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BIRD MIGRATION ACROSS A STRONG MAGNETIC ANOMALY

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SUMMARY

Migratory flights of birds across a strong magnetic anomaly were recorded by tracking radar and, during the daytime, by simultaneous visual observations. The anomaly in central Sweden is about 12 km long and a few kilometres wide, with the total magnetic intensity at low altitude exceeding the normal field by up to 60%, according to aeromagnetic measurements. Migrants change altitude, most often by starting to descend, to a significantly greater extent over those parts of the anomaly where the magnetic field intensity is abnormally high, and particularly where the magnetic inclination is steepest, than over other parts of the study area and at another study area with a normal geomagnetic field. The descents lasted on average about 2 min, with a mean angle of descent of 2·6°, leading to a height loss of about 100 m before level flight was resumed. Flock formations were repeatedly broken up during these temporary descents. The changes in flight altitude were associated with gradients in magnetic inclination along the birds' flight paths across the anomaly. This supports the possibility that birds use the geomagnetic field and associated gradients for continuous guiding and recording of migration. Additional visual observations of migrating birds at the lowest altitudes over the magnetic anomaly suggest that birds sometimes become briefly disturbed (clear weather) or disoriented for longer periods, because of difficulties in finding their way out of the anomaly area (poor visibility).

INTRODUCTION

Much current interest is focused on the exciting possibility that migrating animals use the geomagnetic field to find their way. Localized deviations from the normal geomagnetic field may facilitate or complicate orientation and navigation. The former possibility perhaps applies to whales and other pelagic migrants, which could make use of the large-scale, regular magnetic anomaly pattern over the ocean floor, although, as a secondary effect, whale strandings may occur at sites characterized by an unfortunate combination of local topography and magnetic anomaly pattern (Kirschvink, Dizon & Westphal, 1986). Over continental areas, the magnetic landscape has a quite different character, with anomalies highly localized and

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irregularly scattered. Does this represent a complication to migrating birds visiting or passing such sites?

Birds can use the geomagnetic field for compass orientation (Wiltschko & Wiltschko, 1976; Wiltschko, 1983) and possibly also as a navigational aid providing information about latitude or position along the migratory route and in relation to the homing site (Gould, 1982*a*; Beck, 1984, see also a critical review by Wallraff, 1983). Local geomagnetic anomalies associated with deposits of magnetic minerals may affect migrating birds in at least three fundamentally different ways.

(1) Young birds hatched and raised in nests situated at magnetically anomalous sites may develop an aberrant compass/map sense. Although no studies have been carried out at natural magnetic anomalies, Alerstam & Högstedt (1983) experimentally shifted the magnetic field during the incubation and nestling periods at pied flycatchers' (*Ficedula hypoleuca*) nestboxes. We found that young from nests exposed to a shifted magnetic field showed at least a temporary deviation from the normal orientation during the succeeding autumn migration period. Similar results were obtained for young homing pigeons with respect to their orientation during initial homing flights after growing up in a shifted magnetic field under the natural sky (Wiltschko, Wiltschko, Keeton & Madden, 1983). Further effects of the magnetic field during the ontogeny of the compass sense in migratory birds are reviewed by Bingman, Beck & Wiltschko (1985).

(2) Birds may have difficulties in establishing the proper migratory or homing direction upon departure from a magnetic anomaly. There are no studies of departure directions of migrating birds from such areas. However, releases of homing pigeons at strong anomalies have demonstrated that the pigeons often fail to show their normal homeward orientation in the anomaly area, and that the scatter of orientation increases with increasing deviations in the magnetic field (Walcott, 1978; Kiepenheuer, 1982). The deviations from normal of the total magnetic field intensity at the Iron Mine (Rhode Island, USA) and Kaiserstuhl (FRG) anomalies, where homing pigeons become completely disoriented, range between approx. $-0{\cdot}7$ and $+3\,\mu$T (microteslas) at Iron Mine (about 150 m above ground; Walcott, 1978) and between $-2{\cdot}4$ and $+3{\cdot}2\,\mu$T at Kaiserstuhl (ground level; Kiepenheuer, 1982). Since the normal total intensities at these places are about 56 and $47\,\mu$T, respectively, maximal deviations correspond to 5–7 % of the total field strength. It seems likely that these magnetic conditions have affected the pigeons' navigation system rather than their magnetic compass sense, which would be expected to deviate by only a few degrees from normal in these anomalies.

There are suspicions that the orientation of homing pigeons may also be affected by weak magnetic anomalies, where the total field intensity deviates by merely a few hundred nT (nanoteslas) (<1 %) from normal (Wagner, 1976; Frei & Wagner, 1976; Frei, 1982).

In view of these experiences of pigeon orientation at magnetic anomalies, it is surprising that Lednor & Walcott (1983) failed to demonstrate a deterioration in orientation of homing pigeons released while carrying small pieces of apparatus generating a varying magnetic field across their heads. The conclusion that the disorientation of pigeons released at the above-mentioned magnetic anomalies is due to magnetic disturbances has been questioned by Wallraff (1983), who claims that disorientation of homing pigeons also occurs, for reasons unknown, at certain release sites with normal geomagnetic conditions.

(3) Magnetic anomalies may affect birds passing over on migratory or homing flights. No systematic studies have been carried out to investigate this possibility, although Walcott (1978) mentions some homing pigeons that have been followed by aeroplane or by radio tracking when flying across the Iron Mine anomaly on their way home from more distant release sites. On the basis of these data, Walcott (1978) concluded that once pigeons have established their flight direction, a magnetic anomaly has less effect than if the pigeons are released at the anomaly itself (see illustrations in Gould, 1982*b*).

However, there are some indications from both radar (Richardson, 1976) and ceilometer studies (Moore, 1977) that even small disturbances in the geomagnetic field associated with magnetic storms may affect birds during their migratory flights. Moore (1977) reported a significant correlation between variability in flight directions of nocturnal migrants and geomagnetic fluctuations according to the K index of magnetic disturbance for the 3-h intervals in which the observations of migrating birds were carried out. An increase in the scatter of flight directions was discernible at K values as low as 3 or 4, corresponding to magnetic fluctuations of merely 20–70 nT (but see Skiles, 1985).

Furthermore, Larkin & Sutherland (1977), using tracking radar to follow nocturnal migrants flying over a large alternating-current antenna system, found that the birds turned or changed altitude more frequently when the antenna system was operating than when it was not. Responses were most frequent during the transition phase when the antenna current was switched on or off. These results suggest that the birds could detect the rather weak magnetic field (0·1–0·5 μT, oscillating with a frequency of about 80 Hz) produced by the antenna in operation, and that they responded rapidly, within a few seconds, to on/off changes in this magnetic field.

In the present study, tracking radar was used to register in detail the flights of migrating birds, both during the day and at night, across a strong magnetic anomaly in Sweden. The purpose was to investigate if the migrants show any responses in flight to the magnetic disturbances, and if so, whether there is any consistent correlation between the birds' reactions and the changes in total magnetic field intensity, magnetic inclination or declination in the anomaly area.

MATERIALS AND METHODS

Study area and geomagnetic field

One of the largest deposits of iron ore in Sweden is situated at Norberg (60° 05′ N, 15° 55′ E). It is the oldest known site of highly organized iron mining in Sweden, dating from the 13th century (Justrell, 1974). Deposits of red iron ore and magnetite extend from the surface to at least 2000 m below the ground.

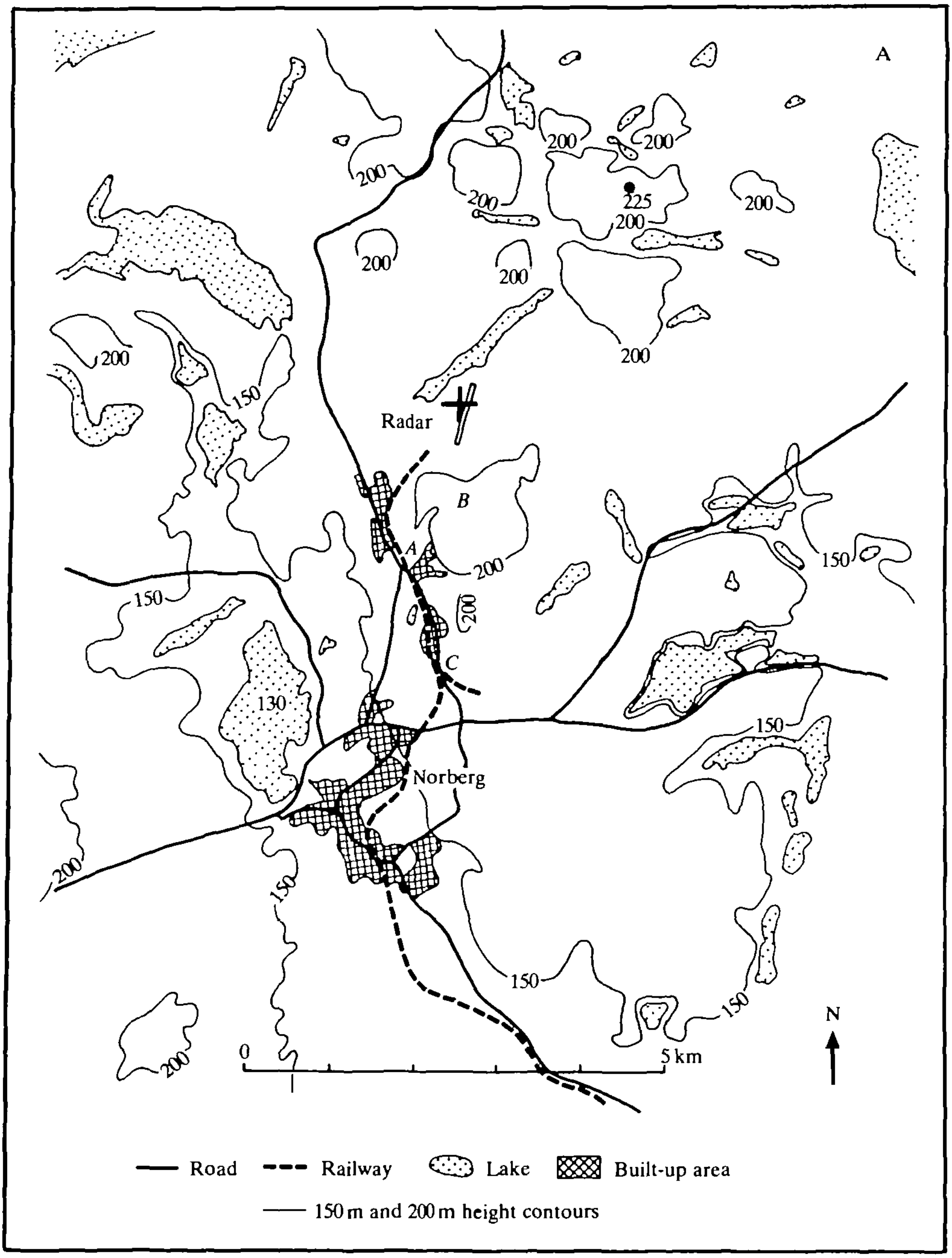

Fig. 1. Topographic (A) and aeromagnetic (B) maps of the study area. The latter is based on the aeromagnetic map of Sweden (Geological Survey of Sweden) with measurements of the total magnetic field intensity (μT) at 30 m above ground level. The normal geomagnetic field intensity is 50·0 μT. Local peak measurements of magnetic intensity are indicated by the dots. The letters *A*, *B* and *C* on the map refer to places where disoriented waders were observed during one night with poor visibility (described in the text).

The topography of the Norberg area is dominated by coniferous forests with scattered oligotrophic lakes, surrounding the community of Norberg (Fig. 1A). There are no dramatic differences in height, which varies between 130 and 200 m

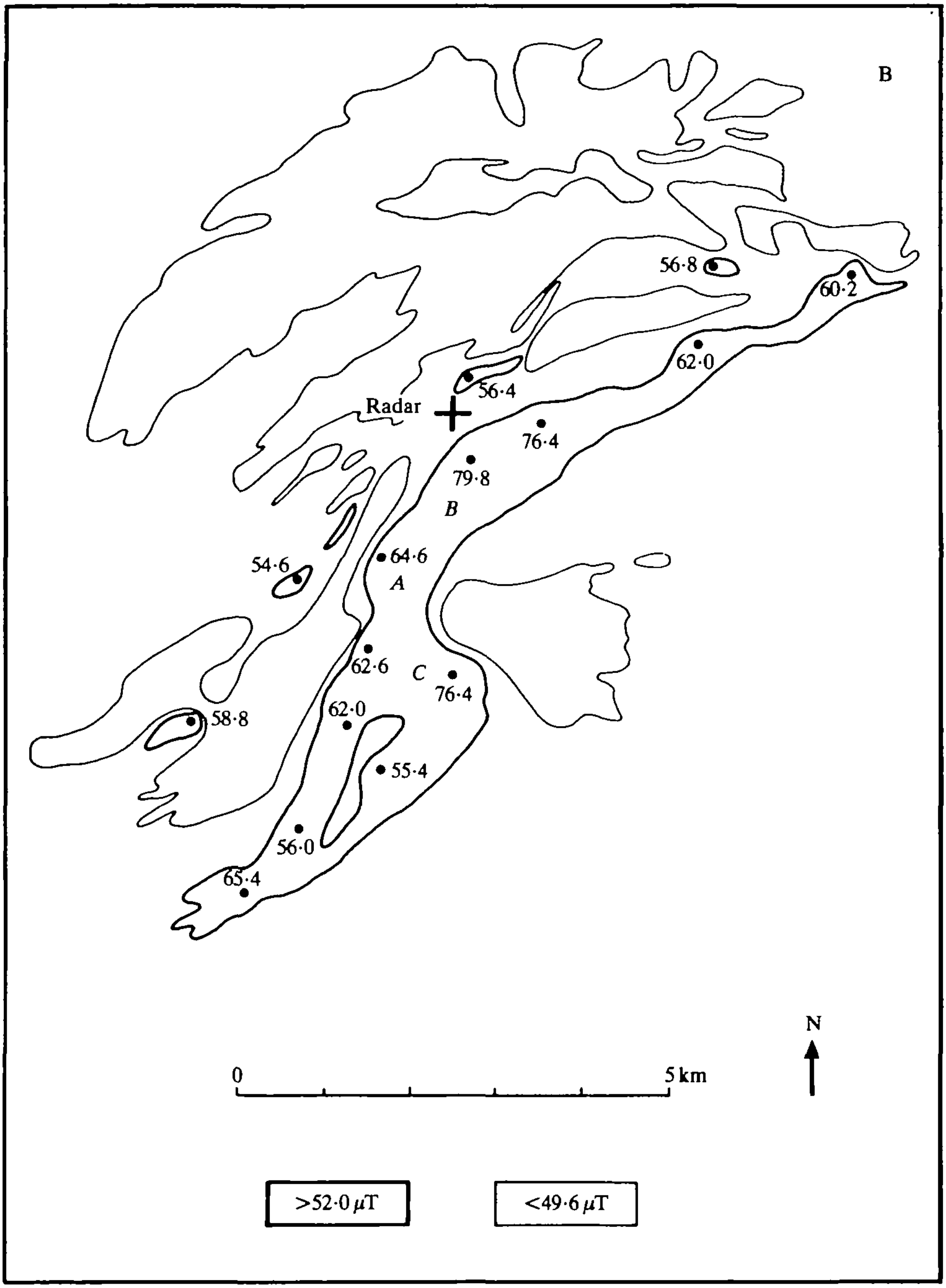

Fig. 1B

above sea level, and with the highest hilltop reaching 225 m above sea level. The tracking radar was placed at a small airfield 185 m above sea level. There is little reason to expect that the unspectacular topography would influence migrating birds to make changes in course or altitude when flying over the area.

The Norberg magnetic anomaly is illustrated schematically in Fig. 1B, based on the aeromagnetic map of Sweden. This map was made from measurements of the total magnetic field intensity measured from a low-flying aircraft by a fluxgate magnetometer held 30 m above ground, with a 200-m spacing between measuring lines and a 40-m spacing between measuring points. The 'magnetic topography' of the Norberg anomaly is characterized by a steep magnetic ridge extending in a SW–NE direction, about 12 km long and 0·5–2 km wide, where the field intensity is considerably (>2 μT) above normal (Fig. 1B). Along this magnetic ridge there is a series of peaks where the magnetic field intensity reaches 5–30 μT above normal. The highest total magnetic intensity, 79·8 μT, was measured close to the site where the radar was placed. On either side of the magnetic ridge, there are wider areas of shallow magnetic depression (wider to the northwest than to the southeast) with a magnetic field intensity 0·2–1·6 μT below normal. A few isolated magnetic peaks, with intensity about 5 μT above normal, protrude from the depression area northwest of the main magnetic ridge.

Hence, in comparison with the Iron Mine (Walcott, 1978) and Kaiserstuhl (Kiepenheuer, 1982) anomalies, the Norberg anomaly is considerably stronger, with the peaks in total magnetic intensity reaching almost ten times higher above the normal level of geomagnetic field strength.

A theoretical three-dimensional model of the Norberg anomaly was developed by Hesselström (1984) in order to estimate different components of the magnetic field at different altitudes for comparison with the radar trackings of birds migrating across the anomaly at various heights. In the model, magnetite deposits in the Norberg area were approximated by a large number of magnetite prisms of different sizes and orientation, arranged so as to give a close fit to the available aeromagnetic measuring profiles of total field intensity at 30 m altitude. The resulting model was used to calculate total intensity, inclination (dip angle) and declination (angular difference between magnetic and geographic north) at points 1 km apart in a square grid over the study area, at 500, 1000 and 2000 m above ground level. For altitudes about 500 m and higher, the theoretical model provides estimates of the magnetic field components that are accurate enough to allow a quantitative evaluation of possible effects on migrating birds (Hesselström, 1984). The different magnetic components as calculated for the 500-m level, with smoothed isomagnetic contour lines computed from the grid data, are illustrated in Fig. 2.

With increasing altitude the anomaly flattens out, extending over a wider area but deviating to a smaller extent from normal geomagnetic values than at lower altitudes. The normal total field intensity, inclination and declination for the geographical position of the study area are 50·0 μT, 72·5° and +0·5°, respectively. At low altitude (30 m) the total intensity in the Norberg anomaly varies between 48·4 and 79·8 μT, as mentioned above. The ranges of total intensity, inclination and declination, as

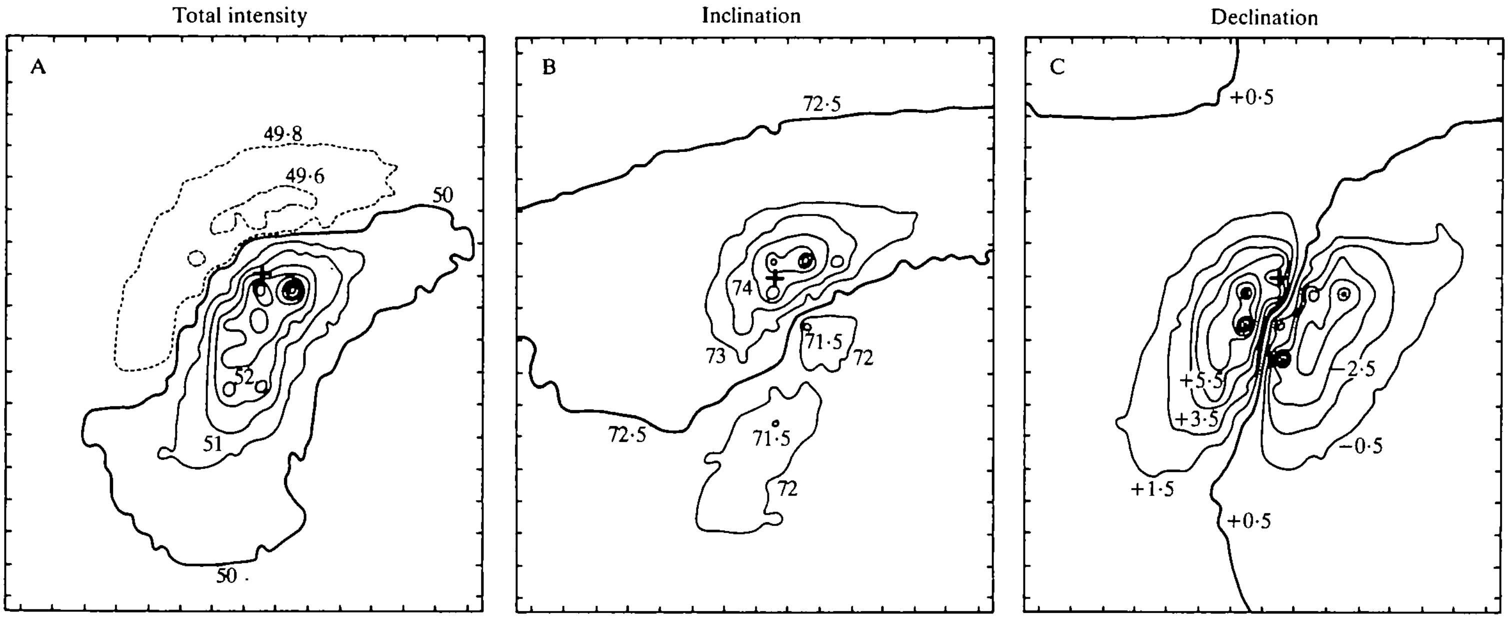

Fig. 2. Total field intensity (μT) and angles of inclination and declination for the Norberg anomaly at 500 m altitude, according to calculations from a theoretical model by Hesselström (1984). The position of the radar is indicated, and frame tics indicate the 1 km^2 grid of the study area used in the model calculations.

calculated from the theoretical model of the Norberg anomaly at 500 m altitude, are 49·4–54·6 μT, 71·3–76·0° and −6·1 to +9·8°, respectively. The corresponding data at 1000 m altitude are 49·7–52·1 μT, 71·9–74·3° and −3·2 to +5·1°, respectively, and at 2000 m altitude they are 49·9–50·8 μT, 72·2–73·2° and −0·9 to +2·3°, respectively. Hence, even as high as 2000 m above ground, the magnetic field strength at the Norberg anomaly deviates by almost 1 μT from normal, with gradients of up to 0·4 $\mu\mathrm{T\,km}^{-1}$, well above the possible magnetic sensitivity in birds implied from previous studies (e.g. Gould, 1982*a*), and at a level of magnetic disturbance causing disorientation among homing pigeons released at magnetic anomalies (Walcott, 1978; Kiepenheuer, 1982).

For comparison it may be noted that, in Scandinavia, the normal N–S (approx.) gradient in total geomagnetic intensity is about 1 μT 450 km^{-1} and in inclination about 1° 200 km^{-1} (both intensity and inclination increase towards the north). The normal E–W declination gradient is about 1° 100 km^{-1}.

Radar observations and analysis of data

Migratory flights of birds were registered by short-range tracking radar (X-band, 40-kW peak power, pulse duration 0·3 μs, pulse repeat frequency 1800 Hz, pencil beam width 2·2°). Range, elevation and bearing to the target were read and stored by computer (HP 85) every 10 s from the radar, which was operated in automatic tracking mode. The radar is equipped with 9× and 18× binoculars which, during the day, permit the two operators to identify the targets and report the birds' flight behaviour onto a tape recorder simultaneously with the computer registrations. Hydrogen balloons carrying aluminium foil reflectors were released and tracked by radar to obtain wind data from different altitudes.

Flocks of birds or individuals were tracked up to about 10 km from the radar, with the majority of trackings within a range of 5 km. Accuracy of position, as measured by the radar, is usually within ±25 m.

Radar observations were carried out during two periods, 19 July–1 August and 12–23 September 1983, during the day as well as at night. Times given in this paper are local summer time (GMT + 2 h). Trackings of local movements, nocturnal flights of swifts, and of birds using thermal air in cross-country soaring migration were excluded from analysis.

All radar tracks were plotted by HP 7225A graphics plotter on a 1:100 000 scale and inspected by ruler for distinct changes in course. This procedure allows course changes of 3° or more to be detected. The majority, about 60 %, of the course changes used in the analysis fell in the range between 3 and 10°, with about 20 % between 10 and 20° and the remaining 20 % being rather more drastic changes of more than 20°. Three categories of changes in course were distinguished, depending on whether the change lasted more than 30 s and the new course was to the right (1) or to the left (2) of the preceding track direction, or whether the change was more temporary and of a zigzag nature (3).

Using a grid overlay on the plotted radar tracks, it was noted for each 1 km^2 square containing tracking data over at least 0·4 km, whether the track was linear or whether any change in course occurred.

Furthermore, flight altitude was plotted in relation to time, and height curves were inspected for distinct changes in rates of climb/descent. Normally there are relatively abrupt and easily detectable incidents of changes between sequences of a fairly uniform vertical speed. Three categories of such changes were distinguished: increases in the vertical speed of at least 0·3 $m\,s^{-1}$ with the succeeding sequence of a new vertical speed lasting more than 30 s (1, upward change in altitude); decreases in the vertical speed of at least 0·3 $m\,s^{-1}$ lasting more than 30 s (2, downward change in altitude); and changes having a more temporary effect appearing as 'notches' in the height curve (3). Information about where changes in altitude took place was transferred for each track to the 1 km^2 grid, in the same way as described for the course data.

Finally, sequences of each track were classified as descent, climb or level flight if the vertical speed was $<-0{\cdot}3\,m\,s^{-1}$, $>0{\cdot}3\,m\,s^{-1}$ or between $-0{\cdot}3$ and $+0{\cdot}3\,m\,s^{-1}$, respectively. This information was transferred to the appropriate squares in the 1 km^2 grid over the study area.

RESULTS

Radar data

Seventy radar tracks of migrating birds, 30 from the study period in July and 40 in September, were available for analysis. The radar observations include a great variety of different types of migrants with airspeeds ranging from about 10 $m\,s^{-1}$ to 23 $m\,s^{-1}$. Generally, track directions fell in the sector between south and west, with SSW as the dominant direction (mean vector of track directions 205°, angular deviation ±21°, $N = 70$). Because winds mostly blew from the sector between SW and N, the migrants most often headed in a southwesterly direction. Taking the effect of wind into account, the mean vector of heading directions was 222°, with angular deviation ±22° ($N = 70$).

Tracking time for the different flocks and individuals ranged between 1 min and 19 min, with an average of 5·4 min, giving a total accumulated tracking time in the study area of 6 h 20·5 min. The length of radar tracks varied between 1 km and 17 km, with an average of 5·0 km and a total accumulated tracking distance of 349·9 km. Ninety-one changes in course (43 to the right, 37 to the left and 11 others) and 64 changes in altitude/vertical speed (33 downwards, 22 upwards and 9 others) were found.

Altitudes at which the migrants were recorded varied between 50 and 2200 m above the radar, and the distribution of radar tracking data obtained from different height intervals is shown in Table 1. There was no significant difference in the incidence, relative to tracking distance, of changes in course ($\chi^2 = 1{\cdot}7$, df = 3) or of changes in altitude ($\chi^2 = 3{\cdot}3$, df = 3) between the four height intervals.

A slightly larger number of tracks was recorded during the night [i.e. more than 30 min after sunset ($N = 38$)] than during the day ($N = 32$). There was no significant difference between the nocturnal and diurnal frequency (relative to tracking distance) of either course changes ($\chi^2 = 0{\cdot}03$, df = 1) or altitude changes ($\chi^2 = 1{\cdot}8$, df = 1).

Most radar observations refer to occasions with fair weather, characterized by good visibility, little cloud cover and with the sun or stars, and sometimes the moon, clearly visible. On a few occasions, cloud cover was more extensive but still permitted a view of the sun or starry sky through gaps in the cloud cover, or of the sun through thin clouds. Radar data are too few to permit an analysis but leave no grounds for suspecting an increased rate of changes in course or altitude on these occasions. Complete overcast prevailed on only 1 day, when a few flocks of migrants were tracked above a layer of stratocumulus, probably about 100 m thick, and with a cloudbase at 250 m above ground. One of these flocks headed straight towards the centre of the magnetic anomaly and showed an unusually drastic reaction, turning back and descending below the cloud cover, before continuing across the anomaly (see below and Fig. 7).

The positions within the study area where changes in course or altitude were registered are related in Table 2 to areas with an anomalously high, low or close to normal total magnetic intensity, inclination and declination, respectively. There is no significant association between changes in course and geomagnetic characteristics, although there may be a tendency for an increased frequency of course changes where declination is anomalous. The course changes of the migrating birds tend to be in the opposite direction compared to the shift in magnetic direction, with anticlockwise course changes predominating where the horizontal direction of the magnetic field is shifted clockwise, and *vice versa* for clockwise course changes. However, this pattern is not statistically significant.

There is a significant association between changes in altitude and total magnetic intensity, and an even more pronounced association between altitude changes and inclination. Changes in altitude – particularly downward changes – were registered predominantly within 1–2 km horizontal distance from the radar, i.e. over those

Table 1. *Number of radar tracks of migrating birds obtained at different altitudes (above radar level) at the Norberg magnetic anomaly*

Mean altitude above ground (m)	No. of tracks	Tracking distance (km)	Tracking duration (s)	No. of changes in: course	altitude
50–500	21	79·3	5480	24	16
500–1000	28	153·7	10310	40	29
1000–1500	13	72·4	4580	19	8
1500–2200	8	44·5	2460	8	11
Total	70	349·9	22830	91	64

Total tracking distance and duration, and number of changes in course and altitude/vertical speed, in the different height intervals are also given.

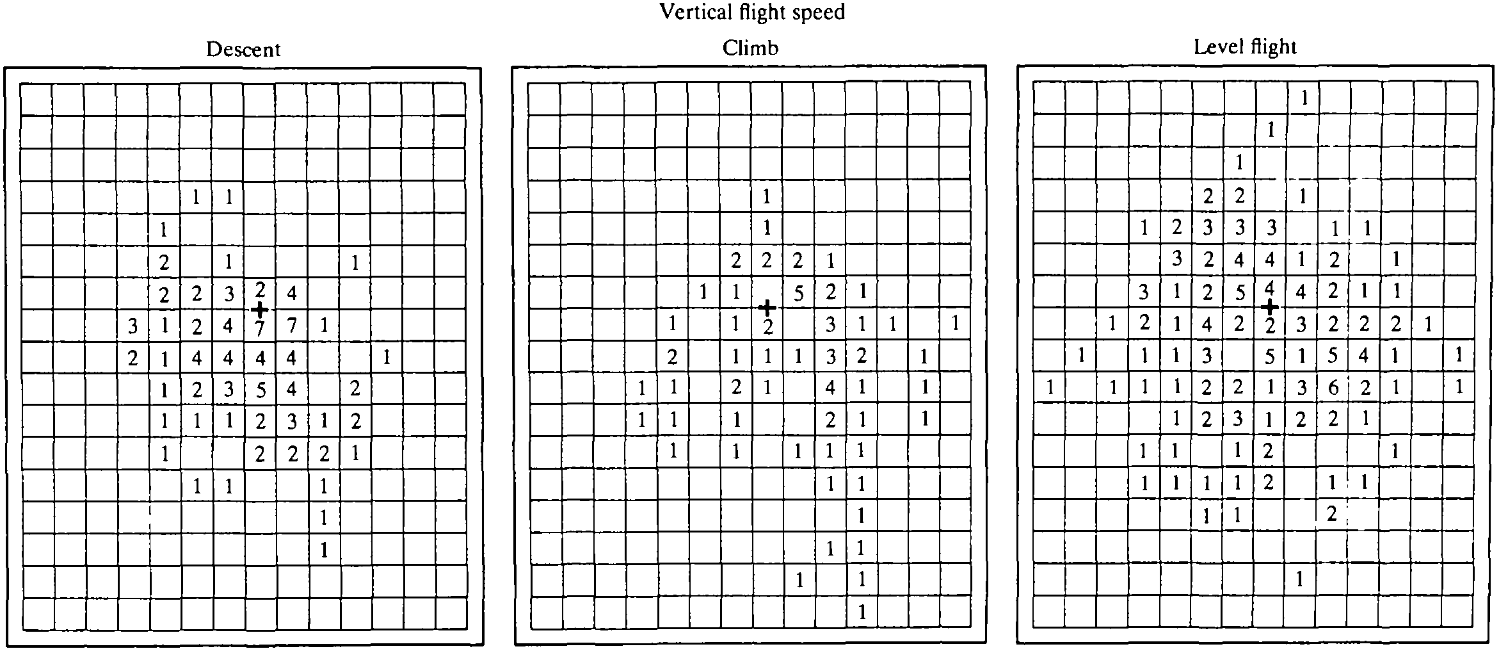

Fig. 3. Number of radar tracks of migrating birds in descending, climbing or level flight in different 1 km^2 squares of the study area. The area shown in the illustrations and the indication of the radar position are the same as in Fig. 2. At least 0·4 km of tracking data in a square is required for inclusion in the analysis. The number of track-squares was 341 (106 descent, 71 climb and 164 level flight, four of the latter falling outside the limit of the illustration).

parts of the anomaly where inclination is abnormally steep (see Fig. 2). As a consequence, sequences of descending flight were more common at, and to the south and southwest of, the radar than were sequences of level flight or climb. In contrast, the two latter modes of flight predominated when the migrants, approaching the magnetic anomaly, were tracked in the sector between northwest and southeast of the radar (Fig. 3). Note that Fig. 3 shows the actual incidence of descent, climb or level flight in the study area, while *changes* in rate of climb/descent are analysed in relation to the magnetic field in Table 2.

The downward changes in altitude were the most striking reactions revealed in this study. A few of the relevant tracks, together with the associated height curves, are illustrated in Figs 4–6. These examples clearly show that the migrants do not change their flight direction to avoid the magnetic anomaly, but fly straight across it with minor, if any, course alterations. In contrast, changes in altitude occur. According to the radar tracking data, of 27 individuals or flocks of migrants passing within 2 km from the radar site at altitudes above 200 m, 19 (70 %) reacted with distinct downward changes in altitude/vertical speed in this area, with another three migrants showing more temporary irregularities in their height curves. However, downward changes in altitude were recorded for only two out of eight migrants tracked in the same area below 200 m (mean altitudes between 50 and 170 m). This may be due simply to the fact that there is little room for steep descents by birds flying at the lowest altitudes.

As judged from tracks that were sufficiently long to include the migrants' flight out of the magnetic anomaly, descents resulting from the downward changes in altitude were temporary, with the migrants resuming level flight after one or a few minutes (see Figs 4, 5, 6A). The durations of 14 such complete sequences of descent, before level flight was resumed, varied between 50 and 240 s with a mean at 132 s. The associated height losses were between 46 and 165 m (mean 100 m), and rates of descent ranged between $-0{\cdot}38$ and $-1{\cdot}4\,\mathrm{m\,s^{-1}}$ (mean $-0{\cdot}81\,\mathrm{m\,s^{-1}}$). Taking into account the ground speed, it was calculated that the angles of descent varied between $-1{\cdot}6$ and $-4{\cdot}6°$, with a mean at $-2{\cdot}6°$ ($N = 14$). There was an indication of a relationship between angle of descent and altitude, in that the three tracks with the lowest mean altitudes, 300–400 m, showed the steepest angles of descent, between $-3{\cdot}8°$ and $-4{\cdot}6°$. The angle of descent was $-1{\cdot}9°$ for the track with highest mean altitude, 2200 m. The Spearman rank correlation coefficient between mean altitude and angle of descent was $0{\cdot}46$ ($P = 0{\cdot}05$, $N = 14$).

The flight behaviour, according to the radar records, of the flock of finches, turning back and descending through cloud cover before continuing migration across the magnetic anomaly, is presented in Fig. 7. In this case, the descent through the clouds was markedly steep, about $-11°$, and the associated height loss was more than 200 m. After resuming SSW migration below the clouds, the migrants continued to descend, although at a smaller angle, $-3{\cdot}6°$.

As seen from Figs 4–6, there are some indications of brief periods of climb, immediately preceding the abrupt changes to descending flights across the magnetic anomaly.

Table 2. *Number of changes in course and altitude (rate of climb/descent) by migrating birds passing over different parts of the study area with geomagnetic components anomalously high (+), low (−) or close to normal*

	Field intensity				Inclination				Declination			
	+	−	normal	χ^2	+	−	normal	χ^2	+	−	normal	χ^2
Changes in course												
All changes, $N = 91$	39 (34·7)	21 (24·6)	31 (31·8)	1·1	35 (32·0)	28 (23·0)	28 (36·0)	3·1	33 (28·6)	40 (34·7)	18 (27·8)	4·9
To the left, $N = 37$	13 (14·1)	13 (10·0)	11 (12·9)	1·3	16 (13·0)	9 (9·3)	12 (14·7)	1·2	18 (11·6)	11 (14·1)	8 (11·3)	5·2
To the right, $N = 43$	17 (16·4)	8 (11·6)	18 (15·0)	1·7	12 (15·1)	15 (10·8)	16 (17·0)	2·3	11 (13·5)	22 (16·4)	10 (13·1)	3·1
Changes in altitude												
All changes, $N = 64$	36 (24·4)	13 (17·3)	15 (22·3)	9·0*	35 (22·5)	15 (16·1)	14 (25·3)	12·1**	21 (20·1)	31 (24·4)	12 (19·5)	4·7
Downwards, $N = 33$	18 (12·6)	7 (8·9)	8 (11·5)	3·8	18 (11·6)	8 (8·3)	7 (13·1)	6·4*	11 (10·4)	17 (12·6)	5 (10·1)	4·1
Upwards, $N = 22$	12 (8·4)	4 (5·9)	6 (7·7)	2·5	11 (7·7)	4 (5·6)	7 (8·7)	2·2	7 (6·9)	10 (8·4)	5 (6·7)	0·7

Expected numbers with an equal probability of changes relative to tracking distance in the different parts of the study area are given in brackets.

Radar trackings of migrating birds were plotted on a 1 km^2 grid over the study area, recording change/no change in course and altitude in 1 km^2 squares with ≥0·4 km tracking distance.

Geomagnetic data calculated for each 1 km^2 square at the 500 m altitude level were used to distinguish between squares with a total field intensity >50·2 μT (+), <49·8 μT (−) or 49·8–50·2 μT (close to normal), an inclination >72·8° (+), <72·2° (−) or 72·2–72·8° (close to normal), and a declination >+1·5° (+), <−0·5° (−) or −0·5 to +1·5° (close to normal).

* $P < 0{\cdot}05$, ** $P < 0{\cdot}01$ (df = 2).

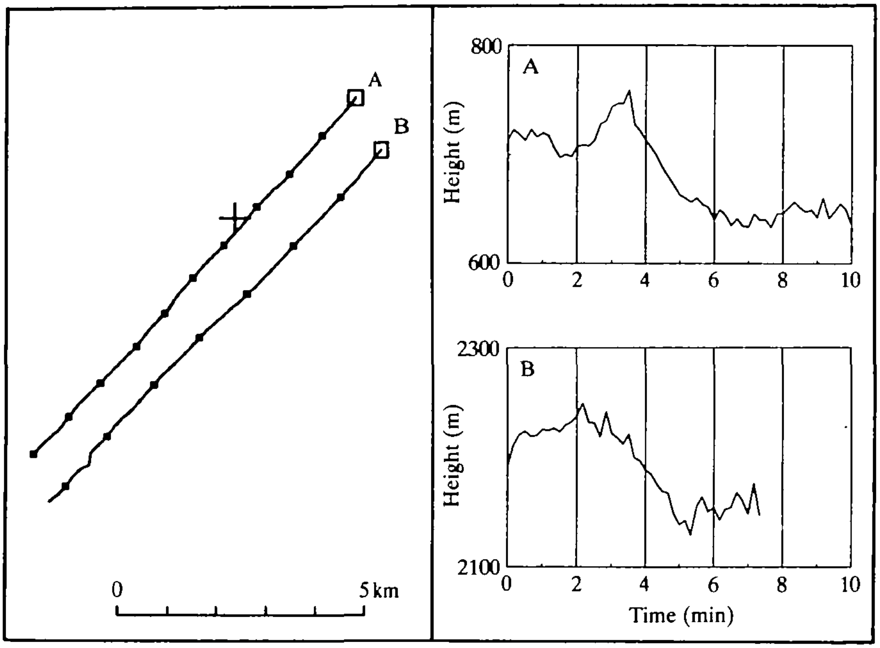

Fig. 4. Radar tracks of birds migrating across the Norberg magnetic anomaly with the associated curves of height (in m above radar level) *versus* time (in min). Position and height are plotted every 10 s. Open squares indicate starting positions of the tracks, with small squares showing positions after each successive minute. The position of the radar is also plotted. Note that there are different lower and upper height limits for different height diagrams. The tracks illustrated are both from clear nights (1–2/8 cloud cover of cirrus and altocumulus) with a low-altitude moon, and with moderate winds from a northwesterly direction. Both probably refer to birds migrating in flocks, although of widely different species as judged from the different air speeds. (A) 1 August, 00.02 h (starting time for the radar registrations). Mean airspeed 14 m s^{-1}. (B) 19 July, 23.24 h. Mean airspeed 23 m s^{-1}.

Visual observations

Widely different species of migrants were identified by visual observations of the birds tracked by radar during daylight hours. Species for which tracking data have been used in the present analysis include curlew/whimbrel *Numenius* spp., arctic/common tern *Sterna* spp., black-headed gull *Larus ridibundus*, heron *Ardea cinerea* and teel *Anas crecca* in July, and chaffinch *Fringilla coelebs*, siskin *Carduelis spinus*, wood pigeon *Columba palumbus*, common buzzard *Buteo buteo* (active flight), greylag goose *Anser anser*, red-throated/black-throated diver *Gavia* spp., lesser black-backed gull *Larus fuscus* and herring gull *Larus argentatus* in September. Of course, many additional species, which could not be identified, are included in the radar tracking data of nocturnal migration. The greater part of the radar data refers to flocks of migrants rather than to birds migrating singly.

The birds' reactions in connection with the downward changes in altitude and the temporary descents, as registered by the radar, have been observed on a few occasions. One such case was a flock of four *Numenius* spp. approaching in the late afternoon at about 950 m in steady formation flight towards the SW. Suddenly the birds dived and banked, interspersed with some gliding, and the flock formation was broken up. Three individuals gradually resumed formation flight after 10–15 s, while the fourth remained separated. A minute later there was a new incident of rather violent banking/diving by the birds when the flock formation was again broken up. The three individuals soon reassembled into formation, and the fourth individual joined them after almost 3 min of descent causing a total height loss of about 100 m.

Similar behaviour was observed in another flock of 11 *Numenius* spp. passing about an hour before sunset at very high altitude (about 1900 m). Over a period of 130 s, when the flock lost about 75 m in height, four incidents of rapid zigzag banking/diving by the birds were observed. Each time, the flock formation was broken up, but after 10–20 s the birds had reassembled to formation flight.

A marked reaction was also observed in two terns *Sterna paradisaea/hirundo*, approaching at sunset in steady pair formation at about 1230 m height. After more than 2 min of such stable formation flight, when the birds passed about 1·5 km to the west of the radar, they suddenly dived and banked and the pair was split with one individual disappearing far below the one that continued to be tracked by the radar. The birds were not seen to reunite during the remaining 2 min of the tracking time. The tern tracked by the radar lost only about 20 m in altitude when the pair was split, but made a clockwise change in course at that moment, from a mean track direction of 206° to 214°.

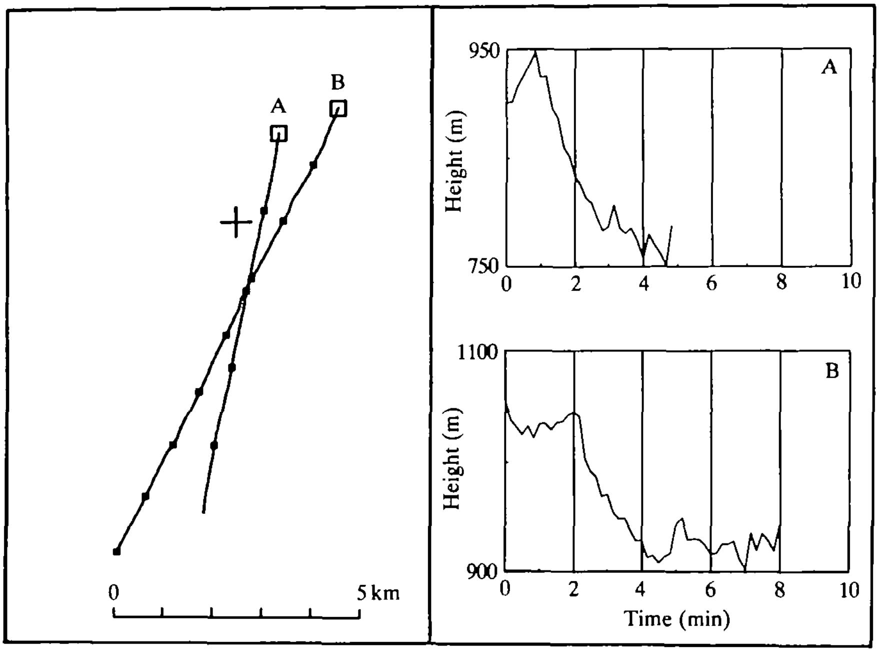

Fig. 5. Radar tracks of birds migrating across the Norberg magnetic anomaly with the associated height curves (illustrated as in Fig. 4). Both tracks are from the same clear night, with very good visibility, as for the track in Fig. 4B. The low-altitude moon set about midnight. (A) 20 July, 00.27 h. Mean airspeed 23 m s^{-1}. (B) 19 July, 23.54 h. Mean airspeed 20 m s^{-1}.

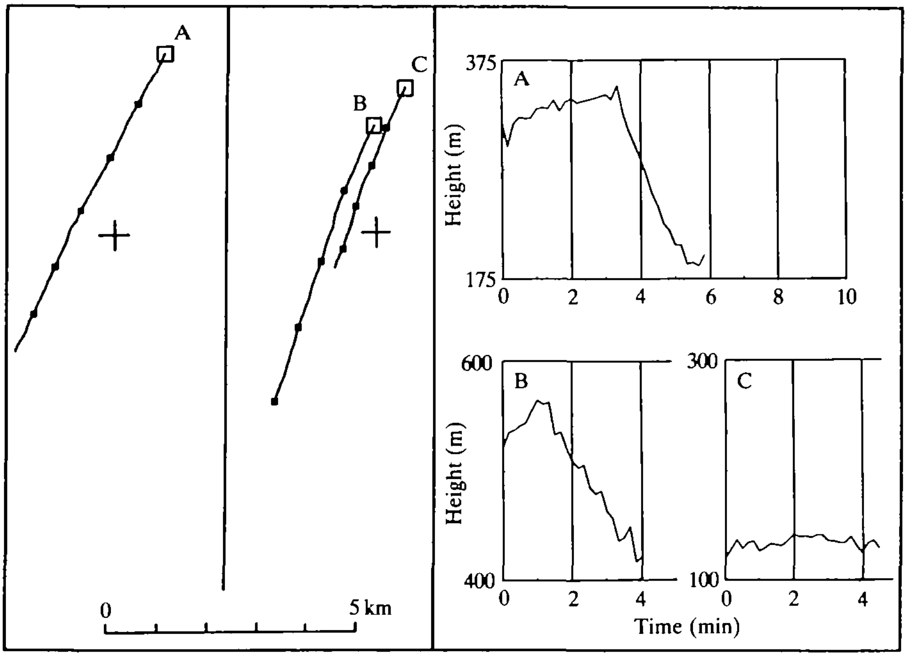

Fig. 6. Radar tracks and height curves of three different flocks of small passerines, probably chaffinches (*Fringilla coelebs*), migrating during the daytime along similar flight paths across the Norberg magnetic anomaly (illustrated as in Fig. 4, with track A shown separately from B and C, to avoid overlapping). The tracks are from the same day which was completely cloud-free, with very good visibility and fairly strong northerly winds. All three flocks showed a slight shift in flight direction, about 4–7° to the left, just north or west of the radar, while the low-flying flock C failed to show any change in altitude like the other two flocks. (A) 23 September, 09.17 h. Flock of eight finches. (B) 23 September, 08.04 h. Flock of about 15 finches. (C) 23 September, 09.10 h. Flock of 10 finches.

Distinct reactions were also observed in some small flocks of wood pigeon, with 3–35 individuals in each, tracked at low altitudes, below 200 m. Flocks passing close to the radar, where total magnetic field intensity is extremely high (see Fig. 1B), showed a clearly visible hesitation, slowed down and veered right and left before continuing rapidly and purposefully on a straight course towards the south. The radar records confirmed that ground speeds were reduced, courses became slightly zigzag, and heights were affected during these brief reactions, which did not last more than 30 s. A few flocks of wood pigeon, not tracked by radar, were even seen to make nervous circling flights with intermittent brief landings or landing attempts close to the radar before finally disappearing on a southerly course. There are no suitable habitats for wood pigeons that could explain this behaviour (the ground at the airfield is covered by fine-grained slag from the mines). We did not observe any hunting by goshawks or other raptors during our studies; it is therefore highly improbable that the migrants' behaviour was caused by the presence of raptors.

One further observation of disoriented migrants in the study area deserves to be mentioned. On 11 September, between 22.00 h and midnight, during conditions of drizzle, poor visibility and very low stratus clouds, flight calls of migrating waders were frequently heard, revealing that several individuals were flying around low over the ground for more than an hour. The birds seemed to fly in wide circuits, passing over and disappearing far away, only to reappear and pass again after a few minutes. The birds, which were heard at sites *A*, *B* and *C* (marked in Fig. 1), comprised at least three different golden plovers *Pluvialis apricaria*, three bar-tailed godwits *Limosa lapponica*, two dunlins *Calidris alpina*, one little stint *Calidris minuta* and one snipe *Gallinago gallinago*. At sites *A* and *C*, where there were some lamps along the road, the birds flew unseen above the illumination except once when a golden plover passed in full view just below a street lamp. In between these passages over the road and adjacent houses and gardens, the birds flew widely over unlit forest areas, as confirmed by audible observations from site *B*. After 23.00 h the drizzle stopped, the cloud base rose and the waders gradually disappeared. Obviously, they had become disoriented and 'trapped' in the area, unable to find their way out until visibility improved. This is suggested by the fact that the disoriented birds flew in circuits just over the central part of the Norberg anomaly, although it cannot be entirely ruled out that they were primarily attracted by the illumination, albeit sparse, along the local road.

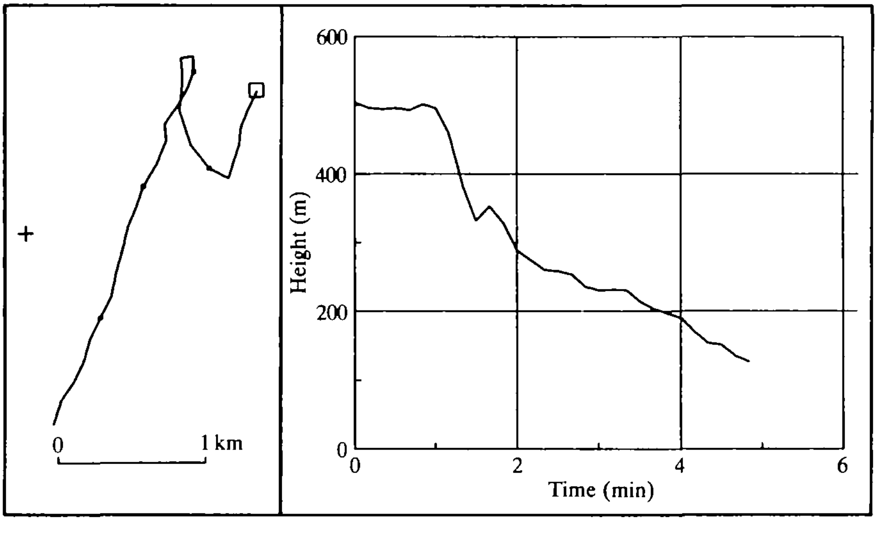

Fig. 7. Radar track and height curve of a flock of small passerines, probably chaffinches, from 15 September, 11.13 h (illustrated as in Fig. 4, although the track has been plotted on a more detailed scale). The weather was overcast, 8/8 stratocumulus with the cloud base at 250 m, moderate visibility (about 10 km) and weak southwesterly winds. Occasionally, the sun was faintly visible through the clouds, indicating that the cloud cover was of a variable thickness, perhaps with an average thickness of 100–200 m. The flock was approaching on a steady SSW course above the cloud cover (radar tracking of this phase of a steady SSW flight started about 1 min before the computer was ready to store the data) and, after 50 s, the migrants turned in a loop to descend steeply through the cloud cover. After 3 min the birds were seen with the binoculars, a flock of five finches, emerging from the clouds and continuing their SSW migration below the clouds.

DISCUSSION

The following conclusions can be drawn from the present results.

(1) Migrating birds show no signs of avoiding a strong magnetic anomaly like the Norberg anomaly, but readily fly towards and across it.

(2) Under most conditions they maintain their orientation without important changes throughout the passage across the anomaly. It is true that there was a tendency for an increase in the rate of (mostly slight) course changes over those parts of the Norberg anomaly where magnetic declination is deviating from normal. However, this tendency was not statistically significant. Certainly, the overall courses of most radar tracks, like those illustrated in Figs 4–6, leave no grounds to suppose that orientation is affected in any important way.

(3) Nevertheless, there are a few observations that indicate that orientation may be affected under special circumstances. Wood pigeons migrating at the lowest altitudes above the central part of the Norberg anomaly, where total magnetic intensity is strongly enhanced (up to 60% above the normal intensity, measured at 30 m altitude) and inclination and declination greatly distorted, seemed to become briefly disoriented, interrupting migration to make nervous landing attempts and circling flights. However, before long they continued migration, disappearing from the anomaly area in the appropriate migratory direction. These wood pigeons were flying in favourable weather conditions on a clear and sunny morning with very good visibility. The observations of disoriented waders flying around in the area for more than an hour during an overcast night with very poor visibility suggest that without visual (celestial or topographical) orientation cues, migrants may have great difficulty in finding their way out of the anomaly area. These interpretations are speculative, and further observations are needed in order to conclude that under certain conditions migrating birds become 'trapped' at strong magnetic anomalies for longer periods of time.

(4) As clearly revealed by the radar registrations, many migrants made abrupt downward changes in altitude/vertical speed when passing the Norberg anomaly. These reactions primarily occurred over those parts of the anomaly where total magnetic intensity is higher than normal and particularly where inclination is abnormally steep. These associations were statistically significant. As a result of these downward changes in altitude/vertical speed, migrants arriving in level or climbing flight from the north or northeast, changed to a temporary descent over the magnetic anomaly, lasting on average 2 min and leading to a height loss of about 100 m, before level flight was resumed. In some cases these descents were immediately preceded by a brief climbing phase. The behaviour of the migrants during these descents, when flock formations were temporarily broken up, was also observed visually.

Can one be sure that these distinct and recurrent reactions were due to the anomalous magnetic field at Norberg and not to other factors? As mentioned earlier, there are no striking features in the local topography at Norberg that might be expected to influence migrants, diurnal or nocturnal, in this way. Furthermore, the weather was mostly clear and cannot provide any explanation for the migrants' reactions.

Another possibility is that the migrants were influenced by the proximity to the radar, and perhaps by the radio waves, rather than by the geomagnetic field. This is a potential source of bias, because the radar was placed near the centre of the magnetic anomaly, where the magnetic inclination is steepest. Hence, as the downward changes in migrants' altitude/vertical speed occurred over areas with an abnormally steep inclination, they also occurred close to the radar. As mentioned earlier, at least 19 out of 27 flocks or individuals tracked within 2 km horizontal distance from the radar above 200 m height showed a downward change in altitude in this area.

At a range of 1 or 2 km from the radar, birds in the radar beam are exposed to a peak radiation flux during the pulses of radio waves of about 35 and $9\,\mathrm{W\,m^{-2}}$, respectively. The associated peak magnetic fields generated by the radio waves amount to approx. 0·5 and $0{\cdot}25\,\mu\mathrm{T}$, respectively, with a frequency of 10 000 MHz (repetition frequency of pulses of radiation is 1800 Hz). It is implausible that birds are significantly influenced by radiation of this magnitude (Eastwood, 1967; Wagner, 1972).

The same radar that was used at Norberg was used later for tracking birds at another inland site, a military airfield at Sjöbo in South Sweden (55°39′ N, 13°38′ E). This area, a rather flat lowland (25–150 m above sea level) of forests mixed with fields and a few nearby lakes, rests on sandy soil and sedimentary rocks, and there is no magnetic anomaly. Of 24 flocks of migrants or individuals tracked by radar during July and September 1984 and 1986, and passing within 2 km from the radar at heights above 200 m (up to 1600 m above the radar), six (25 %) showed downward changes in altitude according to the same criteria used for the Norberg data. This is a much lower incidence of such changes than observed at Norberg ($\chi^2 = 10{\cdot}6$, df = 1, $P = 0{\cdot}001$). In addition, at Sjöbo there was no general pattern of conspicuous descents during which migrants lost 100 m or more in height, as recorded at Norberg. Furthermore, we have used the tracking radar extensively for several years at coastal sites with a normal geomagnetic field, without noting reactions of this kind. Changes in course or altitude by the migrants at these sites generally seem to be attributable to coastal topographical influences. Hence, it is highly improbable that the migrants' responses at Norberg were caused by disturbances due to the proximity of the radar.

Excluding local topography, weather and radar disturbance from having any major effect on the migrating birds passing Norberg, it seems most likely that the distinct and recurrent downward changes in altitude/vertical speed were associated with the magnetic anomaly (that the migrants were affected by the local disturbances in gravity rather than in the geomagnetic field seems improbable, see Lednor & Walcott, 1984). This constitutes an important indication that migrating birds fly with their magnetic sense operating at a high degree of sensitivity.

Why do the migrants respond by temporarily losing height when flying across the anomaly? One possibility is that their reaction is due to some sort of shock when the magnetic characteristics suddenly fall out of range of their sensory mechanism.

Alternatively, they may descend when registering magnetic fluctuations to improve the possibilities of using landmarks for maintaining the exact flight track. Still another possibility is that they respond in a consistent way in relation to changes in some component of the magnetic field.

In Fig. 8 height curves from three of the radar tracks illustrated earlier are compared with the changes in inclination and total magnetic intensity along the migrants' flight paths, according to calculations from the theoretical model of the Norberg anomaly. The overall similarity between height and inclination curves is interesting, indicating that the migrants may respond to the *change* in inclination rather than to absolute inclination angles. Even if not all incidents of temporary descent at Norberg correlate with the estimated changes in inclination as closely as those in Fig. 8 (e.g. descents by migrants have also been recorded at very high altitudes, see Fig. 4B, where estimated inclination gradients are comparatively small), the pattern is consistent enough to warrant consideration of a causal relationship.

Kiepenheuer (1984) suggested that migrating birds orientate by flying at a constant 'apparent angle of inclination' (γ'), i.e. the inclination of the magnetic field vector as projected on a plane orthogonal to the bird's flight trajectory or body axis. As inclination changes with latitude, a migrant must change its course in order to keep γ' constant. As a result, birds will travel along magnetoclinic migration routes, characterized by a fixed γ'. According to Kiepenheuer's hypothesis, migrants are expected to change flight direction when flying across a magnetic anomaly with inclination deviating from normal. Alternatively, where inclination is steeper than normal, they may be expected to climb or descend. Considering migration in the sector between south and west, with flight direction $\alpha°$ to the right of south, the apparent angle of inclination may be determined from:

$$\tan\gamma' = \frac{\tan\gamma\cos\beta}{\sin\alpha},$$

where γ is the magnetic inclination and β is the angle of climb or descent. Hence, at an anomaly with a steeper than normal inclination (γ in anomaly $>$ γ normal), a migrant may keep its apparent angle of inclination constant either by increasing α, i.e. veering to the right, or by climbing or descending ($\beta \neq 0$), or by a combination of both reactions. Encountering a smaller than normal inclination (γ in anomaly $<$ γ normal), a migrant is expected to maintain level flight and decrease α by veering to the left.

Wind causes an angular difference between a bird's heading and its track direction, and predictions from Kiepenheuer's hypothesis differ depending on whether birds perceive the apparent angle of inclination magnetostatically in relation to their body axis (heading direction) or by a magnetic induction process in relation to their trajectory through the magnetic field (track direction).

In the former case, migrants at Norberg, with an average heading close to SW, are expected to change headings on average up to 18°, 8° and 3° to the right when encountering a steeper than normal inclination at 500 m, 1000 m and 2000 m altitude,

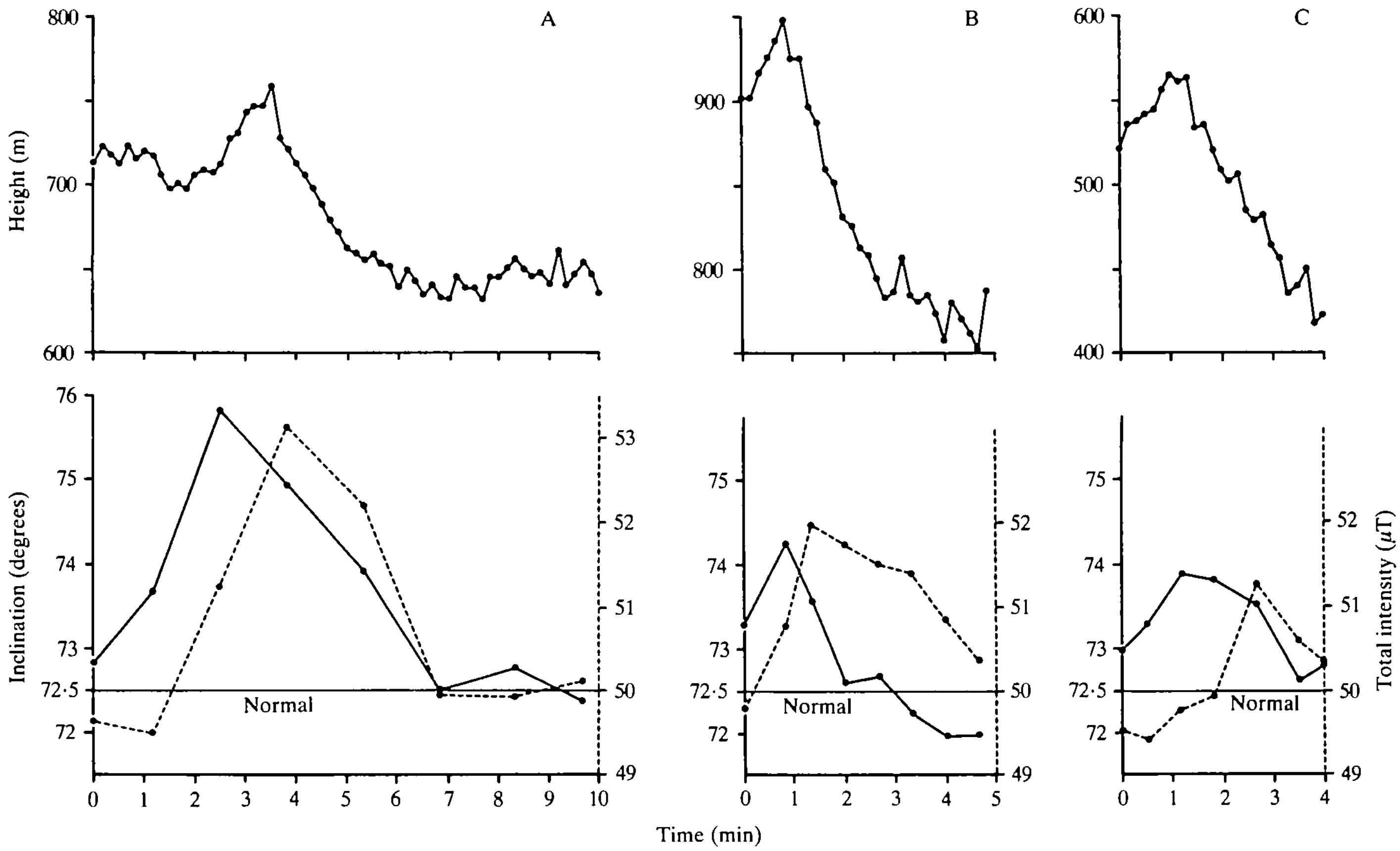

Fig. 8. Height curves of birds migrating across the Norberg magnetic anomaly in relation to the calculated magnetic inclination and total field strength (broken lines) along the migrants' flight paths. Height curves (height *versus* radar tracking time with radar measurements taken every 10 s) are from three radar tracks from different days, illustrated in Figs 4A (A), 5A (B) and 6B (C), respectively. The corresponding magnetic data along the birds' flight paths are shown below, as calculated for the 500 m (A), 1000 m (B) and 500 m (C) height levels, respectively, according to the model by Hesselström (1984).

respectively. The corresponding expected changes in heading with a smaller than normal inclination at Norberg are 4°, 2° and 1° to the left, respectively. Although the latter changes are too small to be readily revealed in the present data, the expected course changes associated with steep inclinations at Norberg should be detectable. However, as concluded earlier, the radar data leave no support for any consistent changes in course (Table 2), a fact which is also clearly illustrated in Figs 4A, 5B and 6A, where tracks are fairly straight although predicted changes in heading according to Kiepenheuer's hypothesis are between 15° and 22° to the right.

If birds fly with a constant γ' in relation to their track rather than their heading direction, the predicted course deviations from an average SSW track direction at Norberg are 6°, 3° and 1° to the right over areas with the steepest inclination at 500 m, 1000 m and 2000 m altitude, respectively. Expected course deviations to the left, where inclination at Norberg is shallower than normal, are even smaller. The radar data do not allow a critical overall evaluation of such small changes in course. However, an examination of specific tracks at lower altitudes or with more southwesterly directions, which are predicted to show detectable course changes (like the track in Fig. 4A with a predicted course deviation 16° to the right), fails to provide any indication that the migrants change flight direction as predicted.

If, as indicated by the radar data, migrants fly across areas at Norberg with a steep inclination without changing flight direction, the remaining means for them to keep γ' constant is to climb or descend by an appropriate angle β. For migrants travelling along a fixed course at 500 m, 1000 m and 2000 m altitude over areas with the steepest inclination at Norberg, predicted values of β are 38°, 27° and 17°, respectively. Predicted angles of climb/descent for the tracks in Figs 4–7 fall between 13° and 38°. These predicted angles are much steeper than the observed angles of descent. An increase in inclination of merely $+0{\cdot}02°$, added to the normal inclination (72·5° at Norberg), is predicted to induce the migrants to descend by the observed mean angle of $-2{\cdot}6°$. One may speculate that the temporary descents recorded at Norberg were caused mainly by repeated brief incidents of diving behaviour (see the visual observations), reflecting aborted attempts by the migrants to adopt the predicted steep angles of descent.

Kiepenheuer (personal communication) suggested another possible explanation, namely that migrants, maintaining a constant track across the Norberg anomaly by visual landmark orientation, interpret a sudden change in perceived apparent angle of inclination as an effect of increased crosswind. In order to avoid such unfavourable winds, the migrants start descending.

Theoretical considerations of magnetoreception in animals (see Kirschvink, Jones & MacFadden, 1985) give no obvious clues why migrating birds should respond to changes in the magnetic inclination as indicated in this study. However, knowledge of the mechanisms of magnetic field sensing in birds and other animals is still extremely scanty and tentative, in spite of the extensive recent theorizing and investigation of this subject.

The present study indicates that birds in migratory flight show consistent responses to local deviations in the geomagnetic field. The implication is that birds use the geomagnetic field and associated gradients for continuous guiding and recording of migration. We do not know how this happens, although analyses, like this one, of the behaviour of migrating birds in relation to different geomagnetic components at strong magnetic anomalies may provide useful clues.

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