

## Interaction of body condition and magnetic orientation in autumn migrating robins, *Erithacus rubecula*

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**Abstract.** Earlier experimental studies have demonstrated that autumn migrating robins, passing a stop-over site in southeastern Sweden, use the geomagnetic field for orientation. However, when exposed to experimentally deflected magnetic fields about half of the test birds preferred magnetic directions that were reverse (northeasterly) from normal (southwesterly), thus resulting in axial (bimodal) distributions. The results were difficult to interpret in terms of orientational mechanisms using either visual sunset cues or geomagnetic information. In an attempt to clarify these results, the influence of different fat loads on the magnetic orientation of the same robins was investigated. The amount of stored fat reserves could be used to predict whether an individual will select a seasonally appropriate southerly direction in relation to the geomagnetic field (large fat reserves) or engage in reverse migration (scant fat reserves). When data were subdivided into different fat class categories, bimodality of orientation disappeared, and the results were no longer in conflict with the magnetic orientation model. The results stress the importance of taking into account the ecological context in which migratory birds are tested for their orientation performance.

Bird migration has attracted scientific interest for centuries. Myriads of birds leave their breeding areas every autumn in search of seasonally more favourable conditions for survival. The distance covered during migration varies considerably, ranging from only a few hundred kilometres to journeys around the world (Baker 1984; Alerstam 1990a). Migration poses a number of different behavioural challenges to the birds involved: for example, they have to meet the energetic costs of migration, which are especially high for species that cross ecological barriers (e.g. seas and deserts). This may involve locating suitable stopover sites with sufficient food supplies to allow renewal of fat reserves (e.g. Bibby et al. 1976; Moore & Simons 1992). The birds have to forage in a fluctuating environment that, apart from having an unpredictable food supply, also contains competitors (Lindström & Alerstam 1986; Moore & Yong 1991) and predators (Lindström 1990 and references therein). In addition, birds must be able to avoid disorientation on their way between species- or population-specific wintering and breeding grounds under variable climatic conditions along their migratory routes (cf. Ralph 1978; Alerstam 1988, 1990b).

Prior to and during migration, birds (especially long-distance migrants) have to store large amounts of fat as fuel for their flights across often inhospitable terrain (Berthold 1975; Blem 1980). How do the fat reserves of migratory birds influence en route behaviour such as the decision to migrate, choice of stopover sites and the orientation of their migratory movements?

When fat deposits are depleted during migration, birds are able to replenish them at rates approaching ca 10% of their live body mass per day, if they manage to find suitable stopover sites (Dolnik & Blyumental 1967; Bairlein 1985; Biebach et al. 1986; Moore & Kerlinger 1987; Loria & Moore 1990). The importance of selecting favourable en route habitat, together with the repeatedly demonstrated correlations between energetic condition, food availability and the amount of activity shown by caged birds in the laboratory (Gwinner et al. 1985, 1988; Terrill 1987), suggests that the decisions made by birds during migration, in an ecological and ecophysiological context, may be critical for successful completion of their annual journeys.

The effect of varying fat reserves on migratory orientation has, so far, received scant experimental attention. Able (1977) tested a number of species of

North American warblers in Emlen-funnels, and investigated the influence of different fat levels on the amount of migratory activity as well as on orientation. The amount of visually estimated fat had no discernible effect on the quantity of migratory activity, but the proportion of individuals that showed oriented migratory restlessness increased significantly with larger fat deposits. In experiments on free-flying robins and pied flycatchers, *Ficedula hypoleuca*, the amount of stored fuel reserves had a pronounced effect on the decision to migrate: birds with low fat levels were significantly less likely to embark on migration (Sandberg et al. 1991; cf. also Berthold 1975; Biebach et al. 1986; Moore & Kerlinger 1991). In addition, those lean birds that did take off on migratory flights often reoriented in directions opposite to that expected for the season. This suggests that if fat reserves are limited, the birds may either stay where they are to replenish their reserves, or engage in reorientation, probably in search of more profitable stopover sites (cf. also Alerstam 1978; Lindström & Alerstam 1986).

Autumn migrating robins, captured at Ottenby Bird Observatory by the Baltic Sea in southeast Sweden (56°12'N, 16°24'E), used directional information from the geomagnetic field for their orientation during twilight (Sandberg et al. 1988a, b; cf. also Pettersson et al. 1991). The robins changed their orientation to maintain their typical axis of migration relative to experimentally shifted magnetic fields. However, some of the birds adopted a reverse orientation in relation to the magnetic field, leading to a bimodal pattern of orientation along an axis aligned approximately east/west (i.e. magnetically north/south), suggesting that additional cues (e.g. celestial cues such as the sunset azimuth, skylight polarization pattern or light distribution in the twilight sky) are involved in the orientation process. These results were difficult to interpret according to suggested mechanisms for orientation involving visual sunset cues (see review by Moore 1987), and did not seem to agree with either of the two currently available hypotheses concerning the functional basis of magnetic orientation (Wiltschko & Wiltschko 1972; Kiepenheuer 1984). Directional bimodality indicated that the robins could not establish magnetic polarity solely on the basis of directional information from the geomagnetic field.

In this paper, I examine the effect of varying amounts of stored fat on the magnetic orientation of autumn migrating robins, using results from

birds captured and tested at Ottenby Bird Observatory in 1984 and 1986.

## METHODS

### General Information

The data presented in this study constitute a subsample of previously published orientation results (see Sandberg et al. 1988a, b). I include in the present analysis only tests in which the body mass and the amount of stored fat of the robins were determined prior to each test. The subsample makes up about 82% of the original sample that was tested at Ottenby (cf. below). For a full description of test birds, equipment and experimental protocol see Sandberg et al. (1988a, b). Here, I give only a brief summary.

The sunset orientation of migrating robins captured at Ottenby Bird Observatory (56°12'N, 16°24'E) was investigated during the autumn passage (September and October) in 1984 and 1986. After being caged 1 or 2 days following capture (to acclimatize them to captivity and ensure they were feeding properly), the test birds were exposed to six different experimental conditions.

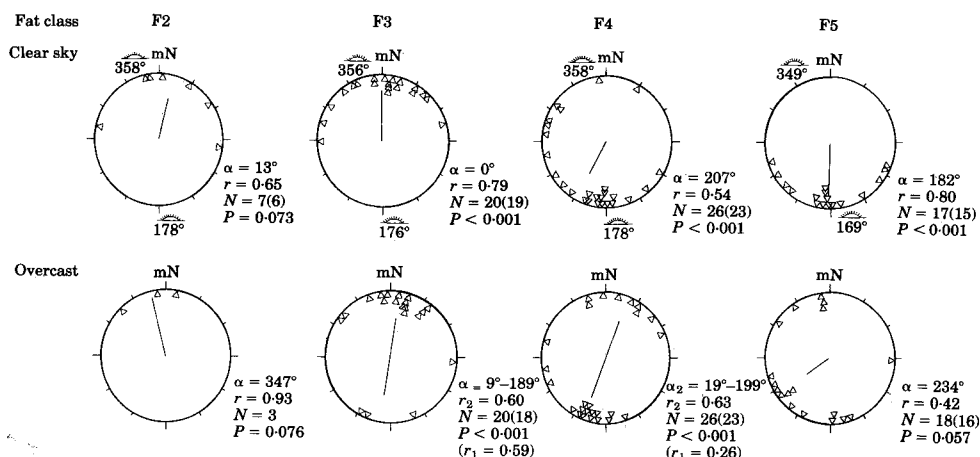
(1) Tests under clear skies: (i) unmanipulated controls; (ii) magnetic north shifted +90° (magnetic north  $\approx$  geographical east); and (iii) magnetic north shifted -90° (magnetic north  $\approx$  geographical west).

(2) Tests under simulated total overcast: (i) unmanipulated controls; (ii) magnetic north shifted +90°; and (iii) magnetic north shifted -90°.

Registration of migratory activity started 10 min after local sunset and lasted for 1 h. Prior to each test, the robins were weighed to the nearest 0.1 g with a Pesola spring balance and fat deposits were estimated visually on the birds' abdomen according to a 7-class scale (see Pettersson & Hasselquist 1985; Sandberg et al. 1988a). The accuracy of the visually estimated fat deposits was ascertained by a strong correlation between fat load and body mass:  $Y = b + aX = 12.94 \text{ g} + 0.87X$ , where  $X$  = fat class ( $P < 0.001$ , linear regression).

### Statistical Evaluation

Each robin was tested only once in each of the experimental conditions described above; consequently an individual bird participated in up to six orientation tests over 2 weeks. In tests performed in



**Figure 1.** Mean sunset orientation of Ottenby robins tested in experimentally deflected magnetic fields during the autumn migration period. Since there were no statistically significant differences between tests where the magnetic field was shifted 90° to the left and 90° to the right from normal, orientation data are pooled for each of the four visually estimated fat classes (cf. Methods). The mean orientation under clear skies and under overcast of robins with fat levels F2, F3, F4 and F5, respectively are shown. Fat levels increase from F2 to F5. For clear sky tests, the average position of the setting sun 40 min after sunset, i.e. in the middle of the test hour, is indicated outside the diagrams. Since individual mean headings are shown in relation to magnetic north (mN), and two different experimental conditions were pooled (cf. above), two mean sunset directions are illustrated for each clear sky test. The number of individuals from each of the two pooled categories was almost equal. Mean vectors are drawn relative to the radius ( $r$ ) or diameter ( $r_2$ ) of the circle = 1. Number of tests ( $N$ ) are shown, with the number of different individuals tested indicated in parentheses. Mean directions ( $\alpha$  and  $\alpha_2$ ), lengths of vectors ( $r$ ) and axes ( $r_2$ ), and probability levels ( $P$ , based on number of individuals) according to the Rayleigh test were calculated by using standard procedures given in Batschelet (1981). For axial distributions, the mean unimodal vector length ( $r_1$ ) is shown (in parentheses) for comparison.

deflected magnetic fields under clear skies, 44 different individuals were tested, 26 of which were tested twice, i.e. under both left and right deflected magnetic fields; but only seven of the latter remained in the same fat class between left and right deflected magnetic field tests (two tests were excluded because activity was less than 40 hops/h, cf. below). In the tests performed under total overcast, the corresponding numbers of individuals were 45 (total), 18 (tested twice) and four (excluded because of low activity). Since data are subdivided into different fat class categories and the majority of individuals changed their fat status between tests, the limited repetition should be of minor consequence. In addition, probability measures are based on the number of different individuals tested within each fat class (cf. Fig. 1). In control tests (valid both for clear skies and overcast), none of the individuals that participated was tested more than once in each experimental category (i.e. when data were subdivided according to fat class).

Vector calculation based on the amount of migratory activity in the eight sectors of the modified Emlen-funnels (cf. Sandberg et al. 1988a), gave

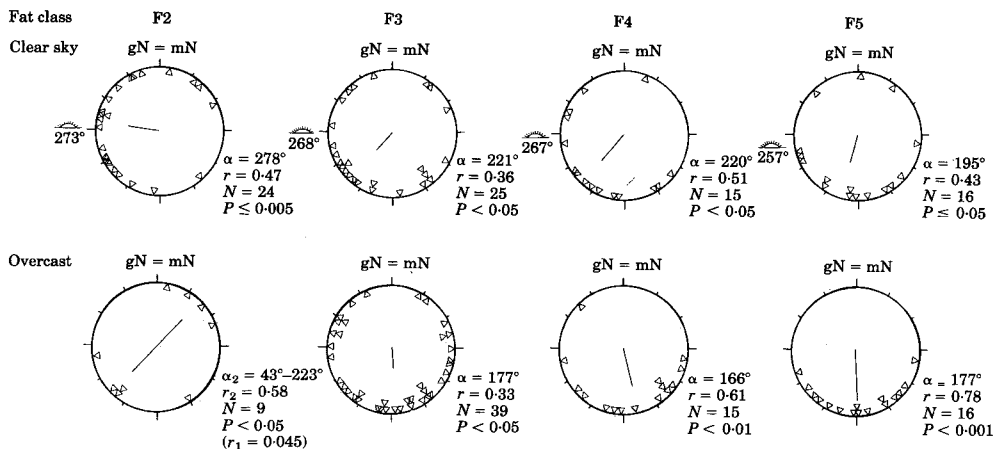
a mean heading for each individual and test. The lower threshold of acceptable migratory activity was set to 40 counts per h (based on this criterion 9 bird-hours were excluded from data analysis).

I used mean headings from individual test-hours to calculate sample mean vectors and axes of orientation, following standard procedures given in Batschelet (1981). When the mean vector length resulting from doubling the angles ( $r_2$ ) was larger, and thus provided a better description of the circular distribution, than the unimodal vector length ( $r$ ), a mean axis of orientation was used as the basis of analysis.

The Rayleigh test was applied to test for significant directional preferences (Batschelet 1981). Other statistical tests are described as appropriate. For further details on statistical procedures, see Sandberg et al. (1988a, b).

## RESULTS

The amount of stored fat had a pronounced effect on the magnetic orientation of the robins tested



**Figure 2.** Mean sunset orientation of Ottenby robins tested in the local unmanipulated geomagnetic field (controls) during autumn migration. Number of tests ( $N$ ) in each fat class category equals the number of different individuals tested within each specific fat class (i.e. no pooling was performed, cf. Fig. 1). For further details, see Fig. 1.

**Table 1.** The proportion of magnetic northerly headings shown by robins with different fat loads

	% Magnetic northerly headings ( $N$ )				$\chi^2$	$df$	$P$
	F2	F3	F4	F5			
Experimental, clear sky	86 (7)	95 (20)	27 (26)	0 (17)	42.2	2	<0.001
Experimental, overcast	100 (3)	80 (20)	38 (26)	28 (18)	14.6	2	<0.001
Controls, clear sky	58 (24)	32 (25)	27 (15)	19 (16)	8	3	<0.05
Controls, overcast	44 (9)	33 (39)	7 (15)	0 (16)	11.2	1	<0.001
Experimental+controls, clear sky	64 (31)	60 (45)	27 (41)	9 (33)	31.2	3	<0.001
Experimental+controls, overcast	58 (12)	49 (59)	27 (41)	15 (34)	15.2	3	<0.005
All tests	63 (43)	54 (104)	27 (82)	12 (67)	45.9	3	<0.001

The robins were classed as magnetic north ( $271^\circ - 90^\circ$ ) and magnetic south ( $91^\circ - 270^\circ$ ) seeking individuals, respectively. ( $N$ ): Number of observations; F: different fat classes.

in deflected magnetic fields (Fig. 1). Birds with fuel reserves corresponding to fat classes 2 and 3 reoriented towards magnetic north under both clear and overcast skies whereas robins with larger fat deposits (i.e. fat classes 4 and 5) chose magnetic southerly directions, appropriate for the season.

For the two control categories tested in normal magnetic fields, the clear relationship between fat load and change in orientation along the magnetic north-south axis failed to emerge (Fig. 2). With the exception of birds with the lowest fat level (i.e. fat class 2), the controls chose headings in more or less southerly directions irrespective of body condition.

However, the agreement in directional choices between individuals, as shown by mean vector lengths, seems to increase with increasing fat deposits. Furthermore, if the data are subdivided into individuals heading in magnetic northerly directions ( $271^\circ - 90^\circ$ ) and individuals that selected magnetic southerly directions ( $91^\circ - 270^\circ$ ), respectively, the overall influence of fat loads on orientation is similar for both experimental birds and controls (Table 1). Robins with small fat reserves were significantly more likely to reorient towards the magnetic north sector than those with large fuel reserves (all chi-squared contingency analyses show statistical significance).

**Table II.** The predictive power of stored fat on magnetic orientation of robins

	Observed changes/ no changes in headings			
	S→N	N→S	N=N	S=S
<b>Clear sky</b>				
Fat→Lean	<b>8 (9)</b>	0 (0)	1 (0)	0 (0)
Lean→Fat	0 (0)	<b>8 (10)</b>	2 (0)	0 (0)
Lean=Lean	0 (0)	0 (0)	<b>2 (2)</b>	0 (0)
Fat=Fat	0 (0)	0 (0)	0 (0)	<b>5 (5)</b>
<b>Overcast</b>				
Fat→Lean	<b>5 (7)</b>	1 (0)	0 (0)	1 (0)
Lean→Fat	0 (0)	<b>2 (4)</b>	1 (0)	1 (0)
Lean=Lean	0 (0)	0 (0)	<b>3 (3)</b>	0 (0)
Fat=Fat	0 (0)	0 (0)	0 (0)	<b>4 (4)</b>

If an individual changes its fat status (lower or higher), it is expected to change its directional preference accordingly, for example, if the bird becomes lean after being fat it should change from a geomagnetic southerly heading (S) to a geomagnetic northerly preference (N) and vice versa. If an individual remains on the same fat level between tests, no change in directional preference (N=N, S=S) is expected. In the table, the observed directional behaviour is given as a function of change/no change in fat load. Values shown in bold correspond to the observed number of instances following expectations (expected values in parentheses).

As some robins were tested more than once I can evaluate the magnetic orientation on the individual level as determined by changes in fat deposits between test conditions. The robins' directional choices (relative to the geomagnetic field) clearly depended on current fat levels (Table II).

The possibility that directions selected by the robins were influenced by differential activity levels between north-seeking and south-seeking individuals, respectively, can be ruled out since there were no significant differences between the two categories either under clear or under overcast skies (mean number of hops per h for clear sky: north=436, south=431 and, for overcast: north=335, south=401). The same holds true in a comparison of mean hops/h between different fat classes (clear skies: F2=559, F3=424, F4=436, F5=497; overcast: F2=329, F3=416, F4=334, F5=305).

Since the mean fat level of birds at capture increased from early (September: mean=2.5) to late (October: mean=3.4) in the season, a possible bias could be introduced if, for example, the majority of robins captured and tested during early

migration were lean and vice versa late in the season. Out of the lean birds (i.e. fat classes 2 and 3) tested under clear skies and in deflected magnetic fields (cf. Fig. 1, top row), 15 were captured and tested during the early part of the season and the remaining 12 experiments were performed late in the season. If the time of season was an important predictor for choices of magnetic northerly and southerly directions, respectively, then almost equal proportions of northerly and southerly headings would have been expected. This was not the case.

## DISCUSSION

### Fat Reserves and Magnetic Orientation of Robins

My results reveal a clear relationship between the amount of stored migratory fuel and the choice of magnetic directions (Fig. 1). When robins were tested in experimentally deflected magnetic fields, the visually estimated fat reserves could be used to predict whether the birds would select seasonally appropriate southerly directions (fat birds), or engage in reoriented migration (lean birds). This is further strengthened by the fact that birds that were tested more than once changed their directional preferences according to expectations based on their current fat deposits (cf. Table II).

The same clearcut connection between fat load and magnetic orientation failed to emerge for robins tested under control conditions (Fig. 2). However, if the heading of each individual is assigned to either the northern half of the circle or to the southern half, the trend is the same among the controls, i.e. lean birds select magnetically northerly directions and fat birds opt for southerly directions (Table I). The reason why the investigated relationship is less pronounced in the control categories, or alternatively, clearer among experimental birds, can only be speculated upon. One possibility is that when the magnetic field is shifted experimentally, the salience of this cue increases in an artificial way which might lead to the observed distinct result shown in Fig. 1.

Reverse migration is well documented during both spring (reorientation towards south) and autumn (reorientation towards north). During spring migration, these reversed movements are most often related to inclement weather situations such as unpredictable cold spells (Lack 1963; Eastwood 1967; Alerstam & Ulfstrand 1974).

Reverse autumn migration, on the other hand, seems to be associated with land birds encountering an ecological barrier for the first time (e.g. before a sea passage, cf. Alerstam 1978). Chaffinches, *Fringilla coelebs*, and bramblings, *F. montifringilla*, migrating through southern Sweden during autumn are often observed flying on northeasterly courses, i.e. moving inland after having met the coastline in southwesternmost Sweden (Lindström & Alerstam 1986). Reoriented finches have significantly lower fat reserves than those who proceed across the Baltic Sea in their normal migratory direction. This behaviour is probably an adaptive response enabling the birds to refuel and at the same time to avoid the strong predation pressure (cf. Lindström 1990) and competition at the coast (Alerstam 1978; Lindström & Alerstam 1986; Moore & Yong 1991).

A similar case of reoriented migration was revealed in an orientation cage study using autumn migrating robins as test subjects. The robins were captured as passage migrants at two nearby stopover sites in southern Sweden (Ottenby and Falsterbo 55°23'N, 12°50'E) and tested under both clear and overcast skies (Sandberg et al. 1988a). Birds passing the two sites are on their way to the same wintering areas in southwest Europe (Roos 1984). Orientation behaviour as well as short-distance ringing recoveries indicated that robins captured at Falsterbo temporarily reoriented towards north after being confronted with the Baltic Sea whereas the Ottenby birds rapidly resumed migration in the normal southwesterly direction. The main difference between the two samples was their migratory experience before capture, i.e. Falsterbo robins arrived at the ringing site after overland migration and were consequently encountering an ecological barrier for the first time. In contrast, the Ottenby birds had already made an extensive sea crossing and had, on average, significantly larger fat deposits than the Falsterbo birds (cf. also Karlsson et al. 1988).

Reorientation of lean birds, as opposed to fat birds, was revealed in release experiments with free-flying pied flycatchers during autumn migration and robins during spring migration (Sandberg et al. 1991). This release study demonstrated that when birds are lean they either stay at their current position or depart in directions opposite to the normal migratory direction, probably in search of more favourable feeding conditions (see also Terrill & Ohmart 1984). In this context it is interesting to note that Able (1977) found no correlation between

the quantity of migratory activity and the amount of visually estimated fat reserves when testing a number of North American warblers in orientation cages, but rather that fat birds were significantly more likely to show oriented restlessness.

All of the above-mentioned experimental studies lend support to a number of stopover studies (Dolnik & Blyumental 1967; Bairlein 1985; Biebach et al. 1986; Moore & Kerlinger 1987; Loria & Moore 1990) that point to a relationship between current fat load and the probability of resuming migration.

### Fat Loads and Mechanisms of Orientation

The results on the magnetic orientation of robins captured and tested at Ottenby (Sandberg et al. 1988b) disagreed with suggested mechanisms for orientation by visual sunset cues (Moore 1987) as well as with the proposed basis of magnetic orientation (the inclination compass, see Wiltschko & Wiltschko 1972). Although the robins changed their headings to maintain their typical axis of migratory orientation relative to the shifted magnetic fields, preferred directions frequently became reverse from normal, resulting in bimodality of mean orientation rather than unimodality. As Fig. 1 shows, when data are subdivided according to fat classes the bimodality disappears.

My results provide information about the basic regulation of directional choices made by birds during migration. Robins engaged in crossing a geographical barrier seem finely tuned to the spatial and temporal characteristics of resource availability of particular stopover sites, i.e. by reorientation, lean birds may increase their probability of finding suitable habitats for restoring depleted fat reserves in an environment less fraught with predation and competition, which usually characterize coastline habitats (Alerstam 1990b; Moore et al. 1990; cf. also Kerlinger 1989). The data may also give insights about what orientation cues are used for the diverse levels of movement that feature in bird migration (see Terrill 1990).

In summary, the current analysis shows on the one hand that the earlier results do not necessarily have to be in conflict with the magnetic inclination compass model, and, on the other hand, serve to stress the complex interplay of a number of environmental and ecological factors in the migratory orientation of robins (cf. also Sandberg 1991).

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