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Effect of geomagnetic field on orientation of the marsh warbler, *Acrocephalus palustris*, in Sweden and Kenya

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Abstract. The orientation of juvenile marsh warblers during autumn migration was investigated at two widely different latitudes, in Sweden and in Kenya, by cage experiments in manipulated magnetic fields during the twilight period after sunset. The objective was to compare responses by birds exposed to different geomagnetic conditions, particularly to the shift in magnetic inclination between the northern and southern hemispheres. Orientation experiments were performed under clear skies and under simulated total overcast. The marsh warblers from the two sites differed markedly in their orientation under clear skies. Marsh warblers in Sweden showed an average orientation in the expected migratory direction (southeast), while in Kenya they oriented towards west-northwest by northwest (significantly different from the sunset point), a direction clearly different from the expected migratory direction in this area (south-southwest). The warblers did not respond in a consistent way to shifts in the magnetic field and they failed to show significant directional tendencies under total overcast conditions, indicating the importance of visual rather than geomagnetic cues for the birds' orientation. In Kenya activity in the orientation cages was strongly reduced under overcast skies in comparison with clear sky conditions. Mean mass and fat deposits of the marsh warblers were much larger in Sweden than in Kenya. These results indicate that migratory marsh warblers captured and tested at different sites along the migration route show markedly different orientational dispositions associated with differences in body condition and migratory strategy.

Orientation using information from the geomagnetic field was first discovered in birds more than two decades ago (Merkel & Wiltschko 1965; Wiltschko 1968). Since then, a large number of reports have revealed that a magnetic compass sense is widespread among birds and other animals (see Kirschvink et al. 1985; Wiltschko & Wiltschko 1988). The magnetic compass sense of robins, *Erithacus rubecula*, is based on the angle of inclination and not on the polarity of the geomagnetic field (Wiltschko & Wiltschko 1972). An inclination compass has also been demonstrated in the garden warbler, *Sylvia borin* (Wiltschko 1974), the pied flycatcher, *Ficedula hypoleuca* (Beck & Wiltschko 1981) and the bobolink, *Dolichonyx oryzivorus* (Beason 1989; but see also Beason & Nichols 1984).

Nocturnal migratory birds are known to make use of other orientational cues, such as the stars (Sauer 1957; Emlen 1967a, b), the sunset point and/or the polarization pattern of the sky (Able 1982; Moore 1982; reviewed by Moore 1987). The interrelationship between different compass systems is poorly understood, but experience and age of the bird (Gauthreaux 1982; Moore 1984; Able & Bingman 1987), migratory status (Sandberg et al. 1988a; Sandberg, in press) and test condition (see Helbig 1991) seem to affect the birds' orientation response. Compass mechanisms may also be species-specific (see Able & Bingman 1987; Helbig 1990).

The geomagnetic field furnishes orientational and navigational information (Skiles 1985). At the geomagnetic poles the field lines are vertically oriented (inclination 90°), at intermediary latitudes there are varying angles of inclination and at the magnetic equator the field lines are oriented parallel to the earth's surface (inclination 0°; Skiles 1985; Fig. 1). An inclination compass reveals no directional information in a horizontal magnetic field and is therefore in theory impossible to use at the magnetic equator. Robins (Wiltschko & Wiltschko 1972) and garden warblers (Wiltschko 1974) tested in artificial horizontal magnetic fields fail to establish a significant orientation. Several bird species migrate between breeding grounds in the Northern Hemisphere and wintering grounds in the Southern Hemisphere (see, e.g. Moreau 1972;

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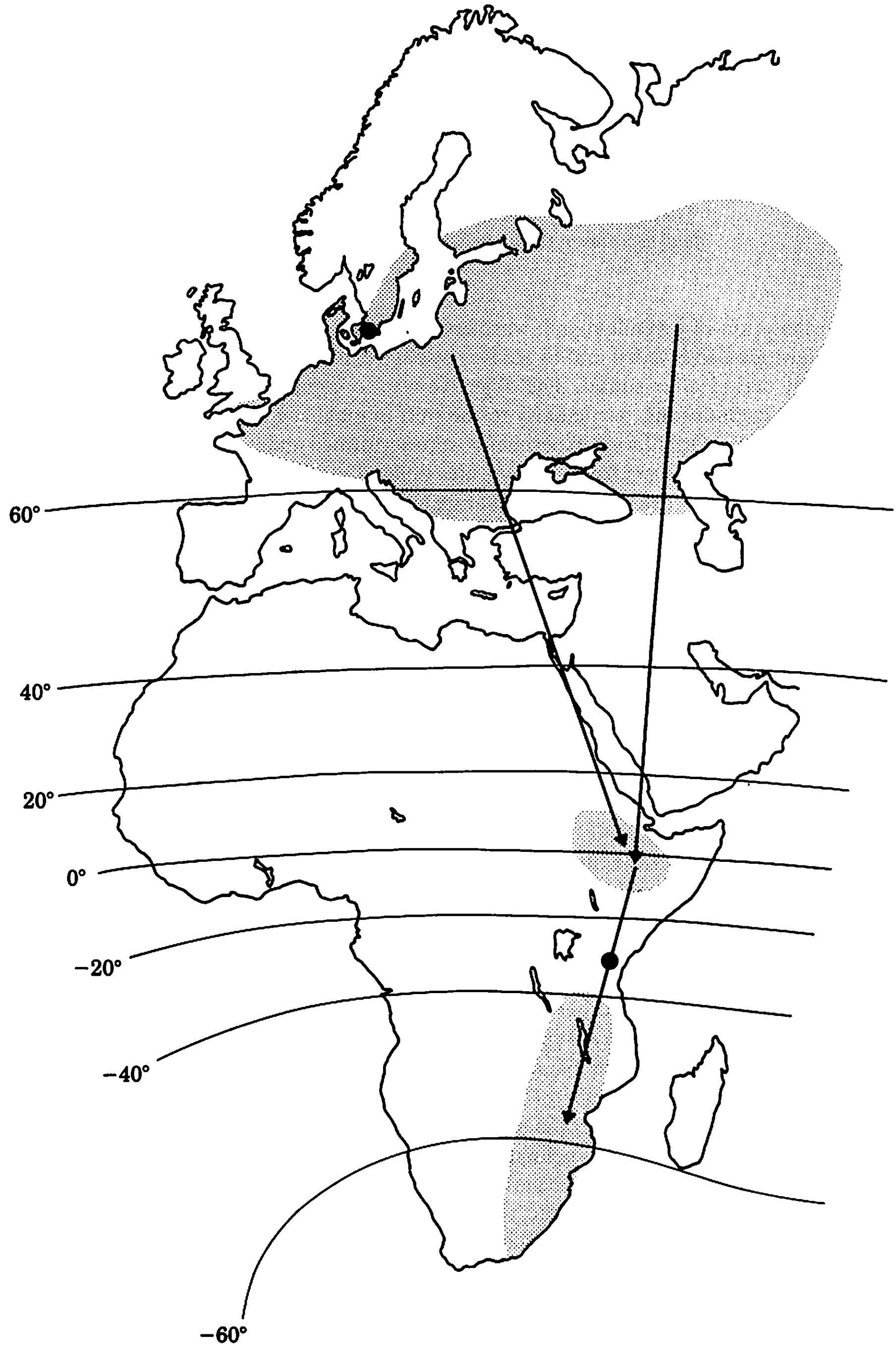

Figure 1. Map of breeding range in Europe, autumn stop-over area in northeastern Africa and wintering grounds in southeastern Africa of marsh warblers. The arrows indicate the suggested migration route. ●: Study sites in Sweden (inclination +70°, declination 0°, 49 μT) and in Kenya (inclination −30°, declination −5°, 35 μT). The isoclines indicate the angle of inclination of the geomagnetic field with the 0°-isocline corresponding to the geomagnetic equator.

Table I. Numbers of marsh warblers tested in orientation experiments under different experimental conditions in Sweden and Kenya, respectively

Experimental condition	Sweden				Kenya			
	Inactive	Disoriented	Included in analysis	Total	Inactive	Disoriented	Included in analysis	Total
Clear sky								
Control	17	6	41	64	8	6	58	72
Deflected	3	2	45	50	18	4	37	59
Vertical	12	4	36	52	—	—	—	—
Simulated total overcast								
Control	23	12	25	60	40	2	7	49
Deflected	17	7	31	55	28	2	2	32
Vertical	15	8	31	54	—	—	—	—

The experiments were performed in local geomagnetic conditions (control), in a deflected magnetic field (magnetic north towards geographical west) and in a vertical magnetic field, under clear sky and simulated total overcast, respectively. Because of inactivity (Inactive, <40 registrations per bird-hour) and disorientation (Disoriented, see text), some birds were excluded from the analysis.

Alerstam 1990), and these birds cross the magnetic equator twice each year. It is interesting that in two of these transequatorial migrants, the garden warbler and the bobolink, the magnetic compass seems to be an inclination compass (Wiltschko 1974; Beason 1989). The intriguing question of how the transequatorial migrants orient close to the magnetic equator has not been resolved.

I carried out comparative orientation tests with transequatorially migrating marsh warblers in manipulated magnetic fields at two sites on their autumn migration route, in Sweden and Kenya, respectively. The purpose was to investigate the relative importance of different orientation cues, and especially the use of the geomagnetic field, at different latitudes along the migration route. Of special interest was to investigate if and how this transequatorial migrant uses the geomagnetic field with a steep inclination (+70°) in Sweden and a low and reversed inclination (−30°) in Kenya after it has crossed the geomagnetic equator. Experiments were performed in local geomagnetic conditions, in a shifted geomagnetic field and in a vertical magnetic field. The experiments were designed so that responses in the birds' orientation to shifts of the magnetic field under clear and overcast skies would demonstrate if they use the geomagnetic field as an orientation cue and to what extent they rely on visual celestial cues.

METHODS

Experimental Subject and Study Areas

Marsh warblers breed in Europe and migrate to winter quarters in southeast Africa (Voous 1960; Moreau 1972; Zink 1973; Fig. 1). The autumn migration is divided into two stages, with a stop-over period from the end of August until mid November somewhere in southwestern Ethiopia or eastern Sudan, before southward migration is resumed on a narrow front through eastern Kenya (Pearson & Backhurst 1976; Backhurst & Pearson 1984; Pearson 1990). Wintering grounds to the south and southwest of Kenya are reached during December and January with the first arrivals in the last week of November (Dowsett-Lemaire & Dowsett 1987).

In Sweden the orientation experiments were conducted between 9 August and 10 September in 1990 and 1991. Juvenile marsh warblers, aged according to Svensson (1984), were captured at stop-over sites in southwestern Sweden, at Falsterbo Bird Observatory (55°23′N, 12°50′E) in 1990 and 1991, and also at Sote Mosse (55°25′N, 13°25′E) in 1991 (for numbers see Table I). The marsh warblers were transported approximately 55 km by car to the northeast to a test site at Stensoffa Ecological Field Station (55°42′N, 13°25′E; northern test site in Fig. 1). At this test site the birds were housed indoors in a room with windows, under the natural photoperiod and local geomagnetic conditions (inclination +70°). The birds were kept individually in spacious cages (350 × 350 × 450 mm), with an unlimited amount of vitaminized water and food (mealworms). Each bird was held in captivity for approximately 10 days, during which it was tested in up to six orientation experiments. In Kenya, juvenile marsh warblers were captured at Ngulia Safari Lodge (3°00′S, 38°13′E, Tsavo West National Park; Fig. 1) and tested in orientation cages between 15 and 27 November and between 12 and 20 December 1990 (for numbers see Table I). The birds were attracted to game-lights at the Lodge on misty and moonless nights while migrating through the area. The timing and procedure of catching at Ngulia Lodge are described in detail by Pearson & Backhurst (1976; see also the yearly ringing reports in *Scopus*). After capture, the birds were immediately placed in individual cages (350 × 350 × 400 mm) with water and food in a separate room at the Lodge, under the natural photoperiod and under local geomagnetic conditions (inclination −30°). The orientation tests were performed in an open area at the Lodge. The majority of the birds were held in captivity only during the day of capture and were released after one test occasion (about 20% of the birds were kept and fed during the following day as well, and tested a second time under a different experimental condition).

To investigate if there was any relationship between body condition and the birds' orientation, the marsh warblers were measured and weighed, in both Sweden and Kenya, to the nearest 0·1 g with a 50-g Pesola spring balance. Fat deposits on the birds' bellies and in the tracheal pits were visually estimated according to a 7-graded scale of fat classification (see Pettersson & Hasselquist 1985), at capture and each evening before the experiments were initiated.

Experimental Set-up and Procedure

The experimental set-up and procedure were principally the same in Sweden and Kenya. The orientation cages used in Kenya were modified Emlen funnels (Emlen & Emlen 1966), with a top diameter of 300 mm and an inner height of 150 mm, allowing the birds to see approximately 160° of the sky. The activity of the birds was registered from the marks in the pigment of typewriter correction paper (Tipp-ex) which was attached to the sloping walls of the cages (see, e.g. Rabøl 1979; Beck & Wiltschko 1981). After the experiments, the paper was subdivided into 24 sectors and the claw scratches across a certain line were counted in each sector. I calculated activity and the mean direction of individual birds on the basis of the registrations in the 24 sectors, using vector addition (Batschelet 1981). Cages of the Emlen type with automatic registration were used in Sweden in additon to the 'Tipp-ex cages' descibed above. These cages had a top diameter of 310 mm, an inner height of 125 mm and also allowed the birds to see approximately 160° of the sky. The sloping walls were subdivided into eight 45°-sectors, under each of which a microswitch was placed and connected to a counter. When the bird jumps on the sector the microswitch closes and the jump is recorded at the specific counter. The mean vector was calculated later on the basis of the recorded registrations in the eight sectors (Batschelet 1981). The orientation cages were all constructed of non-magnetic material and covered with fine-mesh plastic net allowing the birds to see the natural sky. There was no significant difference in the orientation of the birds tested in the two cage types in Sweden, and therefore the data sets from the two types of cages were pooled.

Electromagnetic coils (modified Helmholtz coils, 800 × 800 mm), powered by a car battery (12 V), were arranged in pairs around the orientation cages (for technical specification of the electromagnetic coils see Sandberg et al. 1988b). The coils were constructed to produce a homogeneous magnetic field in the centre and were used to manipulate the horizontal component of the geomagnetic field, (deflecting it by 90° or cancelling it). The same electromagnetic coils were used in both Kenya and Sweden. To simulate total overcast, diffusing Plexiglas sheets were put on top of the orientation cages. Under natural total overcast (8/8, in Sweden only) the birds were exposed to the natural sky instead. The orientation under natural total overcast did not differ significantly from the orientation under simulated total overcast, and these data sets were pooled.

The orientation experiments in Sweden were initiated 10 min after sunset and lasted for 60 min, which allowed the birds to see the horizon glow from the sunset. During the last part of the test period the first stars were visible. In Kenya, the sunset period was much shorter than in Sweden (Civil twilight period in Kenya = 23 min and in Sweden = 45 min) and the experiments were initiated 10 min before

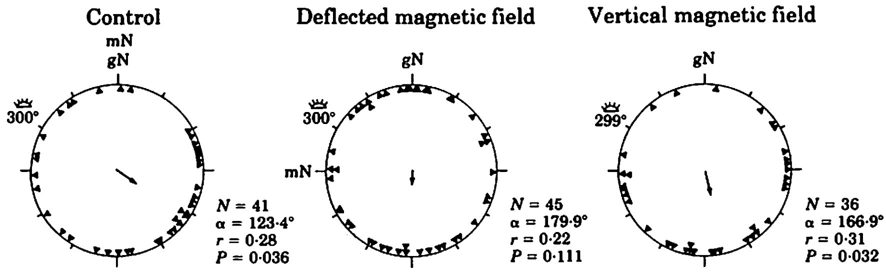

Figure 2. Results of orientation experiments with juvenile marsh warblers during autumn migration in Sweden under clear sky conditions. The experiments were performed in the local geomagnetic field (control: inclination +70°), in a deflected geomagnetic field (magnetic north, mN corresponds to geographical west, gW, inclination +70°) and in a vertical magnetic field (inclination +90°), respectively. ▲: The distributions of mean directions of individual marsh warblers. N = The total number of birds tested. The arrows indicate mean vectors (with α = mean angle of orientation) and the length of the arrows is a measure of the circular distribution (r ranges between 0 and 1, being inversely related to the angular scatter). Significance levels are according to the Rayleigh test (Batschelet 1981). The direction towards geographical (gN) and magnetic north are indicated for each of the test conditions, respectively. The mean direction towards the position of the sun in the middle of the test hour is indicated.

sunset and lasted for 75 min. I used the following three magnetic conditions in the orientation experiments in Sweden: (1) local geomagnetic field (inclination +70°); (2) deflected magnetic field with the horizontal component shifted −90°, i.e. with magnetic north towards geographical west (inclination +70°); (3) vertical magnetic field (inclination +90°). In the local geomagnetic field (1 above) one would expect the warblers to orient towards their preferred migratory direction, which under clear skies may be based on both visual and geomagnetic cues, while under total overcast conditions only the geomagnetic field is available for directional information. If the birds use the geomagnetic field as an orientation cue, one would expect a shift in their orientation corresponding to the deflection of the magnetic field (2 above). A vertical magnetic field provides no directional information (3 above) and therefore we expect to find disorientation under this condition if the birds rely on magnetic information.

In Kenya tests were performed under two different magnetic conditions only (because of the seasonal time restrictions), in the local geomagnetic field (inclination −30°) and in a deflected magnetic field with the horizontal component shifted −90° (inclination −30°, see 1 and 2 above). The birds were tested in each magnetic condition under clear skies as well as under total overcast skies in both Kenya and Sweden. Individual birds were used only once in each of these test conditions, and for each individual the experiments were performed in random order.

I quantified the activity of the birds as the number of counter registrations or scratches (minimum 40) during one test hour. A mean heading of each bird was calculated by vector addition and birds that failed to show a reasonably well-defined orientation (the limit was set to $P > 0{\cdot}05$ according to the Rayleigh test; cf. Batschelet 1981) were excluded. I used this limit as a criterion to exclude highly disoriented and unreliable orientation results from the analysis. Differences in concentration or mean orientation between groups were analysed with Mardia's one-way classification test (Mardia 1972).

RESULTS

The number of marsh warblers tested under different experimental conditions, and the number of birds excluded from the analyses, owing to inactivity or disorientation, are shown in Table I.

Clear Sky, Sweden

The birds showed significantly oriented behaviour in the expected migratory direction (southeast) under unmanipulated magnetic conditions and in a vertical magnetic field, while in a deflected magnetic field the orientation was not significantly different from random (Fig. 2). The orientation in a deflected magnetic field was more scattered but not significantly so, than in local geomagnetic conditions (Mardia's one-way classification test, $t = 0{\cdot}4$, $df = 84$, $P > 0{\cdot}05$) or in a vertical magnetic field (Mardia's one-way classification test, $t = 0{\cdot}6$,

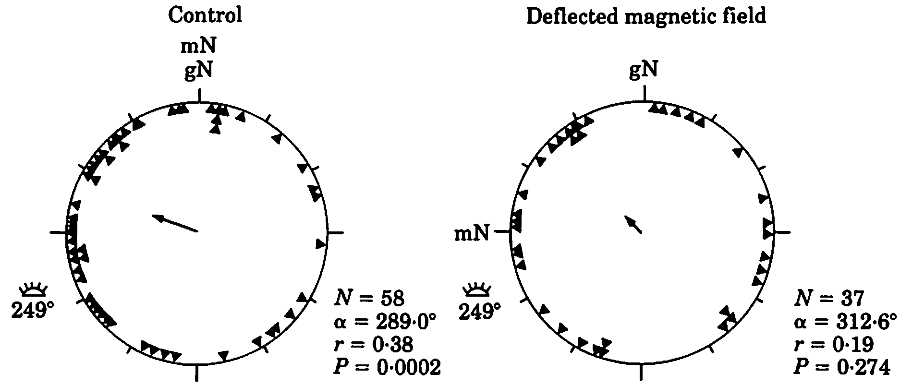

Figure 3. Results of orientation experiments performed with juvenile marsh warblers under clear skies during autumn migration in Kenya. Orientation tests were conducted in the local geomagnetic field (control; inclination −30°) and in a deflected magnetic field (inclination −30°). For further information see Fig. 2.

$df=79$, $P>0.05$). The orientation under local geomagnetic conditions was not significantly different from that in a vertical magnetic field (Mardia's one-way classification test, $\psi=2.2$, F_{75}, $P>0.05$). The mean orientation was significantly different from the direction towards the sunset point in the local geomagnetic field (95% confidence interval ±48°, Batschelet 1981) as well as in the vertical magnetic field (95% confidence interval ±47°).

Clear Sky, Kenya

Control birds showed a highly significant orientation towards west-northwest by northwest, different from the expected migratory direction (south-southwest); they failed to show a significant mean orientation in a deflected magnetic field (Fig. 3), but the difference in scatter was not significant (Mardia's one-way classification test, $t=1.3$, $df=93$, $P>0.05$). The mean orientation of control birds was significantly different from the sunset direction (95% confidence interval ±28°).

Simulated Total Overcast Sky, Sweden and Kenya

Marsh warblers tested under simulated total overcast skies in Sweden failed to show a significant directional tendency in any of the three magnetic conditions (Fig. 4). The activity of the test birds under overcast skies was drastically reduced in Kenya, and the few birds that were active in the orientation cages did not show any significant directional tendency in the local geomagnetic field ($N=7$, the mean angle of orientation, $\alpha,=19.0°$, the mean vector length, $r,=0.30$, $P=0.53$). In a deflected geomagnetic field the activity was even more reduced, and only two birds showed activity above the limit of 40 registrations per test-hour.

Fat, Test Order and Level of Activity

Data sets from the orientation tests in different magnetic conditions were grouped and analysed with respect to the birds' fat content, level of activity and experimental order. One would expect that birds carrying large fat deposits and showing intensive activity during the test-hour would be more inclined than others to respond with a directional tendency corresponding to the expected migratory direction. However, I found no significant relationship between orientation and the birds' fat content under local geomagnetic conditions under clear sky either in Sweden (fat class 1–3 compared with fat class 4–6; Mardia's one-way classification test, $F_{39}=0.007$, $P>0.05$) or in Kenya (fat class 1–3 compared with fat class 4–6, Mardia's one-way classification test, $F_{56}=0.01$, $P>0.05$). The orientation of birds with low activity ($\leqslant 149$ registrations) and high activity ($\geqslant 150$ registrations) under clear skies in the local geomagnetic field did not differ significantly either in Sweden (Mardia's one-way classification test, $F_{39}=0.3$, $P>0.05$) or in Kenya (Mardia's one-way classification test, $F_{56}=1.3$, $P>0.05$).

To investigate whether test order had an effect on the orientation recorded in experiments under clear skies and in a local geomagnetic field in Sweden, the tests were grouped based on whether they were done first in a row of different test conditions or immediately after those performed under clear

Table II. Mass (g) at capture of marsh warblers used in orientation experiments in Sweden and Kenya

	Mass										
	9·0–9·9	10·0–10·9	11·0–11·9	12·0–12·9	13·0–13·9	14·0–14·9	15·0–15·9	16·0–16·9	17·0–17·9	N	$\bar{X}\pm$SD
Kenya	3	26	32	23	8	1	3	1	0	98	11·6±1·8
Sweden	0	0	6	9	18	14	14	5	1	67	14·1±1·4

skies in a deflected magnetic field (a condition with conflicting geomagnetic and visual information). There was no significant difference in the orientation between these two groups of experiments performed under clear skies and in a local geomagnetic field (Mardia's one-way classification test; $F_{29}=0{\cdot}5$, $P>0{\cdot}05$). Further, I found no consistent significant effect of test order on the orientation responses observed in any of the other experimental categories.

The marsh warblers captured in Sweden were markedly heavier than those captured in Kenya ($t=9{\cdot}9$, $df=163$, $P<0{\cdot}001$; Table II). This difference may be explained at least partly by dissimilar average body sizes, if marsh warblers in Sweden are on average larger than those passing through Kenya (Kenya birds originate from a very extensive breeding range). Indeed, the marsh warblers captured in Sweden had, on average, longer wings ($\bar{X}\pm$SD wing length $=70{\cdot}0\pm1{\cdot}4$ mm, $N=66$; maximum wing length, see Svensson 1984) than the birds in Kenya ($68{\cdot}5\pm1{\cdot}5$ mm, $N=77$; $t=6{\cdot}1$, $df=141$, $P<0{\cdot}001$). It is possible to correct for the body size differences by calculating the relative body mass, i.e. mass/(wing-length)^3, assuming isometric scaling. A difference in relative body mass would indicate that the amount of fuel reserves differs, independently of the birds' body sizes. There was a highly significant difference in mean relative body mass between the marsh warblers in Sweden and Kenya ($t=6{\cdot}9$, $df=132$, $P<0{\cdot}001$), demonstrating that the birds in Sweden built up much larger fat reserves than they did in Kenya. Marsh warblers in Sweden put on an average of 23% of extra fuel reserves (their estimated fat-free mass is about 11·4 g). In contrast, birds captured in Kenya carried only about 12% fuel (based on an estimated fat-free mass of about 10·3 g).

The proportion of active birds (Table I) did not differ significantly between different magnetic conditions at either site under overcast conditions (Sweden: $\chi^2=0{\cdot}2$, $df=2$, $P>0{\cdot}05$; Kenya: $\chi^2=0{\cdot}2$, $df=1$, $P>0{\cdot}05$). Under clear sky there was a significant difference in the proportion of active birds in different magnetic conditions in Sweden ($\chi^2=8{\cdot}3$, $df=2$, $P<0{\cdot}05$) and in Kenya ($\chi^2=6{\cdot}5$, $df=1$, $P<0{\cdot}05$). In Sweden the test birds were active relatively more often in a deflected magnetic field than in the other magnetic conditions under clear skies. In contrast, in Kenya the proportion of active test birds was lower in a deflected magnetic field than in a normal geomagnetic one. The activity was significantly reduced under overcast conditions compared with clear sky conditions in Sweden in a deflected magnetic field ($\chi^2=9{\cdot}0$, $df=1$, $P<0{\cdot}01$) but not significantly reduced either in a normal magnetic field ($\chi^2=1{\cdot}5$, $df=1$, $P>0{\cdot}05$) or in a vertical magnetic field ($\chi^2=0{\cdot}7$, $df=1$, $P>0{\cdot}05$). In Kenya the activity was drastically reduced under overcast conditions in a normal magnetic field ($\chi^2=57{\cdot}7$, $df=1$, $P<0{\cdot}001$) as well as in a deflected magnetic field ($\chi^2=24{\cdot}7$, $df=1$, $P<0{\cdot}001$).

The results show that activity in the orientation cages during the experimental hour was strongly reduced under overcast conditions in Kenya. This reduction in activity under overcast was much less pronounced in Sweden.

DISCUSSION

Orientation Under Clear Sky

Under clear skies the juvenile marsh warblers in Sweden oriented towards the southeast, the expected migratory direction (see Zink 1973), in local geomagnetic conditions as well as in a vertical magnetic field (Fig. 2). The results under the latter condition indicate that the magnetic field is not necessary for the birds' orientation.

In Kenya, the orientation in an unmanipulated magnetic field did not coincide with the expected migratory direction, but instead was directed west-

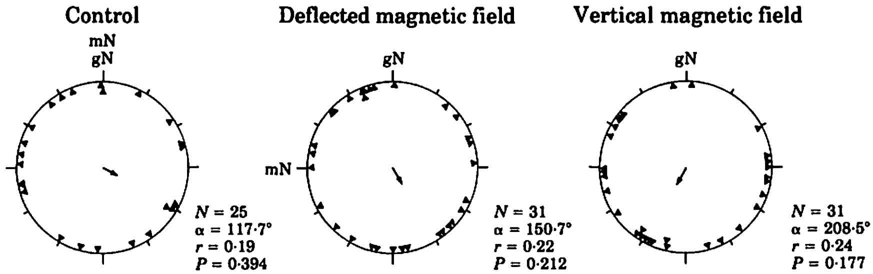

Figure 4. Orientation results of experiments performed with juvenile marsh warblers under simulated total overcast (diffusing Plexiglas sheets) during autumn migration in Sweden. For further information see Fig. 2.

northwest by northwest, a direction significantly different from the sunset point (Fig. 3). A 'nonsense' orientation (towards northwest) has been observed in orientation experiments with starlings, *Sturnus vulgaris* (Kramer 1951) and in release experiments with mallards, *Anas platyrhynchos* (Matthews 1961). A northwest orientation different from the appropriate migratory direction has been reported also in juvenile wheatears, *Oenanthe oenanthe* (Sandberg et al. 1991) and in robins (Wiltschko 1980; Sandberg et al. 1988a), but this divergent and enigmatic orientation has not yet been explained. Under clear skies the orientation in a deflected magnetic field was not significantly different from random either in Sweden or in Kenya. Although the distributions were not significantly more scattered than in unmanipulated magnetic conditions the suggestion of a poor orientation in a deflected magnetic field (see Figs 2 and 3) may indicate that the magnetic field, under conditions when visual and magnetic cues are in conflict, in some way had an effect on orientation performance under clear skies at both sites.

If the magnetic field was of major importance we would expect a shift of the mean orientation of the birds corresponding to the shift of the magnetic field, and also a much more scattered distribution in a vertical magnetic field. A significantly more scattered orientation in a vertical magnetic field has been reported for other night-migrating passerines such as the robin (Pettersson et al. 1991) and in hand-reared savannah sparrows, *Passerculus sandwichensis* (Bingman 1983). This is not what I found for Swedish marsh warblers, which maintained a mean orientation close to the expected migratory direction in a vertical magnetic field.

The orientation experiments under clear skies indicate that the geomagnetic field plays a minor role or no role at all in the orientation of juvenile marsh warblers tested during the evening twilight at different latitudes during autumn migration. One possible explanation is that the marsh warblers do not rely on magnetic orientation because of difficulties in using an inclination compass for transequatorial migrants. However, recent laboratory experiments with garden warblers (Wiltschko & Wiltschko 1992) and bobolinks (Beason 1992), both of which are transequatorial migrants, speak against this possibility. These two spieces were held in captivity during the autumn migration period under changing magnetic conditions, simulating the birds' migratory passage across the magnetic equator. After exposure in a horizontal magnetic field (simulating equator-crossing) the birds changed their orientation approximately 180°, a response corresponding to the shift in the inclination compass which the birds experience when crossing the magnetic equator (Wiltschko & Wiltschko 1992).

Why the marsh warblers captured and tested on actual migration seem to rely primarily on visual cues rather than on their inclination compass, if they are able to adapt it to the changing magnetic conditions along their route, remains to be explained.

Orientation Under Simulated Total Overcast Skies

The results from the orientation experiments under overcast skies support the conclusion that the magnetic field is not used as a major orientational cue either in Sweden or in Kenya. A significant directional tendency failed to emerge in any magnetic conditions under overcast skies (see Fig. 4), in contrast to what has been reported in other night-migrating passerines tested with the same experimental set-up (Sandberg et al. 1988a, 1991). These results indicate that marsh warblers are highly dependent on visual cues for orientation. In Kenya, the activity under simulated total overcast was much reduced (Table I), and only 16% of the birds were active during the test-hour. Hence, the ability to orient properly, or the motivation to migrate in Kenya under overcast conditions, seems to be strongly reduced.

Why do the Birds Orient Differently in Sweden and Kenya?

There are at least two possible causes for the interesting and marked differences in the marsh warblers' orientation between Sweden and Kenya under clear skies in the local geomagnetic field. (1) The birds captured in Kenya may already have reached their winter quarters and therefore exhibit reduced or no migratory activity, compared with Sweden. This is unlikely, since the wintering grounds are situated much further south of Ngulia Lodge (see Moreau 1972; Dowsett-Lemaire & Dowsett 1987). (2) The birds may use different migration strategies in Sweden and in Kenya. The mass and fat reserves probably reflect what overall migration strategy the birds use and it has been demonstrated that body condition and migration strategy have an important effect on the orientation responses recorded in orientation cages (Sandberg et al. 1988a).

In orientation experiments with robins at two stop-over sites in Sweden, Sandberg et al. (1988a) found that, when tested during the twilight period in autumn, robins captured after flights mainly over land were oriented towards west-northwest and carried rather little fat, while birds captured after longer flights across the sea oriented in a direction corresponding to the expected migratory direction and had larger fat reserves (see also Karlsson et al. 1988; Åkesson et al. 1992).

Do the marsh warblers in Sweden and Kenya represent a case that is analogous to that of the robins travelling over sea and land in southern Scandinavia? The marsh warblers in Sweden put on large amounts of fat to prepare for long-distance flights across the Baltic Sea and perhaps further across Central Europe, orienting in the expected migratory direction. In contrast, the marsh warblers in Kenya carry less fuel, presumably migrating by shorter flights through the interior of southeast Africa and exhibiting orientation responses clearly different from the expected migratory direction.

Measurements of migratory activity (Zughunruhe) of marsh warblers held in cages and tested repeatedly during the autumn show a peak of activity during the first part of the migration period (August to September) followed by a comparatively long period of reduced migratory activity (Berthold & Leisler 1980). This supports the suggestion that the last part of the migration may be performed in short jumps rather than long-distance flights, as was also proposed by Berthold & Leisler (1980).

In conclusion, my results indicate that the orientation behaviour of the marsh warbler is flexible and that it is possibly closely connected with the migration strategy used by the bird. However, it remains to be explained why orientation changes with migration strategy and why migration by short successive flights and with small fat reserves may be associated with an orientation response that deviates from the expected migratory direction. For a migrating bird, it is clearly of adaptive value to have a flexible orientation system, but it remains to be shown how different compass systems are interrelated and under what circumstances specific orientation mechanisms are used by the birds.

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REFERENCES

Able, K. P. 1982. Skylight polarization patterns at dusk influence migratory orientation in birds. *Nature, Lond.*, **299**, 550–551.

Able, K. P. & Bingman, V. P. 1987. The development of orientation and navigation behaviour in birds. *Q. Rev. Biol.*, **62**, 1–29.

Åkesson, S., Karlsson, L., Pettersson, J. & Walinder, G. 1992. Body contents and migration strategies: a comparison between robins *Erithacus rubecula* from two stop-over sites in Sweden. *Vogelwarte*, **36**, 188–195.

Alerstam, T. 1990. *Bird Migration*. Cambridge, Cambridge University Press.

Backhurst, G. C. & Pearson, D. J. 1984. The timing of southward night migration of Palaearctic birds over Ngulia, southeast Kenya. *Proc. Pan-Afr. Ornithol. Congr.*, **5**, 361–369.

Batschelet, E. 1981. *Circular Statistics in Biology*. New York: Academic Press.

Beason, R. C. 1989. Use of an inclination compass during migratory orientation by the bobolink *Dolichonyx oryzivorus*. *Ethology*, **81**, 291–299.

Beason, R. C. 1992. You can get there from here: responses to simulated magnetic equator crossing by the bobolink (*Dolichonyx oryzivorus*). *Ethology*, **91**, 75–80.

Beason, R. C. & Nichols, J. E. 1984. Magnetic orientation and magnetically sensitive material in a transequatorial migratory bird. *Nature, Lond.*, **309**, 151–153.

Beck, W. & Wiltschko, W. 1981. Trauerschnäpper, *Ficedula hypoleuca* Pallas, orientieren sich nichtvisuell mit Hilfe des Magnetfelds. *Vogelwarte*, **31**, 168–174.

Berthold, P. & Leisler, B. 1980. Migratory restlessness of the marsh warbler *Acrocephalus palustris*. *Naturwissenschaften* **67**, 472.

Bingman, V. P. 1983. Importance of earth's magnetism for the sunset orientation of migratory naive savannah sparrows. *Monit. zool. ital.*, **17**, 395–400.

Dowsett-Lemaire, F. & Dowsett, R. J. 1987. European reed and marsh warblers in Africa: migration patterns, moult and habitat. *Ostrich*, **58**, 65–86.

Emlen, S. T. 1967a. Migratory orientation in the indigo-bunting, *Passerina cyanea*. I. The evidence for use of celestial cues. *Auk*, **84**, 309–342.

Emlen, S. T. 1967b. Migratory orientation in the indigo bunting, *Passerina cyanea*. II. Mechanisms of celestial orientation. *Auk*, **84**, 463–489.

Emlen, S. T. & Emlen, J. T. 1966. A technique for recording migratory orientation of captive birds. *Auk*, **83**, 361–367.

Gauthreaux, S. A., Jr. 1982. Age-dependent orientation in migratory birds. In: *Avian Navigation* (Ed. by F. Papi & H. G. Wallraff), pp. 68–74. Berlin: Springer-Verlag.

Helbig, A. 1990. Are orientation mechanisms among migratory birds species-specific? *Trends Ecol. Evol.*, **5**, 365–366.

Helbig, A. 1991. Experimental and analytical techniques used in bird orientation research. In: *Orientation in Birds* (Ed. by P. Berthold), pp. 270–306. Basel: Birkhäuser Verlag.

Karlsson, L., Persson, K., Pettersson, J. & Walinder, G. 1988. Fat-weight relationships and migratory strategies in the robin *Erithacus rubecula* at two stop-over sites in south Sweden. *Ring. Migr.*, **9**, 160–168.

Kirschvink, J. L., Jones, D. S. & MacFadden, B. J. (Eds) 1985. *Magnetite Biomineralization and Magnetoreception in Organisms. A New Biomagnetism*. New York: Plenum Press.

Kramer, G. 1951. Eine neue Methode zur Erforschung der Zugorientierung und die bisher damit erzielten Ergebnisse. *Proc. Ornithol. Congr., Uppsala*, **10**, 269–280.

Mardia, K. V. 1972. *Statistics of Directional Data*. London: Academic Press.

Matthews, G. V. T. 1961. 'Nonsense' orientation in mallard, *Anas platyrhynchos*, and its relation to experiments on bird navigation. *Ibis*, **103a**, 211–230.

Merkel, F. W. & Wiltschko, W. 1965. Magnetismus und Richtungsfinden zugunruhiger Rotkehlchen (*Erithacus rubecula*). *Vogelwarte*, **23**, 71–77.

Moore, F. R. 1982. Sunset and the orientation of a nocturnal bird migrant: a mirror experiment. *Behav. Ecol. Sociobiol.*, **10**, 153–155.

Moore, F. R. 1984. Age-dependent variability in the migratory orientation of the savannah sparrow, *Passerculus sandwichensis*. *Auk*, **101**, 875–880.

Moore, F. R. 1987. Sunset and the orientation behaviour of migrating birds. *Biol. Rev.*, **62**, 65–86.

Moreau, R. E. 1972. *The Palaearctic–African Bird Migration Systems*. London: Academic Press.

Pearson, D. J. 1990. The migration of Palaearctic migrants through East Africa. In: *Bird Migration: The Physiology and Ecophysiology* (Ed. by E. Gwinner), pp. 44–59. Berlin: Springer.

Pearson, D. J. & Backhurst, G. C. 1976. The southward migration of Palaearctic birds over Ngulia, Kenya. *Ibis*, **118**, 78–105.

Pettersson, J. & Hasselquist, D. 1985. Fat deposition and migration capacity of robins *Erithacus rubecula* and goldcrests *Regulus regulus* at Ottenby, Sweden. *Ring. Migr.*, **6**, 66–76.

Pettersson, J., Sandberg, R. & Alerstam, T. 1991. Orientation of robins, *Erithacus rubecula*, in a vertical magnetic field. *Anim. Behav.*, **41**, 533–536.

Rabøl, J. 1979. Magnetic orientation in night-migrating passerines. *Ornis Scand.*, **10**, 69–75.

Sandberg, R. In press. Interaction of body condition and magnetic orientation in autumn migrating robins, *Erithacus rubecula*. *Anim. Behav.*

Sandberg, R., Pettersson, J. & Alerstam, T. 1988a. Why do migrating robins, *Erithacus rubecula*, captured at two nearby stop-over sites orient differently? *Anim. Behav.*, **36**, 865–876.

Sandberg, R., Pettersson, J. & Alerstam, T. 1988b. Shifted magnetic fields lead to deflected and axial orientation of migrating robins, *Erithacus rubecula*, at sunset. *Anim. Behav.*, **36**, 877–887.

Sandberg, R., Ottosson, U. & Pettersson, J. 1991. Magnetic orientation of migratory wheatears (*Oenanthe*

oenanthe) in Sweden and Greenland. *J. exp. Biol.*, **155**, 51–64.

Sauer, F. 1957. Die Sternorientierung nächtlich ziehender Grasmücken, *Sylvia atricapilla, borin* and *curruca*. *Z. Tierpsychol.*, **14**, 29–70.

Skiles, D. D. 1985. The geomagnetic field, its nature, history, and biological relevance. In: *Magnetite Biomineralization and Magnetoreception in Organisms. A New Biomagnetism* (Ed. by J. L. Kirshvink, D. S. Jones & B. J. MacFadden), pp. 43–102. New York: Plenum Press.

Svensson, L. 1984. *Identification of European Passerines*. Stockholm: Svensson.

Voous, K. H. 1960. *Atlas of European Birds*. Amsterdam: Nelson, Elsevier.

Wiltschko, W. 1968. Über den Einfluss statischer Magnetfelder auf die Zugorientierung der Rotkelchen (*Erithacus rubecula*). *Z. Tierpsychol.*, **25**, 537–558.

Wiltschko, W. 1974. Der Magnetcompass der Gartengrasmücke (*Sylvia borin*). *J. Ornithol.*, **115**, 1–7.

Wiltschko, W. 1980. The relative importance and integration of different directional cues during ontogeny. In: *Proceedings of the 17th International Ornithological Congress* (Ed. by E. Nöhring), pp. 561–565. Berlin: Deutsche Ornithologen-Gesellschaft.

Wiltschko, W. & Wiltschko, R. 1972. Magnetic compass of European robins. *Science*, **176**, 62–64.

Wiltschko, W. & Wiltschko, R. 1988. Magnetic orientation in birds. In: *Current Ornithology, Vol. 5* (Ed. by R. F. Johnston), pp. 67–121. New York: Plenum Press.

Wiltschko, W. & Wiltschko, R. 1992. Migratory orientation: magnetic compass orientation of garden warblers (*Sylvia borin*) after a simulated crossing of the magnetic equator. *Ethology*, **91**, 70–74.

Zink, G. 1973. *Der Zug europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel. Vol. 1.* Möggingen: Vogelwarte Radolfzell.