

Autumn migratory fuelling: a response to simulated magnetic displacements in juvenile wheatears, *Oenanthe oenanthe*

Jannika E. Boström · Thord Fransson · Ian Henshaw ·
Sven Jakobsson · Cecilia Kullberg · Susanne Åkesson

Received: 21 January 2010 / Revised: 3 May 2010 / Accepted: 16 May 2010 / Published online: 8 June 2010
© Springer-Verlag 2010

Abstract Recent experiments exposing migratory birds to altered magnetic fields simulating geographical displacements have shown that the geomagnetic field acts as an external cue affecting migratory fuelling behaviour. This is the first study investigating fuel deposition in relation to geomagnetic cues in long-distance migrants using the western passage of the Mediterranean region. Juvenile wheatears (*Oenanthe oenanthe*) were exposed to a magnetically simulated autumn migration from southern Sweden to West Africa. Birds displaced parallel to the west of their natural migration route, simulating an unnatural flight over the Atlantic Ocean, increased their fuel deposition compared to birds experiencing a simulated migration along the natural route. These birds, on the other hand, showed relatively low fuel loads in agreement with earlier data on wheatears trapped during stopover. The experimental

displacement to the west, corresponding to novel sites in the Atlantic Ocean, led to a simulated longer distance to the wintering area, probably explaining the observed larger fuel loads. Our data verify previous results suggesting that migratory birds use geomagnetic cues for fuelling decisions and, for the first time, show that birds, on their first migration, can use geomagnetic cues to compensate for a displacement outside their normal migratory route, by adjusting fuel deposition.

Keywords Bird migration · Migration programmes · Fuelling · Magnetic displacement · Wheatear · Geomagnetic cues

Introduction

Birds have been shown to be able to use both magnetic and celestial information for orientation during migratory journeys (for reviews, see Emlen 1975; Able 1980; Wiltschko and Wiltschko 1995; Åkesson and Bäckman 1999; Muheim et al. 2005). Most passerine birds migrate individually during nocturnal flights, using a combination of innate behaviours, and responses to external information met en route to reach their winter destinations (e.g. Beck and Wiltschko 1988; Alerstam 1990; Berthold 1996; Åkesson and Hedenström 2007). In order to be able to perform long migratory flights, birds have to store water and energy, the latter which is most efficiently done by fat accumulation (e.g. Blem 1980; Dawson et al. 1983; see also the review by Bairlein 2002). Since large fat stores lead to increased flight costs, reduced take-off ability and take-off speeds as well as higher predation risks (Alerstam and Lindström 1990; Kullberg et al. 1996, 2000; Lind et al. 1999), most bird species store relatively small amounts

Communicated by W. Wiltschko

J. E. Boström (✉) · S. Åkesson
Department of Biology, Lund University,
Ecology Building,
223 62 Lund, Sweden
e-mail: jannika.bostrom@zooekol.lu.se

T. Fransson
Swedish Museum of Natural History, Bird Ringing Centre,
Box 50 007, 104 05 Stockholm, Sweden

I. Henshaw
Department of Physics and Materials Science, Uppsala University,
751 21 Uppsala, Sweden

S. Jakobsson · C. Kullberg
Department of Zoology, Stockholm University,
106 91 Stockholm, Sweden

of fat (20–30% of lean body mass) and refuel regularly at successive stopover sites (Alerstam and Lindström 1990).

Recent studies have shown that arctic shore birds, however, fuel extensively and perform extreme non-stop migrations for up to 9 days crossing the Pacific Ocean longitudinally (Gill et al. 2009). Greenlandic wheatears (*Oenanthe oenanthe leucorhoa*) have to cross the Atlantic Ocean in one flight step and put on large fuel stores before departure (Ottoosson et al. 1990; Dierschke et al. 2005; Delingat et al. 2008). Juvenile garden warblers (*Sylvia borin*) captured on stopover on the island of Crete during autumn migration have been found to depart with an average fuel load of almost 100% of lean body mass, prepared to cross the Sahara desert (Fransson et al. 2008), and autumn records of birds captured on the island of Capri also show that birds from several different species carry enough fat loads to pass the Mediterranean Sea and the Sahara desert without further fuelling (e.g. Waldenström et al. 2006). The amount and timing of fuelling during migration have been suggested to be controlled by an endogenous programme (Berthold 1996), but several studies have shown that fuelling decisions may also be influenced by external information expected to be met en route (e.g. Fry et al. 1970; Jenni and Schaub 2003), such as exposure to geomagnetic cues (Fransson et al. 2001; Kullberg et al. 2003, 2007; Henshaw et al. 2008).

Juvenile thrush nightingales (*Luscinia luscinia*) trapped in Sweden during autumn migration and exposed to a simulated magnetic field of northern Egypt increased their food intake and attained a higher fuel load than control birds experiencing the ambient magnetic field of Sweden, probably in anticipation for the long non-stop flight crossing the Saharan desert (Fransson et al. 2001; Kullberg et al. 2003, 2007; Henshaw et al. 2008). Kullberg et al. (2007) used the same setup to investigate fuelling in juvenile European robins (*Erithacus rubecula*). Robins reduced their fuel deposition rate in a biological relevant way as a result of a magnetically simulated migratory journey from Sweden to their wintering area in southern Spain compared with control birds experiencing the ambient magnetic field of Sweden. These results are the inverse of what was found in the thrush nightingale, nicely illustrating that a reduction in magnetic field intensity and inclination (a southward flight from Sweden) does not induce a general increase in fuel load in migratory birds but rather trigger either an increase or a decrease in fuel deposition rate depending on the biological relevance for the species and its fuelling requirements (Kullberg et al. 2007).

In this study we used juvenile wheatears (*O. oenanthe*), captured in southern Sweden, to investigate how fuelling is influenced by a magnetic displacement along the natural

migration route compared to a displacement parallel to the west of the migration route, where the birds experience a magnetic field they would normally never encounter during migration. The parallel displacement was performed to investigate if the young wheatears are born with an innate programme taking into account displacements west (or east) of the migration route (e.g. Rabøl 1978; Lohmann et al. 2001; Åkesson et al. 2005) and if they respond to the magnetic field manipulation by altering their fat accumulation. This is the first study investigating fuel deposition in relation to geomagnetic cues in a long-distance migrant using the western passage of the Mediterranean and also the first study investigating fuelling responses to a simulated displacement away from the natural migration route. For our studies we used the actual combination of magnetic parameters (i.e. inclination and field intensity) calculated for the geographic sites. We examined food intake rates of the birds in order to find out if a possible difference in body mass increase between the two treatments could be explained by food intake rates.

The juvenile wheatears could either use a simple clock-and-compass model for orientation during their first migration (e.g. Berthold 1996; Gwinner 1996) or rely on an orientation mechanism encoding geographic (i.e. geomagnetic) positioning and triggering orientation and physiological responses as well as increased activity patterns and movement relative to their current position and their goal (e.g. Rabøl 1978; Phillips 1996; Lohmann et al. 2001; Fransson et al. 2001; Åkesson et al. 2005; cf. Åkesson and Alerstam 1998). Based on these alternatives, we set out to test the following hypotheses: (1) If fat accumulation in the migratory naïve wheatears was strictly endogenously controlled, we would expect no difference in fuelling response between our control and experimental groups to the magnetic displacement, since both groups were tested simultaneously under the same environmental conditions; (2) if the migratory naïve wheatears instead relied on an endogenous migration programme interacting with external information (e.g. a magnetic bi-coordinate map as suggested in sea turtles, lobsters and birds; e.g. Wallraff 1990; Phillips 1996; Lohmann et al. 2001; Boles and Lohmann 2003; Fischer et al. 2003), we would expect wheatears to increase fuelling and possibly also shift their orientation when displaced away from the normal migration route. If information expected to be met en route is strictly inherited, we can expect birds displaced away from these expected magnetic field parameters to respond differently (for example by increasing their fat accumulation) compared to individuals experiencing a simulated migration along the normal route. In this study we have focussed on migratory fuelling and have not studied any orientation responses.

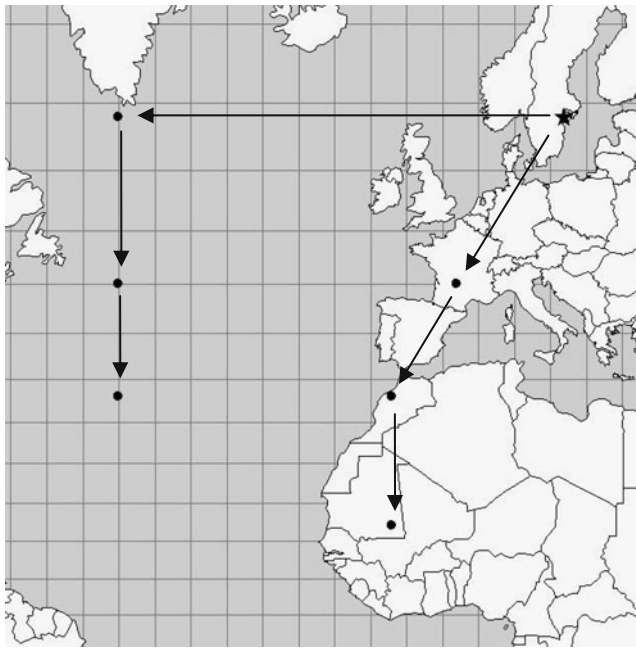


Fig. 1 Map showing the location of Tovetorp Zoological Research Station (*star*) and the simulated displacements of the control group (in Europe and Africa) and the experimental group (south of Greenland, in the Atlantic Ocean). *Arrows* indicate the stepwise displacement experienced by the birds in the two different treatments

Material and methods

Study species and experimental design

We captured the experimental birds, wheatears, at Ottenby Bird Observatory (56°12'N, 16°24'E) in southeast Sweden during late July 2007, using spring (snap) traps. We only used juvenile birds to avoid any effects of age and prior migratory experience on the results. In total, 15 individuals were used in the experiment. After capture the birds were transported to Stensöffa Ecological Field Station (55°42'N, 13°25'E), where they were housed indoors in individual cages for 30 days prior to the transport to the experimental site. During this period the birds were given fresh, vitamin-enriched water and mealworms (*Tenebrio molitor*) ad libitum.

The experiments were performed at Tovetorp Zoological Research Station (58°56'N, 17°08'E) between 31 August and 19 September 2007. The birds were kept in non-magnetic wooden sheds, each containing a magnetic coil system enabling manipulation of the magnetic field (for more information on the experimental setup and technical details on the magnetic coil system, see Kullberg et al. 2007). Individual birds were randomly assigned to either of two experimental treatments: (1) displacement along the migration route (seven individuals) or (2) displacement parallel to the west of the migration route (eight individ-

uals) (Fig. 1). Ringing recovery data from wheatears ringed in Sweden and reported to the Swedish Bird Ringing Centre were used to determine the most probable autumn migration route for wheatears migrating from Sweden to Africa (Fig. 2). The magnetic field data for the positions (calculated for July 15, 2007) used in the simulated displacements were calculated according to International Geomagnetic Reference Field Tenth generation (International Association of Geomagnetism and Aeronomy 2005) WWM 2005 (Table 1).

At the start of the experiments, all birds were kept in the ambient magnetic field of Tovetorp for 5 days. The control group then experienced a simulated displacement in successive steps towards southern Mauritania (Table 1, Fig. 1). The experimental group experienced a similar displacement but displaced to the west of the natural migration route, out in the Atlantic Ocean (Table 1, Fig. 1). The magnetic fields were changed in the morning every 5 days.

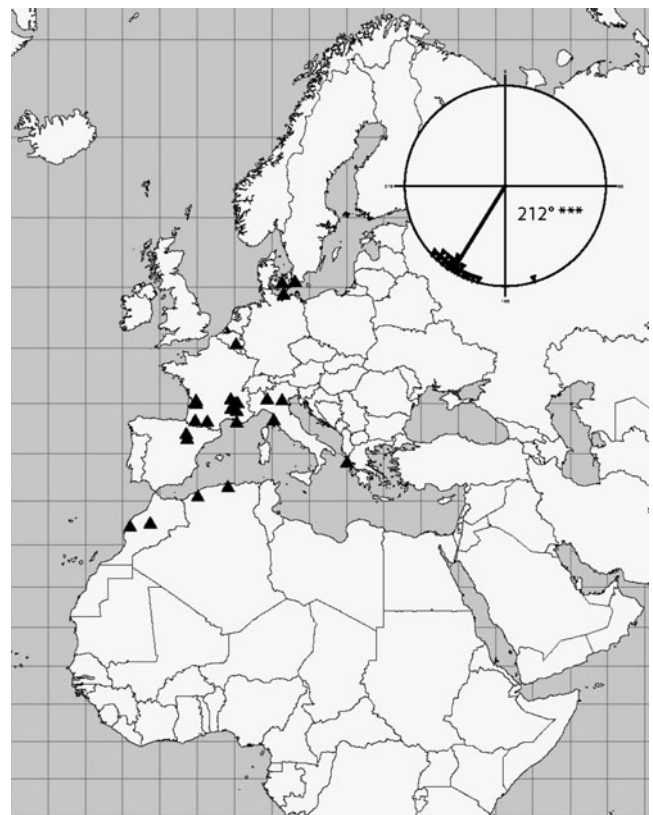


Fig. 2 Autumn and winter ringing recovery data and migratory direction for wheatears ringed in Sweden until year 2008. The map shows places of recovery, each *triangle* representing one individual. The *inlet* shows the initial heading of all individuals recovered, with mean orientation 212°. Our displacements were based on these data, and the control group was magnetically displaced to three locations along the migration route

Table 1 Magnetic fields used during the experiment and their corresponding locations

Day of change	Control				Experiment			
	Location	Position	Total intensity (nT)	Inclination (°)	Location	Position	Total intensity (nT)	Inclination (°)
	Tovetorp	58°56'N, 17°08'E	50,900	72.3	Tovetorp	58°56'N, 17°08'E	50,900	72.3
5	France	44°48'N, 1°50'E	46,600	60.7	Atlantic 1	58°57'N, 45°00'W	53,800	74.7
10	Morocco	33°00'N, 7°00'W	41,200	45.1	Atlantic 2	45°00'N, 45°00'W	49,100	64.0
15	Mauritania	17°00'N, 7°00'W	34,200	13.3	Atlantic 3	33°00'N, 45°00'W	42,800	52.0

All birds were first placed in the ambient magnetic field of Tovetorp for 5 days. Control birds were then magnetically displaced along their migration route, and experimental birds were magnetically displaced parallel to the west of their migration route. Magnetic fields were changed in the morning every 5 days. Magnetic parameters given for the WWM 2005 model

Food trays were placed on electronic scales (Precisa 310C or Precisa XB320C, Precisa Gravimetrics AG, Dietikon, Switzerland) connected to computers, enabling automatic registration of body mass (0.01 g) every time each bird fed. Body mass increase was calculated using weights at time 1830 hour each night (± 15 min). Missing data, due to problems with the scales, were replaced by mean weights of the measurements taken the day before and the day after the missing value (in total four values for control birds and six values for experimental birds, constituting 3% and 4% of total values, respectively).

Birds were fed 20 g of mealworms and given water ad libitum every day. The amount of food left in each tray was weighed daily, and the difference between food given and remaining was used to calculate food intake of each individual.

After termination of the experiment, all the birds were released at Tovetorp Zoological Research Station. The study was carried out with permission from the Swedish Animal Welfare Agency (Linköpings djurförsöksetiska nämnd: permission no. 41-07).

Data analysis

Three birds (one control and two experimental) failed to show any substantial body mass increase during the experimental period (maximum body mass increase ≤ 0.2 g during the 20 days of experiment). In contrast, all other birds showed maximum body mass increase of 1.4 g or more (range: control 1.4–5.6 g, experiment 3.3–8.1 g; Table 2). Furthermore, all three individuals decreased in body mass on at least 17 out of the 20 days of the experiment, while in the rest of the birds, reduction in body mass was only observed in four out of 20 days at the most. Thus, these three birds clearly did not behave as expected of healthy birds being held in captivity during the migration period, given unlimited access to food (e.g. Kullberg et al. 2007; Henshaw et al. 2008), and it seems likely that they may have suffered from some kind of illness or parasite.

Since they did not show a substantial body mass increase, their migratory urge could be questioned, and based on the above-mentioned arguments, they were excluded from further analyses. This resulted in final group sizes of six individuals per treatment.

Results

Fuel deposition rate

There was no difference in temperature in the sheds between the two treatments (ANOVA with repeated measurement days 1–20: $F_{1,4} = 0.4$, $p > 0.99$; mean

Table 2 All individuals subjected to the two different treatments and their maximum body mass increase during the experimental period

Individual	Maximum body mass increase (g)	Treatment	Omitted from further analyses
1EN90816	1.4	Control	
1EN90766	1.5	Control	
1EN90835	2	Control	
1EN90839	4.9	Control	
1EN90719	5.1	Control	
1EN90818	5.6	Control	
1EN90716	3.3	Experiment	
1EN90840	3.6	Experiment	
1EN90838	6	Experiment	
1EN90820	6.3	Experiment	
1EN90829	7	Experiment	
1EN90725	8.1	Experiment	
1EN90827	0	Control	x
1EN90832	0.1	Experiment	x
1EN90831	0.2	Experiment	x

Three birds showed no substantial body mass increase and were omitted from further analyses

Table 3 Repeated measures ANOVA of body mass increase from day 1 for the two different treatments

	<i>df</i>	<i>F</i>	<i>p</i>
Treatment	1	2.27	0.162
Day	18	25.76	<0.001
Treatment×day	18	3.21	<0.001

Factors: treatment (control and experimental) and day (repeated measurement with 19 levels; days 2–20)

morning temperature±SE: control treatment $13.5^{\circ}\text{C} \pm 0.5$, experimental treatment $13.1^{\circ}\text{C} \pm 0.5$), neither was there any difference in wing length nor initial body mass between the birds in the two treatments (wing length: $F_{1,10} = 1.86$, $p = 0.20$, control treatment 98.3 ± 2.9 mm, experimental treatment 96.3 ± 2.2 mm; initial body mass: $F_{1,10} = 1.75$, $p = 0.21$, control treatment 27.3 ± 3.6 g, experimental treatment 29.2 ± 2.0 g).

The birds displaced parallel to the west of the normal migration route increased more in body mass towards the end of the experiment than control birds displaced along the migration route (repeated measurement ANOVA with body mass increase days 1–20: $F_{1,12} = 3.21$, $p < 0.001$; Table 3, Fig. 3). Mean body mass at termination of experiment differed significantly between treatments ($F_{1,2} = 2.7$, $p = 0.027$; mean terminal body mass±SE: control treatment 30.4 ± 3.4 g, experimental treatment 34.7 ± 2.1 g).

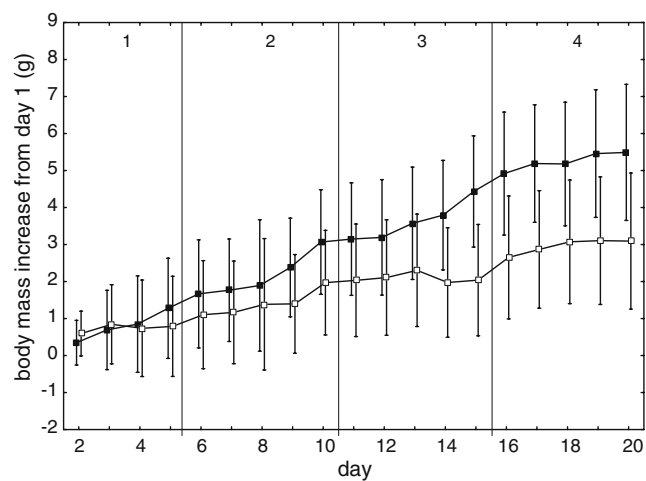


Fig. 3 Effect of magnetic displacement on migratory fuelling in wheatears. Body mass increase from day 1 (mean±SE). The magnetic field was changed every 5 days, and the birds were displaced southwards along their migration route (control group; open squares) or parallel to the west of their migration group (experimental group; filled squares). The geographical positions corresponding to the simulated magnetic displacements were 1 Sweden (ambient magnetic field), 2 France/Atlantic 1 (for the control group and the experimental group respectively), 3 Morocco/Atlantic 2 and 4 Mauritania/Atlantic 3

Table 4 Repeated measures ANOVA of food intake from day 0 for the two different treatments

	<i>df</i>	<i>F</i>	<i>p</i>
Treatment	1	3.03	0.112
Day	19	36.30	<0.001
Treatment×day	19	0.74	0.771

Factors: treatment (control and experimental) and day (repeated measurement with 20 levels; days 1–20)

Food intake

There was no significant difference in food intake between birds in the two treatments (ANOVA with repeated measurement days 0–20: $F_{1,12} = 3.0$, $p = 0.11$; Table 4, Fig. 4). Removal of the insignificant interaction term still resulted in an insignificant effect of treatment (ANOVA with repeated measurement days 0–20: $F_{1,12} = 3.1$, $p = 0.09$). In the beginning of the experimental period, all birds had a relatively stable food intake; during the mid part of the experiment, all birds increased their food intake, and towards the end of the experiment, the birds decreased their food intake again (Fig. 4).

Discussion

We found that the juvenile wheatears exposed to a simulated magnetic displacement parallel, but to the west,

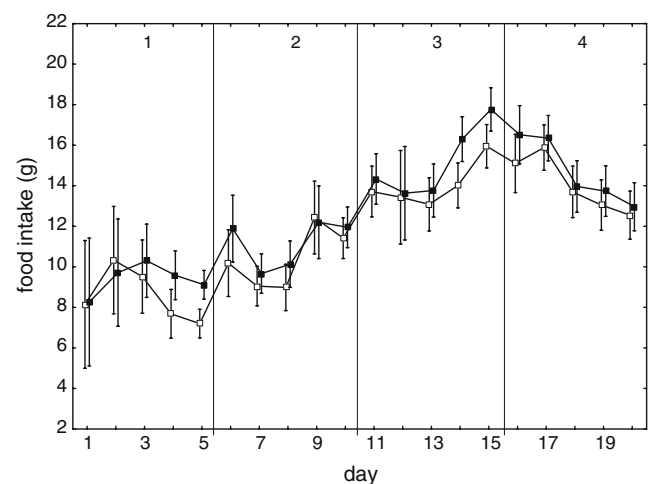


Fig. 4 Effect of magnetic displacement on food intake in wheatears. Diagram showing mean food intake from day 0 (mean±SE). Control group (open squares) and experimental group (filled squares). The geographical positions corresponding to the simulated magnetic displacements were 1 Sweden (ambient magnetic field), 2 France/Atlantic 1 (for the control group and the experimental group, respectively), 3 Morocco/Atlantic 2 and 4 Mauritania/Atlantic 3. Fig. 1

of their autumn migration route showed a higher body mass increase during the last days of experiment than individuals in a control group. The controls were displaced along the expected migration route towards southwest across West Europe, ending up in Mauritania in West Africa. The relatively low fuel deposition in the control group is in agreement with fuel load data collected from wheatears at different stopover sites in Europe (Delingat et al. 2006). The difference in fuelling response between treatments suggests that the experimental birds responded to the new and most probably unexpected combination of magnetic field parameters (i.e. inclination and field intensity) by increasing their fuelling rate. Hence, this indicates that the migratory fuelling is not just simply endogenously controlled but can be modified by magnetic field manipulations as has been suggested in previous work (Fransson et al. 2001; Kullberg et al. 2007). We can expect different physiological responses to simulated magnetic displacements depending on the bird's migratory strategy. For instance, no body mass increase at all as a response to magnetic displacement along the migration route and to the final destination as observed for a short-distance migrant, the European robin, migrating mainly across land (Kullberg et al. 2007), or by increased fuel deposition when magnetically displaced to sites before a large barrier crossing in a long-distance migrant, the thrush nightingale (Fransson et al. 2001; Kullberg et al. 2003; Henshaw et al. 2008). In accordance with previous studies (Fransson et al. 2001; Kullberg et al. 2003), our data suggest that the fuelling response to a specific combination of magnetic field parameters may be innate and the birds may respond independent of the endogenous time programme. However, can we say anything about the character of the migration programme used by our juvenile wheatears? The individuals displaced to the first geographic location in the Atlantic were experiencing both an increase in field intensity and a steeper magnetic inclination compared to the study site, which is not just associated with a displacement to the west of our study site but also with an expected displacement to the north (Skiles 1985). In both situations this would mean that the migration distance to the destination in Sub-Saharan West Africa was experimentally increased. Fuelling rates are often dependent on migration distance (e.g. Berthold 1996; Alerstam et al. 2003; Åkesson and Hedenström 2007), suggesting that a displacement leading to a longer migration distance may also increase fuelling. Both our treatment groups, however, carried relatively large fat reserves at the start of the experiments, possibly limiting the maximum level of fuel deposition. Our results are in agreement with previous studies suggesting that migratory birds use geomagnetic cues to make fuelling decisions during migration, and for the first time, we also show that birds, during their first

migratory event, can use geomagnetic cues to compensate for a displacement away from their normal migratory route, by adjusting their fuel deposition rate. Without orientation data, however, we cannot conclude whether the experimental birds believed that they had been displaced north or west compared to the control group. In this study it is also impossible to unravel whether the birds may respond to any abnormal magnetic field by increased fuelling, but in another experiment (Boström et al. unpublished data), we found that exposure to magnetic fields deviating from the ones expected on route resulted in similar fuelling responses as for individuals kept in the ambient magnetic field. A general fuelling response to any abnormal field can hence be ruled out.

Previous studies have shown that in thrush nightingales magnetically displaced to Egypt, an increased food intake could explain a difference in body mass increase between treatments (Henshaw et al. 2008). Even though the birds in our experiment showed a significant difference in body mass increase towards the end of the experiment, no significant difference in food intake rate was found. However, the groups are relatively small, and there are large variations in food intake within groups some of the days. Judging from the diagram in Fig. 4, there are clear differences in mean food intake some of the days, and overall the experimental group has a higher food intake almost every day throughout the experimental period. The repeated measure ANOVA on food intake was, however, not significant ($F_{1,12} = 3.1$, $p = 0.09$), which may be due to the small group sizes. Although not statistically verified, we cannot completely rule out the impact of food intake rate on body mass increase in our experiment. A study on wheatears on stopover has shown a clear correlation between departure fuel load and fuel deposition rate (Schmaljohann and Dierschke 2005).

Nocturnal as well as diurnal activity may also have had an impact on body mass increase in the two treatments. The amount of migratory restlessness (*Zugunruhe*) in captive migratory birds varies in a predictable pattern throughout the year (Berthold 1993) but has been shown to be affected by external factors such as light regime (Gwinner 1986, 1990). The wheatears in our two treatments experienced the same light regime, but if migratory restlessness can also be altered by magnetic cues, the birds displaced to their wintering area may have shifted their activity pattern to less migratory restlessness during nighttime and more daytime activity as they would do when they reach their wintering area. Orientation cage experiments with migratory birds often show a decreased activity when birds are subjected to conditions complicating the use of one or more compass senses (e.g. Åkesson 1993). If the experimental birds exposed to an unexpected combination of magnetic field parameters were rendered confused, they may have

decreased their activity and hence increased more in body mass than the control group.

Another possible explanation to the observed difference in body mass increase is that one of the groups could have up- or downregulated their basal metabolic rate (BMR), which has been shown to occur in several wader species during migration (e.g. Kersten et al. 1998; Kvist and Lindström 2001; Lindström and Klaassen 2003). If the control group upregulated their BMR, they would use more energy than the experimental group and hence not increase as much in body mass even with equal food intake rates. The same would be true if the experimental group downregulated their BMR, using less energy, and thus gaining more weight than the control group on the same amount of food. We did not expect such a difference between the groups, and further investigations will be needed to determine whether up- or downregulation of BMR may explain the pattern found.

Acknowledgements We are grateful to Christoffer Sjöholm and the personnel at Ottenby Bird Observatory for assistance during capture of the experimental birds and to Heiko Schmaljohann and an anonymous referee for valuable comments on an earlier version of this manuscript. Financial support was received from the Swedish Research Council (to S.Å. and to C.K.). This is report no. 240 from Ottenby Bird Observatory. This is a report from the Centre for Animal Movement Research (CAnMove), with financial support from the Swedish Research Council and Lund University.

The study was carried out with permission from the Swedish Animal Welfare Agency (Linköpings djurförsöksetiska nämnd: permission no. 41-07). The authors declare that they have no conflict of interest.

References

- Able KP (1980) Mechanisms of orientation, navigation and homing. In: Gauthreaux S (ed) *Animal migration, orientation and navigation*. Academic, New York, pp 283–373
- Åkesson S (1993) Effect of geomagnetic field on orientation of the marsh warbler, *Acrocephalus palustris*, in Sweden and Kenya. *Anim Behav* 46:1157–1167. doi:10.1006/anbe.1993.1305
- Åkesson S, Alerstam T (1998) Oceanic navigation: are there any feasible geomagnetic bi-coordinate combinations for albatrosses? *J Avian Biol* 29:618–625
- Åkesson S, Bäckman J (1999) Orientation in pied flycatchers: the relative importance of magnetic and visual information at dusk. *Anim Behav* 57:819–828. doi:10.1006/anbe.1998.1040
- Åkesson S, Hedenström A (2007) How migrants get there: migratory performance and orientation. *Bioscience* 57:123–133. doi:10.1641/B570207
- Åkesson S, Morin J, Muheim R, Ottosson U (2005) Dramatic orientation shift of displaced birds in response to the geomagnetic field. *Curr Biol* 15:1591–1597. doi:10.1016/j.cub.2005.07.027
- Alerstam T (1990) *Bird migration*. Cambridge University Press, Cambridge
- Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. *Oikos* 103:247–260. doi:10.1034/j.1600-0706.2003.12559.x
- Alerstam T, Lindström Å (1990) Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner E (ed) *Bird migration*. Springer, Berlin, pp 331–351
- Bairlein F (2002) How to get fat: nutritional mechanisms of seasonal fat accumulation in migratory songbirds. *Naturwissenschaften* 89:1–10. doi:10.1007/s00114-001-0279-6
- Beck W, Wiltschko W (1988) Magnetic factors control the migratory direction of pied flycatchers. In: Ouellet H (ed) *Acta XIX Congress of International Ornithology*. University of Ottawa Press, Ottawa, pp 1955–1962
- Berthold P (1993) *Bird migration. A general survey*. Oxford University Press, Oxford
- Berthold P (1996) *Control of bird migration*. Chapman & Hall, London
- Blem CR (1980) The energetics of migration. In: Gauthreaux SA Jr (ed) *Animal migration, orientation and navigation*. Academic, Toronto, pp 125–218
- Boles LC, Lohmann KJ (2003) True navigation and magnetic maps in spiny lobsters. *Nature* 421:60–63. doi:10.1038/nature01226
- Dawson WR, Yacoe ME, Marsh RL (1983) Metabolic adjustments of small birds for migration and cold. *Amer J Physiol* 245:755–767
- Delingat J, Bairlein F, Hedenström A (2008) Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in Northern Wheatears (*Oenanthe oenanthe*). *Behav Ecol Sociobiol* 62:1069–1078. doi:10.1007/s00265-007-0534-8
- Delingat J, Dierschke V, Schmaljohann H, Mendel B, Bairlein F (2006) Daily stopovers as optimal migration strategy in a long-distance migrating passerine: the Northern Wheatear *Oenanthe oenanthe*. *Ardea* 94:593–605
- Dierschke V, Mendel B, Schmaljohann H (2005) Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females? *Behav Ecol Sociobiol* 57:470–480
- Emlen ST (1975) Migration: orientation and navigation. In: Farner DS, King JR (eds) *Avian biology*, vol 5. Academic, New York, pp 129–219
- Fischer JH, Munro U, Phillips JB (2003) Magnetic navigation by an avian migrant. In: Berthold P, Gwinner E, Sonnenschein E (eds) *Avian migration*. Springer, Heidelberg, pp 423–432
- Fransson T, Barboutis C, Mellroth R, Akriotis T (2008) When and where to fuel before crossing the Sahara desert—extended stopover and migratory fuelling in first-year garden warblers *Sylvia borin*. *J Avian Biol* 39:133–138. doi:10.1111/j.0908-8857.2008.04361.x
- Fransson T, Jakobsson S, Johansson P, Kullberg C, Lind J, Vallin A (2001) Magnetic cues trigger extensive refuelling. *Nature* 414:35–36. doi:10.1038/35102115
- Fry CH, Ash JS, Ferguson-Lees IJ (1970) Spring weights of some Palaearctic migrants at Lake Chad. *Ibis* 112:58–82
- Gill RE, Tibbitts TL, Douglas DC, Handel CM, Mulcahy DM, Gottschalck JC, Warnock N, McCaffery BJ, Battley PF, Piersma T (2009) Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proc R Soc B* 276:447–458. doi:10.1098/rspb.2008.1142
- Gwinner E (1986) *Circannual rhythms*. Springer, Berlin
- Gwinner E (1990) Circannual rhythms in bird migration: control of temporal patterns and interactions with photoperiod. In: Gwinner E (ed) *Bird migration*. Springer, Berlin, pp 257–268
- Gwinner E (1996) Circadian and circannual programmes in avian migration. *J Exp Biol* 199:39–48
- Henshaw I, Fransson T, Jakobsson S, Lind J, Vallin A, Kullberg C (2008) Food intake and fuel deposition in a migratory bird is affected by multiple as well as single-step changes in the magnetic field. *J Exp Biol* 211:649–653. doi:10.1242/jeb.014183

- Jenni L, Schaub M (2003) Behavioural and physiological reactions to environmental variation in bird migration: a review. In: Berthold E, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Heidelberg, pp 155–171
- Kersten M, Bruinzeel LW, Wiersma P, Piersma T (1998) Reduced basal metabolic rate of migratory waders wintering in coastal Africa. *Ardea* 86:71–80
- Kullberg C, Fransson T, Jakobsson S (1996) Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). *Proc R Soc B* 263:1671–1675. doi:10.1098/rspb.1996.0244
- Kullberg C, Henshaw I, Jakobsson S, Johansson P, Fransson T (2007) Fuelling decisions in migratory birds: geomagnetic cues override the seasonal effect. *Proc R Soc B* 274:2145–2151. doi:10.1098/rspb.2007.0554
- Kullberg C, Jakobsson S, Fransson T (2000) High migratory fuel loads impair predator evasion in sedge warblers. *Auk* 117:1034–1038. doi:10.1642/0004-8038(2000)117
- Kullberg C, Lind J, Fransson T, Jakobsson S, Vallin A (2003) Magnetic cues and time of season affect fuel deposition in migratory thrush nightingales (*Luscinia luscinia*). *Proc R Soc B* 270:373–378. doi:10.1098/rspb.2002.2273
- Kvist A, Lindström Å (2001) Basal metabolic rate in migratory waders: intra-individual, intraspecific, interspecific and seasonal variation. *Funct Ecol* 15:465–473. doi:10.1046/j.0269-8463.2001.00549.x
- Lind J, Fransson T, Jakobsson S, Kullberg C (1999) Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. *Behav Ecol Sociobiol* 46:65–70. doi:10.1007/s002650050593
- Lindström Å, Klaassen M (2003) High basal metabolic rates of shorebirds while in the arctic: a circumpolar view. *Condor* 105:420–427
- Lohmann KJ, Cain SD, Lohmann CMF (2001) Regional magnetic fields as navigational markers for sea turtles. *Science* 294:364–366. doi:10.1126/science.1064557
- Muheim R, Moore FR, Phillips JB (2005) Calibration of magnetic and celestial compass cues of migratory birds—a review of cue conflict experiments. *J Exp Biol* 209:2–17. doi:10.1242/jeb.01960
- Ottosson U, Sandberg R, Pettersson J (1990) Orientation cage and release experiments with migratory wheatears (*Oenanthe oenanthe*) in Scandinavia and Greenland: the importance of visual cues. *Ethology* 86:57–70
- Phillips JB (1996) Magnetic navigation. *J Theor Biol* 180:309–319. doi:10.1006/jtbi.1996.0105
- Rabøl J (1978) One direction orientation versus goal area navigation in migratory birds. *Oikos* 30:216–223
- Schmaljohann H, Dierschke V (2005) Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*. *J Anim Ecol* 74:131–138. doi:10.1111/j.1365-2656.2004.00905.x
- Skiles DD (1985) The geomagnetic field; its nature, history and biological relevance. In: Kirschvink JL, Jones DS, McFadden BJ (eds) Magnetite biomineralization and magnetoreception in organisms. Plenum, New York, pp 43–102
- Waldenström J, Hjort C, Andersson A (2006) Autumn migration of some passerines on the island of Capri, southwestern Italy. *Ornis Svec* 16:42–54
- Wallraff HG (1990) Conceptual approaches to avian navigation systems. In: Berthold P (ed) Orientation in birds. Birkhäuser, Basel, pp 128–165
- Wiltschko R, Wiltschko W (1995) Magnetic orientation in animals. Springer, Berlin