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The Influence of Fat Stores on Magnetic Orientation in Day-migrating Chaffinch, *Fringilla coelebs*

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Abstract

Earlier experimental studies have demonstrated the ability of day-migrating birds to perform migration under overcast skies, thereby indicating use of cues other than solar. The orientation behaviour of the chaffinch, a diurnal migrant, was investigated in orientation cage experiments during the autumn migration period. The aim of our experiments was to examine the relationship between different orientation cues and the influence of body condition on directional choices. We obtained the following results: 1. Chaffinches displayed a bimodal distribution of headings along a SW–NE axis when tested in the local geomagnetic field (controls); 2. When the geomagnetic field was experimentally deflected 90° counterclockwise, the chaffinches responded by changing their preferred axial orientation to SE–NW; and 3. The predictive power of stored fat reserves became evident when both the control and experimental samples were subdivided into fat and lean individuals. The majority of fat controls orientated towards a seasonally appropriate SW direction, whereas lean controls chose mean directions towards the NE. Experimentals followed the same pattern, but with the expected deflection, i.e. fat birds selected SE headings and lean individuals chose a NW mean direction.

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Introduction

Abundant research on the orientation behaviour of nocturnally migrating passerines has revealed that these migrants use several kinds of environmental sources of directional information including the geomagnetic field, the stars, the sun and skylight polarization patterns (ABLE 1980, 1993; BAKER 1984; MOORE 1987; W. WILTSCHKO & R. WILTSCHKO 1991). In contrast, very few studies have examined the orientation mechanisms used by diurnal migrants (R. WILTSCHKO & W. WILTSCHKO 1995). KRAMER (1950) demonstrated a role for the sun compass in the orientation

system of day migrants by employing mirror experiments with starlings, *Sturnus vulgaris*, and for a long time it was believed that orientation based on the sun was of major importance for diurnal migrants (VLEUGEL 1953; EMLEN 1975). Later experiments with both starlings and meadow pipits, *Anthus pratensis*, indicated that day migrants can show well-directed movements under overcast skies as well (ORTH & WILTSCHKO 1981; WILTSCHKO 1981; HELBIG et al. 1987). So far, only one day-migrating species, the yellow-faced honeyeater, *Lichenostomus chrysops*, has been thoroughly investigated with respect to orientation mechanisms. This species seems to use geomagnetic information as a primary directional reference, with sun and polarized skylight as auxiliary compass cues (MUNRO & R. WILTSCHKO 1993, 1995; MUNRO & W. WILTSCHKO 1993).

Apart from possible differences in orientation mechanisms between species with different migratory habits (HELBIG 1990), the priority and use of available directional cues seem to vary between conspecifics. Differences in age and experience (MOORE 1984; ABLE & BINGMAN 1987), migratory situation (SANDBERG et al. 1988a,b; PETTERSSON et al. 1991; SANDBERG 1991) and body condition (KARLSSON et al. 1988; SANDBERG 1994) may cause different orientation responses to the same set of environmental conditions. For example, field data have shown that reorientated migration regularly occurs among finches that migrate through southern Sweden during autumn. Birds involved in reverse migration have significantly lower body mass than birds that migrate in the seasonally appropriate direction (LINDSTRÖM & ALERSTAM 1986). Reorientating birds probably search for a suitable stopover site to increase their fat reserves before attempting to cross the Baltic Sea, as proposed by ALERSTAM (1978). Furthermore, SANDBERG (1994) reanalysed data from orientation experiments with robins, *Erithacus rubecula*, that showed a bimodal (axial) response when exposed to experimentally shifted magnetic fields (SANDBERG et al. 1988b). He subdivided each experimental sample according to visually estimated fat loads and found that relatively fat birds orientated in the seasonally appropriate magnetic direction, whereas lean birds orientated in the opposite direction.

In this study we have used the currently available information to focus on two main questions to elucidate the migratory orientation of the chaffinch, *Fringilla coelebs*: 1. Do day-migrating chaffinches utilize geomagnetic directional information for their orientation? and 2. How does the energetic status of the birds influence their directional choices?

Materials and Methods

Test Species and General Information

The chaffinch is one of the most common breeding birds in Scandinavia, distributed over the whole area except for the alpine zone (SOF 1990). According to ringing recoveries, their migratory direction in autumn is predominantly towards the SW (PETTERSSON et al. 1986). Most Swedish chaffinches winter in the Netherlands, Belgium, western France and western Iberia while the Finnish breeding population winters chiefly in France and Iberia (PETTERSSON et al. 1986; CRAMP & PERRINS 1994). Chaffinches caught on passage migration at Ottenby Bird Observatory (56°12'N, 16°24'E) during autumn, originate mainly from

breeding areas in Finland (LILJEFORS et al. 1985). The chaffinches used in this study were captured and ringed during autumn migration in 1993 (9 Sep.–13 Nov.) and 1994 (10 Sep.–13 Nov.), as part of the regular ringing scheme at Ottenby Bird Observatory.

Experimental Equipment and Treatments

After capture, the birds were moved to a nearby test site 3 km north of the observatory. At this site, the birds were housed indoors in wooden cages covered with fine-meshed plastic nets and fed ad libitum with rape seeds, *Brassica napus*, mealworms, *Tenebrio* sp., and vitamin-enriched water. Chaffinches were held in captivity for up to 14 d. All experimental birds were kept in the local geomagnetic field (inclination $\approx 70^\circ$) and under the natural photoperiod. At capture and prior to each experiment, the amount of subcutaneous fat was estimated visually according to a scale developed by PETTERSSON & HASSELQUIST (1985). The scale scores the amount of visible fat on the abdomen and in the tracheal pit of the bird from 0 (no visible fat) to 6 (underparts almost completely covered with fat). This method is widely used as a measure of how much stored energy birds carry, and the estimate of fat is strongly correlated with body mass (SANDBERG 1994). We labelled birds with fat score 0–3 as lean and birds with score 4–6 as fat.

The orientation cages used were modified Emlen funnels (EMLEN & EMLLEN 1966), of the same design as described by SANDBERG et al. (1988a), with the exception that the cages were connected to a computer for automatic recording of the activity. The circular cage has a diameter of 0.3 m and an inner height of 0.12 m, and is constructed entirely out of non-magnetic materials. During the test, the bird is standing on the bottom of the cage and jumps towards the roof. When the bird slides back, a section of the wall is pressed down and a switch is closed. Because the computer records the state of the switches very fast, it was programmed to accept only one reading per s from each switch, so as to get only one record from each jump. The experimental manipulation of the geomagnetic field was carried out by using pairs of electric coils, about 0.8 m in diameter, which were placed around each orientation cage. The artificially produced magnetic fields had the same total strength and the same inclination as the local geomagnetic field (detailed description: SANDBERG et al. 1988b). All tests were performed outdoors and lasted for 1 h. The start of experiments varied from between 1 and 2 h after sunrise. All experiments were carried out at a test arena in an open meadow about 3 km north of the observatory. The funnels were placed on top of plastic crates, to position the cage 0.5 m above ground level. No screening devices were used: the birds could see $\approx 160^\circ$ of the sky overhead (SANDBERG 1991). Orientation cages were always covered with a plastic diffuser when carried to the test arena. The distance between the cages during tests was 3–4 m.

Chaffinches were tested both under clear sky and under simulated total overcast (see below). The sky was considered clear if the cloud cover was less than 50%, and then the cages were covered only by a thin plastic net. If there was more than 50% cloud cover we always covered the cages with a 3 mm opaque diffusing plexiglass panel during the experiment. This diffusing disc effectively prevented any view of the surroundings and of the position of the sun, thereby making the geomagnetic field the sole source of available directional information. All the experimental birds were tested both in the local geomagnetic field and in an artificial field with magnetic north deflected 90° counterclockwise.

Individual chaffinches were tested once in each of the two above-mentioned magnetic conditions (control and deflected) and a second time only if an individual changed energetic status from lean to fat or vice versa. We did this to investigate if it is the amount of fat per se that influences the directional preference. Chaffinches were allocated randomly to experimental categories.

Data Analysis and Statistical Evaluation

A mean heading for each individual and test was obtained by using vector calculation based on the computer records. We excluded bird-hours that either showed too little migratory activity (40 records minimum) or failed to show a reasonably well-defined orientation, where the criterion for exclusion was arbitrarily set to $p > 0.05$ where p is calculated according to the Rayleigh test (BATSCHELET 1981). Because within-test data points are not independent, this p -value was not used as a measure of statistical significance, but simply as a yardstick for exclusion of bird-hours that yielded unreliable estimates of orientation.

Mean headings from individual test hours were used to calculate mean sample vectors and axes of orientation, following standard procedures described in BATSCHELET (1981). When the mean vector length resulting from doubling the angles (r_2) was larger and hence provided a better description of the circular distribution than the unimodal vector length (r), we used a mean axis of orientation as the basis of analysis. Tests for statistically significant directional preferences are according to the Rayleigh test. Comparisons of

Table 1: Comparison of mean directions under clear sky and simulated total overcast, respectively. Birds tested in normal and deflected geomagnetic field are treated separately. Differences in mean direction were tested with Mardia's 'one-way' classification test' (see Methods). Both unimodal (r_1 : single values) and bimodal (r_2 : paired values) vectors are given. When $r_2 > r_1$, we used the axial distribution as a baseline for analysis (see Methods). In these cases, paired values are presented first. There were no statistical differences between weather conditions, in mean directions of samples. Asterisks indicate significant vectors according to the Rayleigh test (BATSCHULET 1981)

Condition	Mean direction	r_1	r_2	n
Control				
Clear Sky	34° (35–215°)	0.87*	0.57*	13
Overcast	34–214° (161°)	0.40	0.42	16
Deflected				
Clear Sky	102° (122–302°)	0.59*	0.52*	12
Overcast	114–294° (306°)	0.23	0.51*	12

the level of scatter around the mean angles between samples were made by using the 'test for the homogeneity of concentration parameters' (MARDIA 1972). Differences in mean headings between test groups were examined with the 'one-way classification test' (MARDIA 1972).

Results

Ten of the test hours with chaffinches were excluded from the analysis because of low activity (7) or failure to show a well-directed orientation behaviour (3). The excluded bird-hours were evenly distributed over the different experimental groups (4 in control and 6 in experimental condition). The analysis was (after exclusions) based on 53 tests in total, of which 29 were unmanipulated controls and 24 experimentals.

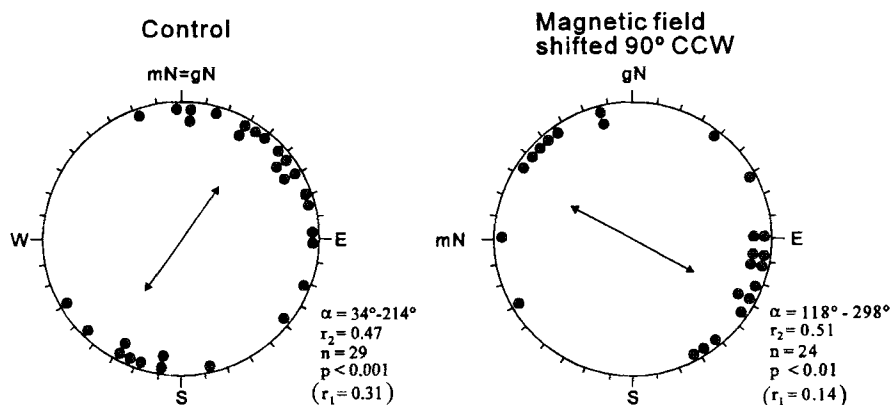


Fig. 1: Mean morning orientation of chaffinches in autumn. Each dot represents the mean heading of an individual during a 1-h experiment. Individual mean headings are shown in relation to geographical north (gN) and magnetic north (mN). Axes show the average direction of the whole sample. The bimodal vectors are drawn relative to the diameter of the circle = 1. Left diagram: birds tested in control condition, i.e. in the local geomagnetic field. Some individuals were tested twice, but only if they had changed their fat score between lean and fat. Right diagram: experimental birds, geomagnetic field deflected 90° counterclockwise.

Significance levels according to the Rayleigh test (BATSCHULET 1981)

Experiments were performed both under clear sky and under overcast. In both circumstances, experimental birds showed a clear response to the induced shift in direction of the geomagnetic field. When the amount of stored fat was taken into account (see below), there was no difference in choice of direction between birds tested under clear sky and overcast (Table 1). Data from both weather conditions are hereafter pooled. Because the vast majority of the tests were performed with juvenile birds (84%), it was difficult to evaluate a possible difference in behaviour between chaffinches of different ages. There were no statistically significant differences in activity levels between any of the experimental categories.

Magnetic Orientation of Chaffinch

Orientation tests performed in the local geomagnetic field (controls) resulted in statistically significant mean orientation along a SW–NE axis (Fig. 1, compare unimodal mean vector: $\alpha = 72^\circ$, $r_1 = 0.31$, $p > 0.05$).

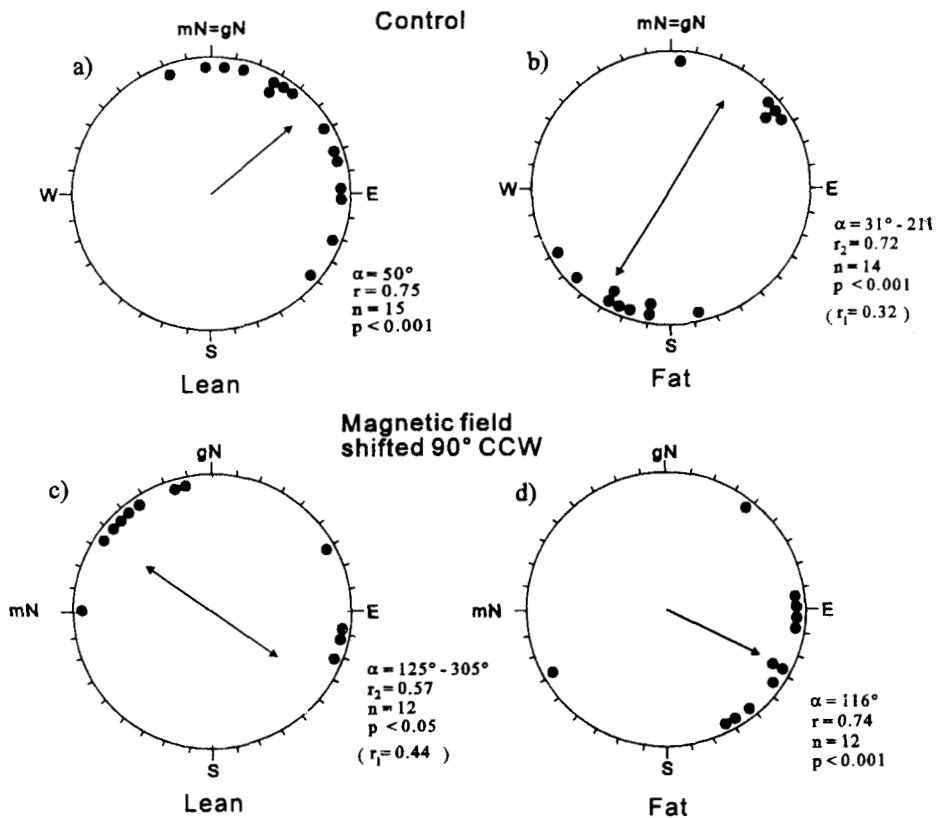


Fig. 2: Morning orientation of chaffinches in normal and deflected geomagnetic fields, subdivided into lean and fat individuals: (a) normal geomagnetic field, lean individuals; (b) normal geomagnetic field, fat individuals; (c) deflected magnetic field, lean individuals; and (d) deflected magnetic field, fat individuals.

Unimodal vectors are drawn relative to the radius of the circle = 1. See Fig. 1 for further details

When the finches were exposed to a geomagnetic field where the direction towards magnetic north was experimentally deflected 90° counterclockwise (CCW), they responded by shifting their axial mean orientation 84° CCW (Fig. 1, unimodal mean vector: $\alpha = 79^\circ$, $r_1 = 0.14$, $p > 0.05$). This angular distribution differed significantly from that of controls ($p < 0.001$).

Influence of Body Condition on Directional Choices

The birds in each sample (control and experimental) were subdivided into two different groups according to the amount of subcutaneous fat they carried at test. This was to examine the possible influence of energetic condition on orientation behaviour. There was a clear relationship between the amount of fat reserves and the directional choices made by the finches (Fig. 2). Under control conditions, lean chaffinches chose northeasterly mean headings (Fig. 2a), whereas the majority of the fat individuals orientated in the expected south-westerly direction (Fig. 2b; unimodal vector: $\alpha = 180^\circ$, $r_1 = 0.32$, $p > 0.05$). When the magnetic field was deflected 90° CCW, both lean (Fig. 2c; unimodal vector: $\alpha = 347^\circ$, $r_1 = 0.44$, $p > 0.05$) and fat birds (Fig. 2d) showed significant responses to the experimental manipulation ($p < 0.05$ in both cases). Of the 12 chaffinches that were tested more than once, only three made the same directional choice in subsequent tests. The other nine individuals responded to the change in energetic and magnetic condition as predicted. In control condition, a relatively higher number of lean chaffinches showed reversed orientation between NW and SE (within 304–123°), as compared with fat individuals which preferred directions within the SE–NW sector (124–303°). This difference was statistically significant ($\chi^2 = 10.6$, $df = 1$, $p < 0.01$). The same was true for experimental birds where a majority of the fat birds chose headings within a south-easterly sector (28–207°), while most lean birds were found within a north-westerly sector (208–27°) ($\chi^2 = 9.3$, $df = 1$, $p < 0.01$, Fig. 2).

Discussion

Magnetic Orientation of Chaffinch

In the local geomagnetic field, the chaffinch showed a bimodal orientation with one end of the axis pointing towards the expected south-westerly direction. The behaviour of the birds when exposed to an experimentally manipulated magnetic field clearly demonstrates that day-migrating chaffinches can utilize geomagnetic information for their orientation. A change in the direction towards magnetic north resulted in a bimodal distribution that was shifted in the correct direction and by almost exactly the expected amount. Furthermore, it did not matter if the chaffinches had access to celestial cues or not — the shift was distinct and significant under both clear and overcast morning skies. Our interpretation is that magnetic directional information overrules celestial stimuli in the orientation system of chaffinches.

To the best of our knowledge, only one other day-migrating species has been subjected to experimental deflections of magnetic directions, the Australian yellow-faced honey-eater (MUNRO & W. WILTSCHKO 1993). By testing yellow-faced honey-

eaters indoors during autumn migration, MUNRO & W. WILTSCHKO (1993) were able to establish that these birds possess a magnetic compass, and moreover, in outdoor tests during spring migration they found that honey-eaters respond readily to an experimental reversal of the magnetic vertical component even if they have access to celestial cue information. The authors concluded that for yellow-faced honey-eaters, the magnetic compass seems to be of primary importance during migration (MUNRO & R. WILTSCHKO 1993, 1995). The only other diurnal migrants to have had their orientation performance studied are starling (KRAMER 1950; WILTSCHKO 1981) and meadow pipit (ORTH & WILTSCHKO 1981; HELBIG et al. 1987), and in both cases, there is observational and experimental evidence that these species are capable of showing well-defined orientation even under overcast conditions. Taken together, there are no a priori reasons to expect differences in the general use of orientation cues between diurnal and nocturnal migrants (VLEUGEL 1953; EMLEN 1975).

Influence of Energetic Status on Directional Selections

The choice of magnetic direction by chaffinches shows a strong relationship with their body condition. Most birds with a large amount of stored subcutaneous fat chose south-westerly, seasonally appropriate directions, while the majority of birds with smaller fat reserves chose opposite directions, i.e. towards the north-east. This clear connection between body condition and orientation behaviour was maintained when the birds were tested in a deflected magnetic field. However, a few chaffinches with high fat loads, tested under control conditions, did not orientate in the expected direction. Of these five individuals, all had fat score 4, which was the lowest score a bird could have and still be considered as a 'fat' bird according to our subdivision. As our subdivision is necessarily artificial, it is possible that those individuals regarded themselves as not yet prepared to migrate with respect to their energetic state, and therefore did not show an appropriate response. The same reasoning can be applied to explain some of the discrepancies among birds with small fat reserves, tested in deflected magnetic fields.

Reorientated migration is a well-known phenomenon as described both from field observations and from experimental studies. During spring migration, reorientated movements are often related to inclement weather like strong northerly winds, cold spells and snow which force spring migrants to retreat (SVÄRDSON 1953; LACK 1963; EASTWOOD 1967; ALERSTAM & ULFSTRAND 1974). Reorientated autumn migration, on the other hand, seems to be connected with encountering an ecological barrier (ABLE 1977; ALERSTAM 1978; RICHARDSON 1978; BRUDERER & JENNI 1988) which may cause migrants to hesitate before attempting to cross this obstacle, especially if they do not have sufficient energy stores to successfully negotiate a crossing (ALERSTAM 1978; SANDBERG & MOORE 1996). In southernmost Sweden, migrating chaffinches and bramblings, *Fringilla montifringilla*, are often observed flying NE from the coast, i.e. opposite to the direction towards their wintering area. At inland sites, 20–40 km from the coast, the most intense migration of this kind can be observed on average 3.5 h later than the morning departure in the normal direction (LINDSTRÖM & ALERSTAM 1986). Finches that engage in reorientated movements have significantly less fat than those

which proceed in the normal south-westerly direction. This behaviour is consistent with a need to build up larger fat reserves before crossing the Baltic Sea barrier, but at the same time the birds may avoid the stronger predation pressure and competition at the coastline (LINDSTRÖM & ALERSTAM 1986; LINDSTRÖM 1990; MOORE & YONG 1991).

Our results are in agreement with this explanation of reorientated orientation behaviour. They are also very similar to those reported by SANDBERG (1994) who investigated the twilight orientation of robins during autumn migration, at the same test site. He found that the amount of stored fat could be used to predict whether an individual robin would select a seasonally appropriate southerly direction in relation to the geomagnetic field (fat birds), or engage in reverse migration (lean birds). Furthermore, the fact that chaffinches orientated almost exactly in the opposite direction is consistent with BAKER's (1978) concept of exploratory migration. One could imagine that a bird which encounters a barrier would orientate in almost any other possible overland direction, randomly searching for a suitable stop-over site. In his theory, BAKER considers reverse migration as a flight back along the track it has flown, returning to a site which the bird already noticed en route. However, many of the chaffinches captured at Ottenby during autumn migration most likely originate from Finland (LILJEFORS *et al.* 1985). If they do, then they are not encountering an ecological barrier after previous overland migration, but rather, they have stopped after having performed a long journey across the Baltic Sea.

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