

Food intake and fuel deposition in a migratory bird is affected by multiple as well as single-step changes in the magnetic field

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SUMMARY

Recent studies have shown that migratory thrush nightingales (*Luscinia luscinia*) experimentally treated with multiple changes of the magnetic field simulating a journey to their target stopover area in northern Egypt, increased fuel deposition as expected in preparation to cross the Sahara desert. To investigate the significance of food intake on the body mass changes observed, in the work described here we analysed food intake of the nightingales under study in those earlier experiments. Furthermore, to study whether a single change in the magnetic field directly to northern Egypt is sufficient to provide information for fuelling decisions, we performed a new experiment, exposing thrush nightingales trapped in Sweden, directly to a magnetic field of northern Egypt. Our results show that an experimentally induced magnetic field of northern Egypt, close to the barrier crossing, triggers the same response in fuel deposition as experiments with multiple changes of the magnetic field simulating a migratory journey from Sweden to Egypt, suggesting that migratory birds do not require successive changes in field parameters to incorporate magnetic information into their migratory program. Furthermore, irrespective of experimental set up (single or multiple changes of the magnetic field parameters) increase in food intake seems to be the major reason for the observed increase in fuelling rate compared with control birds, suggesting that geomagnetic information might trigger hormonal changes in migratory birds enabling appropriate fuelling behaviour during migration.

Key words: geomagnetic cues, bird migration, food intake, fuel deposition.

INTRODUCTION

Migratory flights in many songbirds are performed alone nocturnally using a combination of innate (Beck and Wiltschko, 1988) and external information about migratory direction (Alerstam, 1990; Berthold, 1996). The migratory journey requires birds to store energy in the form of fat accumulated at stopover sites along the migration route (Blem, 1990). Most migrants store relatively small amounts of fat (<25% of lean body mass) and regularly refuel at successive stopover sites (Alerstam and Lindström, 1990). Nevertheless, large ecological barriers such as the Gulf of Mexico or the Sahara desert require large fuel loads for a successful crossing (Berthold, 1993). Migratory flights over the Sahara desert involve distances of at least 1500 km, and birds can double their mass (100% increase relative to lean body mass) by storing fat prior to crossing the desert (Fry et al., 1970). Mostly, endogenous mechanisms have been thought to control various aspects of a migrant's physiology and behaviour including both timing and amount of fuelling during migration (Berthold, 1996). Recent evidence now strongly suggests that temporal and spatial precision of bird migration incorporates additional external cues along with the inherited migratory program (Fransson et al., 2001; Thorup and Rabøl, 2001; Jenni and Schaub, 2003; Fransson et al., 2005; Alerstam, 2006; Kullberg et al., 2007). In order to find confined species-specific areas it seems likely that birds must use some additional external cues in combination with clock-and-compass orientation (Fransson et al., 2005).

Both celestial cues (e.g. Emlen, 1970; Able, 1982; Moore, 1987) and information from the Earth's magnetic field are known to be used by birds to determine and maintain migratory direction

(Wiltschko and Wiltschko, 1995). Beck and Wiltschko (Beck and Wiltschko, 1988) showed that hand-reared juvenile pied flycatchers (*Ficedula hypoleuca*) use the magnetic field to trigger directional changes, suggesting that they respond to changing magnetic field values or perhaps values specific to a geographic position. Orientation responses of adult Australian silvereyes (*Zosterops l. lateralis*) subjected to experimental manipulations of the magnetic field simulating displacements along the migration route indicate that they may use the magnetic field as part of a navigational map in order to find their wintering area (Fischer et al., 2003). Evidence for physiological reactions to geomagnetic cues in migratory birds come from studies of fuelling decisions in two migratory species, the thrush nightingale (*Luscinia luscinia*) (Fransson et al., 2001; Kullberg et al., 2003) and European robin (*Erithacus rubecula*) (Kullberg et al., 2007). Fransson et al. (Fransson et al., 2001) and Kullberg et al. (Kullberg et al., 2003) exposed first-year thrush nightingales to four successive changes in magnetic field parameters, simulating a migratory journey from Sweden to northern Egypt, where extensive fuelling could be expected prior to passage over the Sahara desert. Experimental birds showed increased fuel deposition rate compared to control birds remaining in the ambient magnetic field of southeast Sweden.

In preparation for migration, many birds develop a state of hyperphagia or over-eating (e.g. King, 1961; Bairlein, 1985), and together with an increased efficiency of food utilization (Bairlein, 1985; Klaassen and Biebach, 1994), this provides an important mechanism for migratory fuelling. The cause for the observed

increase in body mass in response to a simulated geomagnetic field remains, however, to be determined.

To investigate the significance of food intake on the body mass changes observed in the earlier studies (Fransson et al., 2001; Kullberg et al., 2003) in the work reported here we analyze food intake of the nightingales. Furthermore, to study whether a single shift in magnetic field value is sufficient to provide information for fuelling decisions we performed a new experiment, exposing thrush nightingales trapped in Sweden, directly to a magnetic field of northern Egypt. If birds use the successive change in the magnetic field experienced during a natural migration for fuelling decisions, we would expect experimental birds directly exposed to the magnetic field of Egypt to show similar amount of food intake and fuel deposition rate as control birds experiencing the ambient magnetic field of southeast Sweden.

MATERIALS AND METHODS

The effect of single-step change in the magnetic field on fuel deposition rate

Thrush nightingales (*Luscinia luscinia* Linnaeus 1758) were trapped using mist nets and playback of song during August 2004, close to Tovetorp Zoological Research Station, in southeast Sweden (58°56'N, 17°08'E). First-year birds were used to avoid the potential effects of previous migration experience, and had completed post-juvenile moult and carried small amounts of visible fat; fat score 0–2 (Pettersson and Hasselquist, 1985).

Birds were randomly assigned to either a treatment group, experiencing a manipulated magnetic field implemented by a magnetic coil system, or to a control group experiencing only the ambient magnetic field and surrounded by a wooden dummy coil. The magnetic coil system consisted of two independent series of four quadratic coils each, arranged orthogonally (Lohmann and Lohmann, 1994). For technical details of the magnetic coil system see Kullberg et al. (Kullberg et al., 2003).

Each coil system (magnetic or dummy) was placed in a shed built of non-magnetic materials and placed 15 m apart. Within each coil system, birds were placed individually in four separate cages, separated by sound absorbing baffles. Semi-transparent plastic roofs prevented access to potential celestial cues. Each shed had two daylight bulbs (HP1-T Plus Philips Powertone 400 W; Philips Sweden AB, Stockholm) following the natural daylight to compensate for the reduction in light spectra caused by the plastic roofs.

Control birds experienced no manipulation of the magnetic field and remained in the ambient magnetic field of Tovetorp, southeast Sweden (58°56'N, 17°08'E; total intensity: 50 800 nT, inclination: 72°20') during the 11 days of the experiment. Experimental birds were exposed to a magnetic field of northern Egypt (31°00'N, 29°00'E; total intensity: 43 200 nT, inclination: 45°10') during the 11 days of the experiment. This experiment was replicated twice, birds in the first replicate started on the 5th August ± 2 days, and birds in the second replicate started on the 18th August ± 3 days. These dates correspond to the early and the late phases of the onset of autumn migration for thrush nightingales, respectively (Kullberg et al., 2003). Thus a total of 16 birds were used in the experiment, eight received the magnetic treatment, experiencing the geomagnetic field of northern Egypt, and eight experienced no manipulation but remained in the ambient magnetic field of southeast Sweden. In order to record body mass of the birds, food trays were attached to electronic scales (Precisa 310C, Precisa Gravimetrics AG, Dietikon, Switzerland) connected to computers, enabling automatic registration of body mass (to 0.01 g) for each bird. Body mass increase was calculated using weights at time 19:30 h.

The study was carried out with permission from the Swedish Animal Welfare Agency (permission no: 26-02).

Recording of food intake in the present experiment and the earlier experiments

In both the present experiment (2004) and the earlier experiments in 2000 and 2001 (Fransson et al., 2001; Kullberg et al., 2003) birds were fed daily with a mixture containing meal worms (*Tenebrio molitor*; 30 g) and dry food (10 g) (Berthold et al., 1990) and given water *ad libitum*. For each bird the amount of food remaining in the trays was weighed daily. The difference between the amount fed and remaining was used to calculate food intake.

RESULTS

The effect of single step change in the magnetic field on fuel deposition rate

Initial body mass and wing length did not differ between either replicates (body mass: $F_{1,14}=1.57$, $P=0.46$; wing length: $F_{1,14}=0.092$, $P=0.76$) or treatments (body mass: $F_{1,14}=0.03$, $P=0.85$; wing length: $F_{1,14}=0.09$, $P=0.76$). All birds increased in body mass during the experiment and overall experimental birds showed a higher body mass increase than controls (ANOVA with body mass increase from day 1 as repeated measurement with 10 levels: $F_{1,12}=4.98$, $P=0.04$).

In experimental birds, body mass increase was equally high between early and late season replicates whereas control birds showed a lower body mass increase during the course of the experiment in the early season replicate compared with the late season replicate (Table 1, Fig. 1).

The effect of magnetic field change on food intake

Birds trapped early in the season in all three years differed in food intake; experimental birds had a higher food intake during the course of the experiment compared with controls (Table 2, Fig. 2). Birds trapped late, however, showed no difference in food intake between treatments (Table 2, Fig. 2).

DISCUSSION

Thrush nightingales exposed to a single step change of the magnetic field from Sweden to northern Egypt, where a high fuel load would be required prior to crossing the Sahara, showed overall a higher body mass increase than control birds experiencing the ambient magnetic field of southeast Sweden. Just as in the earlier studies, in which experimental birds were subjected to multiple changes in the magnetic field from Sweden to Egypt (Fransson et al., 2001; Kullberg et al., 2003) (Fig. 3), birds directly experiencing the magnetic field of northern Egypt, reached a high fuel load irrespective of time of season, while control birds (experiencing the ambient magnetic field in southeast Sweden) by contrast, gained higher fuel loads only in the

Table 1. ANOVA of body mass increase from day 1 in thrush nightingales, when experimental birds were treated with a single-step change in magnetic field

Factor	d.f. effect, d.f. error	Control birds		Experimental birds	
		F	P	F	P
Replicate	1, 6	1.08	0.33	0.03	0.86
Day	9, 54	41.61	<0.001	33.60	<0.001
Day \times replicate	9, 54	2.83	0.008	0.59	0.79

Factors: replicate (early or late) and day (repeated measurement with 10 levels; days 2–11).

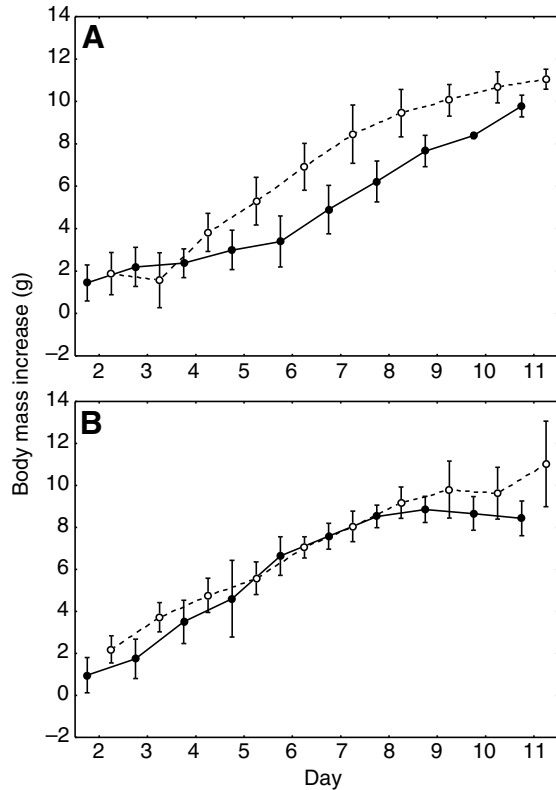


Fig. 1. The effect of a single-step change in magnetic field and time of season on migratory fuelling in thrush nightingales. Body mass increase from day 1 (mean \pm s.e.m.) for the early (A) and late (B) replicate, respectively. Experimental birds receiving a magnetic treatment are represented by open symbols; control birds are represented by filled symbols.

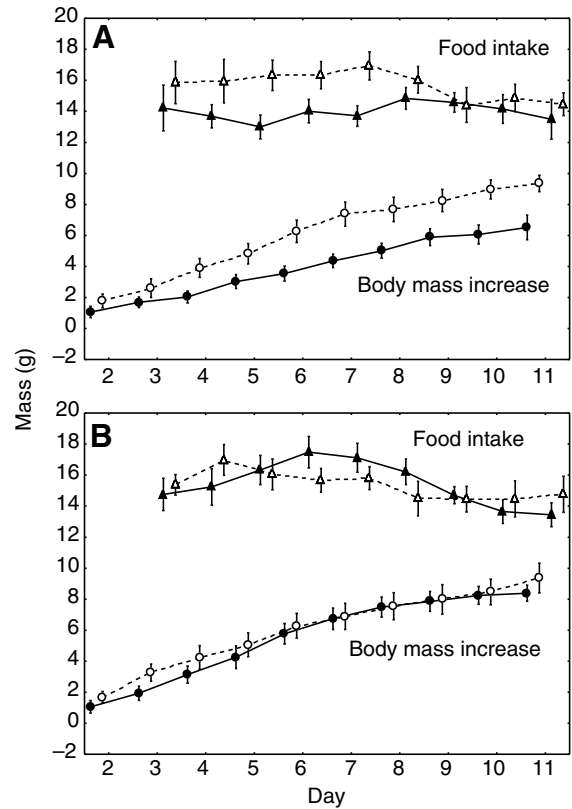


Fig. 2. Body mass increase (circles) from day 1, and daily food intake (mean \pm s.e.m.; triangles) for the early season (A) and late season (B) replicates in all three years (2000, 2001 and 2004). Experimental birds receiving a magnetic treatment (single-step or multiple changes in magnetic field value) are represented by open symbols; control birds are represented by filled symbols.

late replicate. This is in line with observations that birds late in the migratory season are likely to be increasingly time constrained and increase their fuel load (Fransson, 1998; Därnhardt and Lindström, 2001; Kullberg et al., 2003) and that late birds show a tendency to migrate with higher speeds (Ellergren, 1993; Fransson, 1995; Schaub and Jenni, 2000a; Schaub and Jenni, 2000b). Our results thus confirm the earlier studies on thrush nightingales suggesting that migratory birds can use information from the Earth's magnetic field during migration for fuelling decisions (Fransson et al., 2001; Kullberg et al., 2003). Furthermore it indicates that nightingales do not require a successive change in magnetic field in order to incorporate magnetic information into their migratory program.

Nevertheless, whether the effect shown is triggered by any latitudinal change or is a response evolved to a specific area where a large fuel load is needed remains to be investigated. Evidence so far suggesting that experienced adult birds might use magnetic map information to determine their relative position comes from orientation responses of Australian silvereyes (*Zosterops l. lateralis*). The birds under study showed the expected orientation responses when experimentally tested to changes of the magnetic field that simulated displacements to different locations along their migratory route (Fisher et al., 2003). Whether our manipulated nightingales use any change

in the magnetic field as trigger signal to initiate weight gain, use geomagnetic cues to determine their position as a component of a bi-coordinate navigational map or whether they can also use regionally specific magnetic fields as signposts indicating important areas, such as prior to ecological barriers, or to locate their wintering and breeding areas, remains to be investigated.

Experimental birds in the early season replicate receiving either a successive change in magnetic field (Fransson et al., 2001;

Table 2. ANOVA of cumulative food intake from day 3 in early and late replicates for all three years

Year	Factor	d.f. effect, d.f. error	Early replicate		Late replicate	
			F	P	F	P
2004	Treatment	1, 6	2.2	0.19	0.6	0.46
	Day	8, 48	422.4	<0.001	811.9	<0.001
	Day \times treatment	8, 48	2.1	0.05	1.0	0.41
2001	Treatment	1, 6	21.7	0.003	0.6	0.46
	Day	8, 48	502.2	<0.001	294.6	<0.001
	Day \times treatment	8, 48	2.4	0.03	0.9	0.51
2000	Treatment	1, 6	0.8	0.42	1.7	0.27
	Day	8, 48	655.6	<0.001	446.5	<0.001
	Day \times treatment	8, 48	2.3	0.03	1.2	0.29

Factors: treatment (experimental or control) and day (repeated measurement with 9 levels; days 3–11).

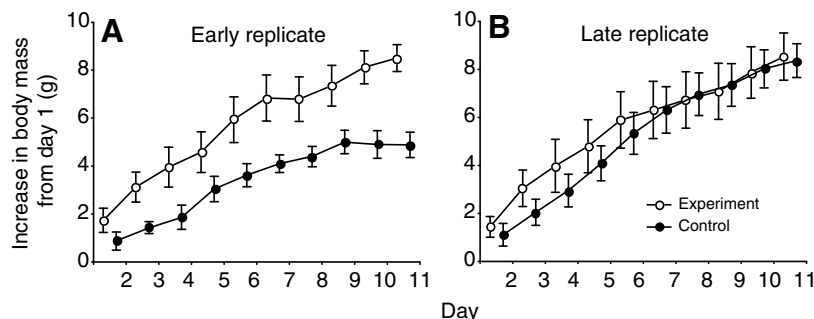


Fig. 3. The effect of multiple step changes in the magnetic field and time of season on migratory fuelling in thrush nightingales. Data from experiments in 2000 and 2001 are pooled. Body mass increase from day 1 (mean \pm s.e.m.) for the early (A) and late (B) replicate, respectively. Experimental birds receiving a magnetic treatment are represented by open symbols; control birds are represented by filled symbols. In the early replicate, experimental birds increased more in body mass than control birds, whereas in the late replicate there was no difference between the treatments (ANOVA with repeated measurement; early replicate: $F_{1,12}=8.1$, $P=0.02$; late replicate: $F_{1,12}=0.1$, $P=0.8$). From Kullberg et al. (Kullberg et al., 2003).

Kullberg et al., 2003) or a single-step change to a magnetic field of northern Egypt (this study) showed higher food intake compared to control birds. Birds trapped late however, showed no difference in food intake between experimental and controls. The fact that the pattern of food intake in the experiments performed in all three years was nicely reflected by observed body mass patterns (Fig. 2) strongly suggests that birds react to the magnetic treatment by increasing food intake, causing an increase in fuel deposition. The increased energy and nutrient demands needed for migratory fuelling are known to be mostly achieved through an increase in food intake or hyperphagia (Bairlein, 2003), probably combined with an increase in assimilation efficiency of food eaten (Bairlein, 1985; Bairlein, 1999). Furthermore our result is in line with earlier findings of food intake and fuel deposition in migratory European robins. Robins showed lower food intake and fuel loads when experiencing a magnetic treatment simulating a migratory journey from Sweden to their wintering area in southern Spain where their migratory fuel load is expected to decline (Kullberg et al., 2007).

The physiological mechanism by which the manipulated magnetic field affects nightingales to increase food intake remains to be investigated; however, regulation of foraging behaviour is believed to be influenced by corticosterone (e.g. Gray et al., 1990; Long and Holberton, 2004), the primary glucocorticoid hormone in birds. Corticosterone has recently been shown to affect foraging behaviour, lipid stores, migratory activity and orientation behaviour in migratory birds (Holberton et al., 2007; Holberton, 1999; Piersma et al., 2000; Löhmus et al., 2003). Recently Löhmus et al. (Löhmus et al., 2006) observed that migratory red-eyed vireos (*Vireo olivaceus*) treated with increased levels of corticosterone visited feeding bowls more often than control birds. Corticosterone further correlates with the stages of refuelling and flight and has been suggested to serve as a cue when birds prepare to reinstate flight at a stopover site (Landys-Cianelli et al., 2002). Our results thus suggest that geomagnetic information might trigger hormonal changes in migratory birds enabling appropriate fuelling behaviour during migration. Further investigation is, however, required to determine the links between geomagnetic cues, hormones and feeding behaviour, when birds are fuelling in preparation for a barrier crossing.

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