field under clear skies increased the scatter in individual mean headings in three species in spring and one in autumn, which indicates the importance of directional magnetic information for proper orientation under clear skies.

Species' Differences in Orientation Mechanism?

The different species responded in a rather similar way in the different experimental situations; however, some cases stand out from the general pattern.

The marsh warblers (autumn migration) clearly oriented away from the sunset point and in the expected migratory direction (Fig. 2); however, the mean vector length was surprisingly small. If

the birds were subjected to conflicting urges caused by solar attraction on the one hand and orientation in the migratory direction on the other hand, this may explain the different resulting orientation, with respect to both direction and scatter, for the marsh warbler in comparison with the other species. This is because the migratory direction of the marsh warbler is almost opposite to the sunset point, while the migratory direction falls within 90° of the sunset direction in all other cases (spring migration and southwest migrants in autumn). In the latter situation the birds may be relatively more prone to deviate towards the sunset direction. Hence, the peculiar orientation of the marsh warbler does not necessarily imply any difference in principle in the function of the orientation mechanism between the species.

The pied flycatcher and the redstart were significantly oriented in their spring migratory direction under overcast, indicating a successful use of the magnetic compass sense. This raises the interesting possibility that migrants that are not confronted with orientation problems at the magnetic equator (e.g. pied flycatcher and redstart) use the magnetic compass more readily on migration than do trans-equatorial migrants (e.g. marsh warbler, thrush nightingale; cf. Åkesson 1993). However, the present evidence is not sufficient to permit such a conclusion. The experiments with a deflected magnetic field failed to confirm that the pied flycatchers and redstarts really are guided by the magnetic field under overcast (Table III).

Wiltschko & Wiltschko (1975a, b) reported that there may be differences in the calibration time of the star and the magnetic compasses between short-distance (robins) and long-distance (*Sylvia* warblers) migratory bird species. There was a few days' delay in the response to a magnetic shift in robins, while the warblers responded immediately and changed their orientation according to the magnetic field, obviously ignoring information from the stars. Wiltschko & Wiltschko suggested that long-distance migrants calibrate the magnetic compass against the stars more often than short-distance migrants. If this is correct, we would expect that long-distance migrants would rely mainly on magnetic information. However, in my study the experimental birds did not respond to the deflections of the magnetic field and they were less well oriented under overcast conditions,

Table V. Orientation experiments performed in the local geomagnetic field (control) and in a vertical magnetic field under natural clear skies with different species of migratory birds during the spring (S) and autumn (A) migration period

Species	Season	Mean vector length		Time of test	References
		Control	Vertical		
Dunnoch	S	0.45 (***)	0.37 (*)	Twilight	Bingman & Wiltschko 1988
Robin	A	0.45 (***)	0.20 (NS)	Twilight	Pettersson et al. 1991
Robin	S	0.39 (***)	0.33 (**)	Twilight	Pettersson et al. 1991
Robin	S	0.51 (**)	0.35 (*) total	Night	Wiltschko & Wiltschko 1975b
Robin	S	0.39 (**)	0.23 (NS)	Night	Bingman 1987
Thrush nightingale	S	0.55 (***)	0.31 (**)	Twilight	This study
Redstart	S	0.63 (***)	0.36 (**)	Twilight	This study
Redstart	A	0.43 (**)	0.30 (NS)	Twilight	This study
Wheatear	A	0.38 (**)	0.42 (**)	Twilight	Sandberg et al. 1991
Wheatear	A	0.39 (*)	0.35 (*)†	Twilight	Sandberg et al. 1991
Marsh warbler	A	0.28 (*)	0.31 (*)	Twilight	This study
Garden warbler	A	0.56 (**)	0.16 (NS)	Night	Wiltschko & Wiltschko 1975a
Pied flycatcher	S	0.69 (***)	0.17 (NS)	Twilight	This study
Pied flycatcher	A	0.51 (***)	0.24 (NS)	Twilight	This study
Savannah sparrow	S	0.56 (**)	0.09 (NS)	Twilight	Bingman 1983
Savannah sparrow	A	—	0.21 (NS)	Twilight	Bingman 1983

Mean vector lengths and significance levels according to the Rayleigh test (Batschelet 1981) are given.

† r_2 ; $r_1 = 0.26$ (NS).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

indicating that they did not rely on magnetic information for orientation in the twilight period after sunset.

I conclude that my results do not imply any clear differences in the function of the orientation mechanism, and in the relative importance of different cues, between the species studied. In all species, the orientation responses seem to have been affected in a similarly complex way by celestial as well as magnetic cues. The birds' behaviour under clear skies may be the outcome of conflicting urges to orient towards the brightest part of the twilight sky (presumably by visual cues) and in the migratory direction (by magnetic/visual cues). However, the observed pattern of orientation under the different experimental conditions is too multifaceted to be fully explained as a simple composite vector sum of visual and magnetic directional preferences according to two such main urges. How the birds' multicue orientation system operates during actual migration still defies our attempts to understand it.

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