

## Information from the geomagnetic field triggers a reduced adrenocortical response in a migratory bird

Ian Henshaw<sup>1</sup>, Thord Fransson<sup>2</sup>, Sven Jakobsson<sup>1</sup>, Susanne Jenni-Eiermann<sup>3</sup> and Cecilia Kullberg<sup>1,\*</sup>

<sup>1</sup>Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden, <sup>2</sup>Swedish Museum of Natural History, Bird Ringing Centre, Box 50 007, SE-104 05 Stockholm, Sweden and <sup>3</sup>Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

\*Author for correspondence (cecilia.kullberg@zoologi.su.se)

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### SUMMARY

**Long-distance migrants regularly pass ecological barriers, like the Sahara desert, where extensive fuel loads are necessary for a successful crossing. A central question is how inexperienced migrants know when to put on extensive fuel loads. Beside the endogenous rhythm, external cues have been suggested to be important. Geomagnetic information has been shown to trigger changes in foraging behaviour and fuel deposition rate in migratory birds. The underlying mechanism for these adjustments, however, is not well understood. As the glucocorticoid hormone corticosterone is known to correlate with behaviour and physiology related to energy regulation in birds, we here investigated the effect of geomagnetic cues on circulating corticosterone levels in a long-distance migrant. Just as in earlier studies, juvenile thrush nightingales (*Luscinia luscinia*) caught during autumn migration and exposed to the simulated geomagnetic field of northern Egypt increased food intake and attained higher fuel loads than control birds experiencing the ambient magnetic field of southeast Sweden. Our results further show that experimental birds faced a reduced adrenocortical response compared with control birds, thus for the first time implying that geomagnetic cues trigger changes in hormonal secretion enabling appropriate behaviour along the migratory route.**

Key words: bird migration, fuelling decisions, hormones, corticosterone, geomagnetic cues.

### INTRODUCTION

Most songbirds perform their migration alone during nocturnal flights often over long distances. The main fuel for migratory flights is fat, deposited at stopover sites *en route* (Klaassen, 1996). As large fat stores entail increased flight costs, maintenance and increased predation risk (Alerstam and Lindström, 1990; Kullberg et al., 1996), most bird species accumulate rather small fat deposits (<25% of lean body mass) and refuel at several successive stopover sites (Alerstam and Lindström, 1990; Schaub and Jenni, 2000a; Schaub and Jenni, 2000b). When facing large ecological barriers like the Sahara desert that cover at least 1500 km with hardly any possibilities to refuel, extensive fuel loads (100% of lean body mass) are needed for a successful passage (Alerstam and Lindström, 1990; Fransson et al., 2008). In preparation for migratory flight birds develop a state of hyperphagia or over-eating (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 annual timing of migration and normal seasonal progression of migratory disposition such as migratory restlessness and body mass increase has also been shown to appear in seasonal constant environments in the laboratory (reviewed by Gwinner, 2003; Gwinner and Helm, 2003). These apparent circannual rhythms have led to the assumption that juvenile songbirds rely on an inherited endogenous programme, fine tuned by photoperiod and possibly other synchronizers, defining the migratory journey in terms of direction, distance and fuelling behaviour along the route (Gwinner, 1990; Berthold, 1996). The behavioural and physiological changes during migration not only occur at the onset of the initial departure but also will be repeated throughout the journey during substages (Jacobs and Wingfield, 2000) of moderate to extreme fuelling bouts with feeding, mass gain

and preparation for departure, and flight bouts of different lengths. Migratory birds will thus alternate between different physiological stages, varying from extremely fast energy deposition to prolonged bouts of energy expenditure (Jenni-Eiermann and Jenni, 1991; Jenni and Schaub, 2003).

Even though the hormonal regulation of migration is not fully understood, probably being extremely complex and relying on several hormones and their relationships and interactions, the primary glucocorticosteroid hormone corticosterone seems to play a major role in controlling behavioural and physiological traits in migratory birds (Wingfield, 2003; Ramenofsky and Wingfield, 2007). Elevated corticosterone plasma levels have been shown for many species during the migratory period (Ramenofsky et al., 1995; Holberton et al., 1996; Romero et al., 1997; Piersma and Ramenofsky, 1998; Holberton, 1999; Piersma et al., 2000), and have been found to correlate with behaviours such as hyperphagia (Landys et al., 2004a; Lohmus et al., 2006), migratory activity (Landys et al., 2004b; Holberton et al., 2007) and orientation behaviour (Lohmus et al., 2003). During the adrenocortical response to an acute stress, plasma levels of corticosterone can increase within minutes and enable behavioural and physiological adjustments redirecting the individual to life-saving activities during unpredicted stressful events (Wingfield et al., 1998). Some studies suggest elevated baseline corticosterone levels and a reduced adrenocortical response in migratory birds compared with pre-migratory birds (Holberton et al., 1996; Holberton, 1999; Long and Holberton, 2004). The migration modulation hypothesis (Holberton et al., 1996) suggests that during migration birds should express elevated baseline corticosterone levels to facilitate migratory fattening while the adrenocortical response should be reduced to prevent the already high level of plasma corticosterone becoming too high during a

stressful event, and thus causing breakdown of skeletal muscles. It has been suggested that corticosterone might play multiple roles in the control of migratory behaviour and mobilization of energy stores along the migratory route (Piersma et al., 2000; Long and Holberton, 2004). High levels of baseline corticosterone are suggested to induce hyperphagia in lean birds; in contrast, in birds with extensive fuel loads it stimulates physiological and behavioural changes that induce them to leave the stopover site (Piersma et al., 2000; Landys-Ciannelli et al., 2002).

Recent studies have shown that information from the geomagnetic field affects fuelling behaviour in migratory birds. First year thrush nightingales (*Luscinia luscinia*) exposed to a magnetic treatment simulating a migratory flight from southeast Sweden to northern Egypt increase food intake and attain a higher fuel load compared with control birds experiencing the ambient magnetic field in southeast Sweden (Fransson et al., 2001; Kullberg et al., 2003; Henshaw et al., 2008). These results are in line with the suggestion that migratory birds use external cues to get more precise information than the endogenous time programme alone would allow in deducing their latitudinal position (Gwinner, 1996; Thorup and Rabøl, 2001; Fransson et al., 2005), and suggest that geomagnetic information might act as an external synchronizer affecting hormonal secretions during migration, leading to adaptive fuelling behaviour along the migratory route (Henshaw et al., 2008). In order to investigate the effect of geomagnetic information on corticosterone secretion in migratory birds we here repeated our earlier studies and also measured baseline corticosterone levels and the adrenocortical response in juvenile thrush nightingales trapped in southeast Sweden during autumn migration and exposed to either the ambient magnetic field of southeast Sweden or the magnetic field of northern Egypt. We expected to observe a difference in hormone levels in the two treatment groups, providing insight into the importance of external geomagnetic cues for hormonal changes, and thus optimal fuelling along the migratory route.

## MATERIALS AND METHODS

### Subjects

Thrush nightingales (*Luscinia luscinia* L.) were trapped using mist nets during August 2007, in the vicinity of Tovetorp Zoological Research Station, in southeast Sweden (58°56'N, 17°08'E). To avoid the effects of age and experience from an earlier migration only first year birds were used in the study. Individuals were chosen that had completed their post-juvenile moult and had small amounts of visible fat stores [fat score 0–2 according to Pettersson and Hasselquist (Pettersson and Hasselquist, 1985)]. The study was carried out with permission from the Swedish Animal Welfare Agency (permission number: 41-07) and the experiment was conducted in accordance with Animal Behaviour Society Guidelines for the Use of Animals in Research and with the legal requirements in Sweden.

### Animal husbandry during the experiment

Experiments were performed in four wooden sheds (5 m × 5 m × 5 m) built of non-magnetic material and placed 20 m apart. Each shed contained a magnetic coil system enabling manipulation of the magnetic field. Semi-transparent plastic roofs blocked potential celestial cues but allowed some light through. The reduction in light spectra caused by the plastic roof was compensated for using four daylight bulbs in each shed (HP1-T Plus Philips Powertone 400 W; Philips Sweden AB, Stockholm, Sweden) following the natural daylight. In each shed, four birds were housed in separate circular cages (70 cm diameter and 70 cm height) constructed of non-

magnetic material with a wooden perch in the middle of the cage. Plastic baffles (0.5 cm thickness) between each cage were used to separate birds visually. In addition the baffles were covered with sound-absorbing material (Acusticell VF, 15 mm thickness; Odecon Sweden AB Sontech, Stockholm, Sweden) to reduce sound disturbance between cages. Birds were fed a dry food mixture (10 g per day) (Berthold et al., 1990), mealworms (*Tenebrio molitor*; 30 g per day) and water *ad libitum*. Fresh food and water were provided daily in the morning and the amount of food eaten was recorded by weighing the remaining food. Automatic and continuous registration of body mass was achieved by placing food trays on electronic scales (Precisa 310C or Precisa XB320C, Precisa Gravimetrics AG, Dietikon, Switzerland) connected to computers. When calculating the increase in body mass during the 12 days of the experiment, daily body mass at 19:00 h was used.

### Treatments

Two of the sheds were used for the control treatment; birds housed in these sheds received no manipulation and experienced the ambient geomagnetic field of Tovetorp (total intensity: 50,900 nT; inclination: 72°5') during the 12 days of the experiment. In the two other sheds experimental birds were exposed to a simulation of the magnetic field of northern Egypt (31°00'N, 29°00'E; total intensity: 40,100 nT; inclination: 44°23') during the 12 days of the experiment. The magnetic field of northern Egypt was calculated according to IGRF 10th generation (International Association of Geomagnetism and Aeronomy, 2005). The chosen location in northern Egypt is based on autumn ring recoveries of thrush nightingales in the eastern Mediterranean area ringed in northern Europe, suggesting that they prepare for crossing the Sahara desert in a confined species-specific area (Fransson et al., 2005; Kullberg et al., 2003). In total eight birds were subject to the magnetic treatment and eight birds were used as controls.

### The magnetic coils

To generate a volume of 1.5 m × 1.5 m × 0.75 m in which four caged birds could be subjected to a manipulated homogeneous magnetic field, each shed contained a magnetic coil system of aluminium profiles (3 m × 3 m × 3 m). The system consisted of three independent series of four quadratic coils each, arranged to control the X- (north–south), Y- (east–west) and Z-components (vertical) of the magnetic field. For further information on the magnetic coil systems see Kullberg et al. (Kullberg et al., 2007).

### Blood sampling procedure

A generally accepted method of recording plasma corticosterone is based on measurement of the baseline level and the adrenocortical response. The baseline levels of plasma corticosterone can be measured in a blood sample taken within 3 min from the time a bird flew into the mist net or from the time the experimenter entered the holding room, while the individual's responsiveness to a stressful situation is measured by taking an additional sample after at least 30 min from when the handling started (Wingfield et al., 1998). Directly after being trapped, birds were housed in separate cages in the laboratory on a restricted diet (8 g of mealworms and water *ad libitum*) to prevent accumulation of large fuel loads before the actual experiment started. After 2 days of acclimatization an initial blood sample was taken, after which the birds were taken to the experimental sheds and the experiment begun. Thereafter two more blood samples were taken: in the middle (day 6 of the experiment) and at the end of the experiment (day 12 of the experiment). All blood sampling took place in the morning between 08:00 and 09:30 h. At each of the

Table 1. Body mass increase from day 2

Factor	d.f. effect, d.f. error	F	P
Treatment	1,14	1.3	0.29
Day	8,112	11.7	<0.0001
Day×treatment	8,112	3.3	0.002

Statistics from ANOVA with day as repeated measurement with 9 levels (days 3–11) and treatment (experimental and control) as independent factor.

three blood sampling occasions (before, in the middle and at the end of experiment) a baseline sample was collected for each bird as soon as possible after entering the holding room (mean±s.e.m.: 3.1±0.16 min; range: 1.6–6.0 min), and a second sample to evaluate the adrenocortical response was collected after 30 min (mean±s.e.m.: 34±0.73 min; range: 27–52 min). Between the two samples the birds were held in individual cloth bags hung inside the test cages. Body mass was recorded for each bird after the second blood sample. Blood samples were obtained by puncturing the alar vein with a sterile 27-gauge needle and collecting the blood into heparinized microhaematocrit capillary tubes. Blood samples were then immediately placed on ice and centrifuged within 30 min at 3000 r.p.m. (centrifugal radius: 6.6 cm) for 5 min. Plasma was removed and frozen in microcentrifuge tubes at –20°C until being transferred on dry ice to the laboratory of S.J.-E. for corticosterone analysis. Because of technical problems with obtaining enough blood, the sample size was sometimes lower than the total of 16 birds used in the study (baseline sample day 6:  $N=13$ ; baseline sample day 12:  $N=15$ ). Data were normally distributed and the assumption of equal variance was met, thus Student's *t*-test and ANCOVA were used.

#### Corticosterone assay

Plasma total corticosterone concentration was determined using an enzyme-immunoassay (Munro and Stabenfeldt, 1984; Munro and Lasley, 1988) following Müller et al. (Müller et al., 2006); 5 µl plasma was added to 195 µl water, and from this solution we extracted corticosterone with 4 ml dichloromethane, which was re-dissolved in phosphate buffer and measured in triplicate in the enzyme-immunoassay. The dilution of the corticosterone antibody (Chemicon Int., Temecula, CA, USA; cross-reactivity: 11-dehydrocorticosterone 0.35%, progesterone 0.004%, 18-OH-DOC 0.01%, cortisol 0.12%, 18-OH-B 0.02% and aldosterone 0.06%) was 1:8000. We used HRP (1:400,000) linked to corticosterone as the enzyme label and ABTS as the substrate. The concentration of corticosterone in plasma samples was calculated using a standard curve run in duplicate on each plate. Internal controls were included on each plate. Intra-assay variation was 6.08% and inter-assay variation 13.9%.

#### RESULTS

##### The effect of the magnetic field on fuel deposition rate

Initial body mass and wing length did not differ between treatments (Student's *t*-test; body mass:  $t=-0.22$ , d.f.=14,  $P=0.82$ ; wing length:  $t=0.32$ , d.f.=14,  $P=0.76$ ). All birds increased in body mass and experimental birds showed a greater increase over the course of the experiment than control birds (Table 1; Fig. 1). Experimental birds also tended to eat more food during the second part of the experiment (cumulative food intake days 7–12, Student's *t*-test;  $t=-2.01$ , d.f.=14,  $P=0.06$ ).

##### The effect of the magnetic field on corticosterone level

There was no difference in baseline corticosterone or adrenocortical response levels between treatments before the experiment

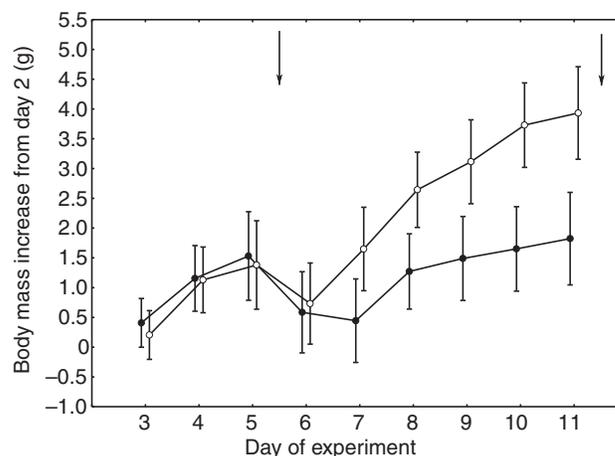


Fig. 1. Mean (±s.e.m) body mass increase from day 2 for experimental (open circles) and control birds (filled circles). The arrows mark the time of blood sampling.

(ANCOVA with corticosterone level as dependent variable, treatment as categorical predictor and time to take blood sample as covariate: baseline:  $F_{1,13}=1.5$ ,  $P=0.23$ ; adrenocortical response:  $F_{1,13}=0.07$ ,  $P=0.79$ ) (Fig. 2). Baseline levels, however, were in some cases very high (minimum: 2.2 ng ml<sup>-1</sup>; maximum: 93.0 ng ml<sup>-1</sup>; mean±s.d.: 19.7±24.1 ng ml<sup>-1</sup>). Baseline corticosterone levels did not differ between treatments during the course of the experiment (Table 2; Fig. 2). Experimental birds, however, had a lower adrenocortical response than control birds, and there was an overall reduction in the response during the course of the experiment (Table 2, Fig. 2).

#### DISCUSSION

Our results for the first time imply that geomagnetic information triggers changes in corticosterone secretion in birds, enabling appropriate behaviour along the migratory route. Birds in the present study were all trapped at the onset of the migratory period and should be in a migratory disposition with an urge to increase fuel loads and migrate. The only difference between the two treatment groups

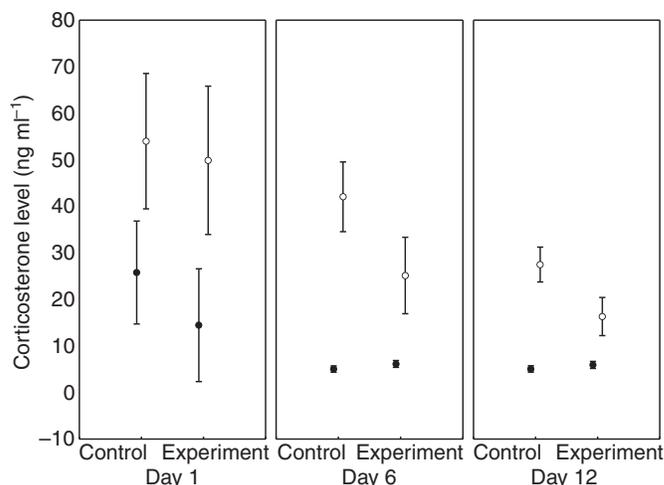


Fig. 2. Mean (±s.e.m) corticosterone levels at the three sampling occasions for experimental and control birds. Filled circles represent baseline levels and open circles represent the adrenocortical response.

Table 2. Baseline plasma corticosterone concentration and the adrenocortical response during the experiment

Factor	Baseline			Adrenocortical response		
	d.f. effect, d.f. error	F	P	d.f. effect, d.f. error	F	P
Treatment	1,10	0.1	0.72	1,13	6.1	0.04
Day	1,10	0.001	0.98	1,13	7.6	0.02
Time	1,10	2.7	0.13	1,13	0.2	0.89
Day×treatment	1,10	0.5	0.47	1,13	0.7	0.41

Statistics from ANCOVAs with day as repeated measurement with two levels (day 6 and 12), treatment as independent factor and time to take blood sample (Time) as changing covariate.

is the manipulation of the geomagnetic field experienced over the 12 days, giving the birds different information about where they are located along the migratory route. Birds experiencing the simulated geomagnetic field of northern Egypt are expected to prepare for a much longer flight (crossing more than 1500 km with no feeding possibilities) than birds experiencing the ambient magnetic field of southeast Sweden where more moderate fuel loads are required (Alerstam and Lindström, 1990). Birds experiencing a simulation of the geomagnetic field of northern Egypt not only increased fuel deposition rate compared with control birds experiencing the ambient magnetic field of southeast Sweden but also showed a reduced adrenocortical response. This result is in agreement with the hypothesis that birds facing severe environments, e.g. during reproduction (Romero et al., 1997) and migration (Ramenofsky et al., 1995; Holberton et al., 1996), inhibit the adrenocortical response to environmental stressors, thus allowing the animal to carry on with breeding and feeding activities, respectively, during stressful conditions. Accordingly, and just as in earlier studies of thrush nightingales experiencing a simulation of the geomagnetic field of northern Egypt, the elevated fuel deposition rate seems to be due to an increase in food intake (Henshaw et al., 2008). The reduced adrenocortical response could thus be an adaptive response enabling birds to spend more time feeding in spite of stressful events (e.g. predator risk) encountered at stopover sites, and thus be able to more rapidly accumulate extensive fuel loads in anticipation of a long energy-demanding non-stop flight.

We furthermore observed a difference in body mass increase between the two treatment groups after the stressful event of blood sampling in the middle of the experiment, which might be linked to the reduced adrenocortical response (Fig. 1). Birds exposed to the ambient magnetic field of southern Sweden seemed to be more affected by the stressful treatment and did not increase their body mass for 2 days, while birds exposed to the magnetic field of northern Egypt recovered much faster and continued to accumulate fuel loads the day after the stressful event. Accordingly, it has recently been shown that raised corticosterone levels can cause substantial increases in oxygen uptake leading to increased energy expenditure (DuRant et al., 2008). It might be argued that birds exposed to the magnetic field of northern Egypt do not react to the magnetic field of Egypt *per se*, but that any change in the magnetic field causes chronic stress resulting in a reduced adrenocortical response and hyperphagia. In an earlier study we have, however, shown that European robins (*Erithacus rubecula*), being medium-distance migrants, reduce their fuel deposition rate in a biologically relevant way as a result of a magnetically simulated migratory journey from Sweden to their wintering area in Spain compared with control birds experiencing the ambient magnetic field of Sweden (Kullberg et al., 2007). This nicely illustrates that a reduction in magnetic field intensity and inclination (a southward flight from Sweden) does not

induce a general stress response causing hyperphagia in migratory birds but, rather, triggers either an increase or a decrease in fuel deposition rate depending on the biological relevance for the species. Furthermore, there were no differences in baseline levels of corticosterone between experimental and control birds in the present study, suggesting that the magnetic treatment *per se* did not impose additional stress on the birds. The lower adrenocortical response in birds exposed to magnetic field changes is thus not linked to a change in baseline corticosterone levels, which is in accordance with the suggestion that baseline corticosterone and adrenocortical responses are regulated differently, with baseline corticosterone levels showing more seasonal rhythms than the adrenocortical response (Romero, 2002). Furthermore, a large variation in adrenocortical responses in birds during migration has been observed, suggesting that the level of adrenocortical response is more dependent upon the current ecological context and fuel load requirements (Ramenofsky et al., 1995; Jenni et al., 2000; Breuner et al., 2008). Before the experiment started we recorded unusually high baseline corticosterone levels, which is not surprising given the birds had only been in captivity for 2 days and thus had not acclimatized to captivity. Furthermore, they were held on a restricted diet during these first days, which is known to increase baseline levels in some birds (Reneerkens et al., 2002) (but see Schwabl et al., 1991). During the later part of the experiment both experimental and control birds showed similar low levels of baseline corticosterone (mean±s.d.: 5.6±1.6 ng ml<sup>-1</sup> at the end of the experiment) to those measured in seven passerine species trapped during autumn migration in Europe (Gwinner et al., 1992) and in garden warblers (*Sylvia borin*) stopping over in the Sahara desert during autumn migration (Schwabl et al., 1991). This indicates that the birds under study, after habituation to captivity, showed no extreme stress due to the experimental set-up.

Birds sampled just prior to a long non-stop flight, have been reported to show moderately elevated baseline corticosterone levels compared with birds of the same species sampled when there is no need for extended energy stores [red knots (*Calidris canutus*) (Piersma et al., 2000); bar-tailed godwits (*Limosa lapponica*) (Ramenofsky et al., 1995; Landys-Ciannelli et al., 2002); western sandpipers (*Calidris mauri*) (O'Reilly and Wingfield, 2003)], suggesting that a high energetic demand and unpredictable environmental circumstances ahead induce elevated baseline corticosterone levels in migratory birds (Piersma et al., 2000; Landys-Ciannelli et al., 2002). The lack of an increased baseline corticosterone level in experimental birds in the present study might thus seem puzzling. However, a high level of baseline corticosterone prior to a long non-stop flight has been shown to correlate with extensive fuel loads and has thus been suggested to stimulate physiological and behavioural changes that induce birds to leave the stopover site (Piersma et al., 2000; Landys-Ciannelli et al., 2002). As none of the experimental birds under study at the end of the

experiment (maximum of 34% of lean body mass in this study) had reached a sufficient amount of fuel to successfully be able to pass the Sahara desert [80–100% of lean body mass (Alerstam and Lindström, 1990; Fransson et al., 2008)], baseline levels would not be expected to rise until a higher fuel load had been obtained. The lack of a complete response in the experimental birds resembling natural fuelling patterns is probably due to constraints in the experimental set-up (for example the very fast change to the magnetic field of Egypt and the absence of all other natural cues birds will obtain during migration) (Kullberg et al., 2003).

Corticosterone levels in birds are known to vary with social and environmental factors (Raof et al., 2006; Rubenstein, 2007; Jenni-Eiermann et al., 2008), but observed seasonal variation in corticosterone levels has been suggested to be mediated through photoperiodically induced seasonal changes in physiology rather than variation in environmental factors like temperature, storms or habitat condition (Romero et al., 1997; Romero and Wingfield, 1998; Romero, 2002; Landys et al., 2004b; Romero and Rich, 2007; Holberton et al., 2008). Annual variation of the geomagnetic field has been suggested to act as a seasonal synchronizer affecting the circannual rhythm of the neuroendocrine system in mammals [(see Löscher and Fiedler, 1996; Burch et al., 1999; Meyer et al., 2006) and references therein]. Our results for the first time show that geomagnetic information affects corticosterone levels of birds, reflecting an intrinsic change in migratory status due to an external cue (the geomagnetic field) signalling for ‘substages’ of migration (Jacobs and Wingfield, 2000) that require different hormonal levels to enable birds to prepare for a forthcoming long non-stop flight. In accordance, a recent study of fuelling behaviour before the Saharan crossing in first-year garden warblers suggests that inexperienced birds switch from a fuelling programme used throughout Europe to a programme preparing for the desert crossing with stopover times that are twice as long and accumulation of extensive fuel loads very close to the desert (Fransson et al., 2008). This precise fuelling strategy close to the crossing indicates an allostatic change bringing birds to a different internal physiological state (McEwens and Wingfield, 2003; Landys et al., 2006) that, according to our novel finding, may be induced by geomagnetic information.

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