Magnetic cues and time of season affect fuel deposition in migratory thrush nightingales (*Luscinia luscinia*)

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Bird migration requires high energy expenditure, and long-distance migrants accumulate fat for use as fuel during stopovers throughout their journey. Recent studies have shown that long-distance migratory birds, besides accumulating fat for use as fuel, also show adaptive phenotypic flexibility in several organs during migration. The migratory routes of many songbirds include stretches of sea and desert where fuelling is not possible. Large fuel loads increase flight costs and predation risk, therefore extensive fuelling should occur only immediately prior to crossing inhospitable zones. However, despite their crucial importance for the survival of migratory birds, both strategic refuelling decisions and variation in phenotypic flexibility during migration are not well understood. First-year thrush nightingales (*Luscinia luscinia*) caught in the early phase of the onset of autumn migration in southeast Sweden and exposed to a magnetic treatment simulating a migratory flight to northern Egypt increased more in fuel load than control birds. By contrast, birds trapped during the late phase of the onset of autumn migration accumulated a high fuel load irrespective of magnetic treatment. Furthermore, early birds increased less in flight-muscle size than birds trapped later in autumn. We suggest that the relative importance of endogenous and environmental factors in individual birds is affected by the time of season and by geographical area. When approaching a barrier, environmental cues may act irrespective of the endogenous time programme.

Keywords: bird migration; fuel; magnetic cues; flight muscle; endogenous time programme

1. INTRODUCTION

Long-distance migration is a common life-history trait in birds, and most songbirds perform their migration alone during nocturnal flights using innate information about migratory direction (Alerstam 1990; Berthold 1996). It has been shown that songbirds use both celestial cues and information from the Earth's magnetic field to choose and maintain migratory direction (Able 1993; Wiltschko & Wiltschko 1995). The main fuel for migratory flights is fat, deposited at stopover sites en route (Blem 1980). Since large fat stores entail increased flight costs and an increased predation risk (Alerstam & Lindström 1990; Kullberg *et al.* 1996), most bird species accumulate rather small fat deposits (20–30% of lean body mass) and refuel at several successive stopover sites (Alerstam & Lindström 1990). However, when facing large ecological barriers, such as the Gulf of Mexico or the Sahara desert, large fuel loads are necessary for a successful passage. The passage of the Sahara desert involves flight distances of at least 1500 km, and birds have been found to double their mass (100% increase in relation to lean body mass) by means of fat storage prior to crossing this barrier (Fry *et al.* 1970).

It has been assumed that the amount and timing of fuelling during migration are governed by a circannual rhythm fine-tuned by photoperiod (Berthold 1996). However,

variation in the time of breeding affects the timing of the onset of migration, and unpredictable weather and feeding conditions affect timing en route. Hence, a bird cannot safely deduce its latitudinal position from the calendar date (Gwinner 1996). Consequently, it is reasonable to assume that birds use external cues to time crucial fuelling events (e.g. to enable barrier crossing; Fransson *et al.* 2001; Jenni & Schaub 2003). In a recent study, we have shown that birds might use geomagnetic information to decide where to accumulate the extensive fuel loads necessary for successful trans-Saharan flights. Thrush nightingales (*Luscinia luscinia*) caught in Sweden during their first migration and exposed to a magnetic field simulating a migratory flight to northern Egypt extended their fuelling period compared with control birds experiencing the ambient magnetic field in southeast Sweden (Fransson *et al.* 2001). This finding shows that a change in the magnetic field can trigger not only directional changes in migratory animals (birds: Beck & Wiltschko 1988; Wiltschko & Wiltschko 1992; sea turtles: Lohmann *et al.* 2001) but also processes such as extensive fuel deposition. How much fuel a bird accumulates is flexible and is probably determined by complex trade-offs between present environmental and endogenous factors (Schaub & Jenni 2000). In several species, late-migrating individuals have larger fuel deposits and seem to travel faster than early individuals (Dänhardt & Lindström 2001). Jenni & Schaub (2003) suggest that early migrants may be able to adjust more easily behaviourally to environmental factors than late and time-pressed birds, which could be expected

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to be more controlled by their endogenous time pro-
gramme.

Besides accumulating fuel, birds also show adaptive
phenotypic flexibility in several organs during migration.
Dissections of individuals of several species, sampled at
different periods during migration, have shown that flight-
muscle mass often increases before migratory flights while
the size of various nutritional organs is reduced (Piersma
1998), presumably to increase flight-muscle size relative to
wing load during extensive migratory flights (Pennycuick
1989). An enlarged flight muscle may also serve to
increase protein sources before long-distance migration
(Bauchinger & Biebach 1998, 2001; Jenni & Jenni-Eierm-
ann 1998). How interactions between endogenous and
external factors in late and early migrants may affect birds'
bodily changes is not well understood (Jenni & Schaub
2003).

In order to study whether changes in the size of fuel load
and flight muscle depend on the time within the migratory
season, we replicated our study of migratory fuelling in
relation to geomagnetic cues in first-year thrush night-
ingales (Fransson *et al.* 2001). Because the experiments in
both years (2000 and 2001) were performed in two repli-
cates during autumn, when thrush nightingales leave
Sweden (birds in the first replicate were trapped early and
those in the second replicate were trapped late during the
onset of autumn migration), it is possible to study the
effects of both timing of migration and magnetic infor-
mation on fuelling decisions. We also investigated how the
increase in body mass during the fuelling period affects
the size of the pectoral muscle by measuring the muscle
of all birds in 2001 at the beginning and end of the experi-
ment using a non-invasive technique.

2. MATERIAL AND METHODS

(a) *Subjects*

Thrush nightingales were trapped by mist nets during August
2000 and 2001, in the vicinity of Tovetorp Zoological Research
Station, in southeast Sweden (58°56′ N, 17°08′ E). The effects
of age and, thereby, experience from earlier migration were
avoided by using only first-year birds in the study. Furthermore,
only birds about to prepare for migration were included by
choosing individuals that had completed their post-juvenile
moult and had small amounts of visible fat reserves (fat scores
0–2 according to the scale in Pettersson & Hasselquist (1985)).

(b) *Husbandry*

Individual birds were randomly assigned either to a shed with
magnetic coils, or to a shed with a wooden dummy coil where
birds experienced the ambient magnetic field. Both sheds
(4 m × 4 m × 3.5 m) were built of non-magnetic materials, and
were placed 15 m apart. Roofs were made of semi-transparent
plastic, which allowed some light through but blocked potential
celestial cues. To compensate for the reduction in light spectra
caused by the plastic roof (Wiltschko *et al.* 1993), each shed
had two daylight bulbs (HP1-T Plus Philips Powertone 400 W)
following the natural daylight. In each shed, four birds were
housed in separate cages (55 cm × 55 cm × 55 cm), and baffles
of sound-absorbing material were placed between the cages to
reduce sound transmission and to separate the birds visually.
Birds were fed with mealworms (*Tenebrio molitor*), a dry food
mixture (Berthold *et al.* 1990) and water *ad libitum*. Food and
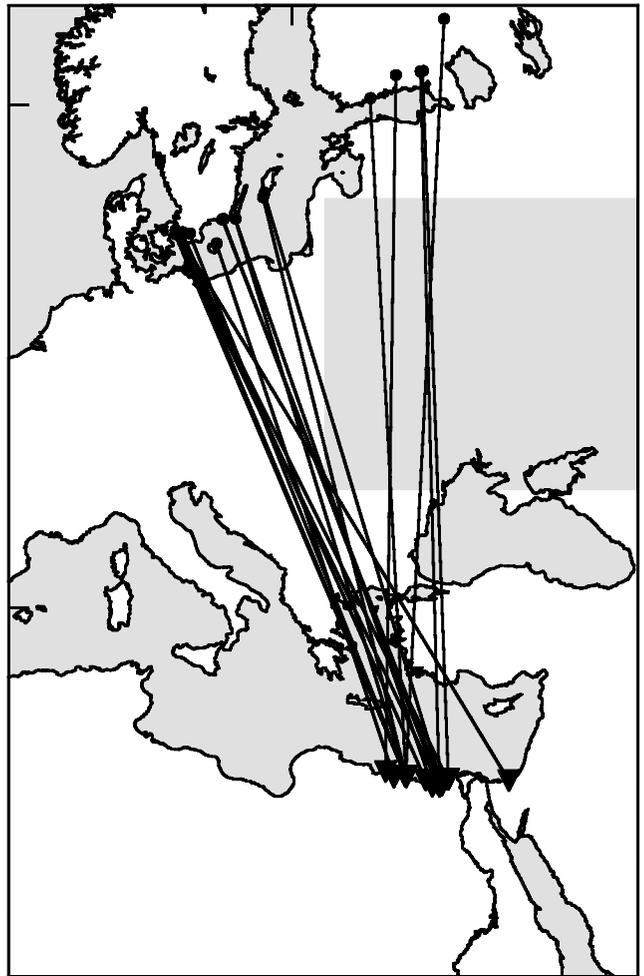
Figure 1. All autumn recoveries of thrush nightingales in the
eastern Mediterranean area that were ringed in Denmark
($n = 5$), Sweden ($n = 9$) or Finland ($n = 5$). Data received
from the Zoological Museum in Copenhagen, the Swedish
Museum of Natural History and the Finnish Museum of
Natural History.

water were exchanged daily. Food trays were placed on scales
(Precisa 310C) connected to computers, allowing automatic and
continuous registration of individual body mass. When calculat-
ing the increase in body mass, weights at 20.00 were used.

(c) *Treatments*

Control birds experienced no manipulation of the magnetic
field during the whole experiment, which ran for 11 days. At
the start of the experiment, morning day 1 (trapping day), both
experimental and control birds remained in the ambient mag-
netic field (total intensity of 50 800 nT; inclination of 72°20′).
In order to simulate the gradual change in magnetic field that
birds experience during migration, the field of the experimental
birds was changed to that of four different localities during the
course of the experiment, calculated according to IGRF2000
(International Association of Geomagnetism and Aeronomy
2000). We based the simulated migration on data from autumn
recoveries of thrush nightingales ringed in Denmark, Sweden
and Finland. Since all recoveries are found in northern Egypt
(figure 1), suggesting they prepare for crossing the Sahara desert
in this area, we simulated a migratory route from Sweden to
northern Egypt for the experimental birds. The autumn
recoveries available indicate that this migratory trip lasts for

approximately one month. At evening day 1 the magnetic field of the experimental birds was changed to that of northern Poland (49 900 nT, 69°30′), at evening day 2 the magnetic field was changed to that of southern Poland (48 900 nT, 65°50′), at evening day 4 the magnetic field was changed to that of northern Greece (46 400 nT, 57°20′) and at evening day 6 the magnetic field was changed to that of northern Egypt (43 200 nT, 45°10′). Experimental birds then remained in the magnetic field of northern Egypt (31°00′ N, 29°00′ E) until the end of the experiment at day 11 when all birds were released into the wild. This protocol was replicated once each year, thus 16 birds were subjected to the magnetic treatment and 16 birds were used as controls. Birds for the first replicate each year were trapped on 5 August (± 2 days) while birds in the second replicate were trapped on 19 August (± 2 days). The number of trapped thrush nightingales per day during the autumn (1990–2001) at a bird observatory in southeast Sweden (56°55′ N, 18°11′ E) gives a median date for the onset of autumn migration of 13 August (90% of the birds were trapped between 30 July and 19 August, $n = 143$, Sundre Bird Ringing Group, unpublished data). Thus, birds used in the first replicate were trapped in the early phase of the onset of autumn migration while birds used in the second replicate were trapped late in the onset of migration.

(d) *The magnetic coil*

To generate a volume of 1.2 m³, in which four caged birds could be subjected to a manipulated homogenous magnetic field, we constructed a magnetic coil system of aluminium profiles. The system consisted of two independent series of four quadratic coils each, arranged orthogonally (Lohmann & Lohmann 1994). Since the difference in declination between southeast Sweden and northern Egypt is less than 1°, the declination was left unchanged.

The magnetic field of the coil system (2.4 m × 2.4 m × 2.4 m) was calculated using the Biot–Savart law. We found, numerically, a configuration of the coils giving an inhomogeneity of lower than 1% in the experimental area. Coils were wound with copper wire (0.7 mm diameter), the four outer coils in 25 turns and the four inner coils in 10 turns. By connecting each of the two coil systems to a power supply (Delta Elektronika ES 030-10) we could change the vertical and horizontal components of the magnetic field independently by changing the current (stability of the power supply = ± 0.0011 A).

Before the experiment began, we set the vertical and horizontal components of the magnetic field for the stopover sites, using a fluxgate magnetometer (Zeiss Jena theodolite with Bartington Instruments fluxgate magnetometer). Furthermore, we verified the homogeneity of the field using a proton magnetometer (GEM Systems). At this point, we also checked that the field from one coil did not affect the field of the other more than expected, thus showing that the coils were sufficiently orientated.

(e) *Measurement of pectoral muscle and wing load*

In order to study changes in the flight muscle, we measured the size of the pectoral muscle of each bird in 2001 at trapping (day 1) and at the end of the experiment (day 11). The size of the muscle was estimated using a body mould in dental alginate (TopDent, DAB Dental, Sweden) (Selman & Houston 1996). By cutting the mould dorsoventrally through the middle of the pectoral muscle, we obtained a measure of the cross-sectional area of the muscle, which was recorded by making four ink prints per mould on a paper. A horizontal line was drawn 6 mm perpendicular to the sternal keel of each print (6 mm being used as a standard measure of keel depth, obtained from dissection of a dead thrush nightingale). The enclosed area was then measured using the computer program SCION IMAGE FOR WINDOWS, BETA 4.0.2; Scion Corporation, and an average area was calculated for the four prints from each mould. The cross-sectional pectoral-muscle area established with this moulding technique has been shown to correlate with pectoral-muscle lean dry mass in zebra finches (*Taeniopygia guttata*) (Selman & Houston 1996). Before making a mould, we examined each bird, thereby confirming that subcutaneous fat did not cover the pectoral muscle, which would have given an incorrect estimate of pectoral-muscle size. In order to calculate wing load we traced the outline of the left wing of each bird at day 11. The area of the wing was then measured using the computer program SCION IMAGE and the wing load of each bird was calculated according to Pennycuick (1989). The muscle ratio for individual birds was calculated as muscle area per wing load.

3. RESULTS

There were no differences in either initial body mass or wing length between replicates (body mass: $F_{1,24} = 0.1$, $p = 0.8$; wing length: $F_{1,24} = 0.1$, $p = 0.8$), treatments (body mass: $F_{1,24} = 0.6$, $p = 0.4$; wing length: $F_{1,24} = 0.1$, $p = 0.8$) or years (body mass: $F_{1,24} = 0.4$, $p = 0.5$; wing length: $F_{1,24} = 3.8$, $p = 0.6$) and all birds increased in body mass during the study (ANOVA with body-mass increase from day 1 as repeated measurement with 10 levels: $F_{9,216} = 121.5$, $p < 0.001$; table 1). Since birds in the early replicates increased less in body mass over time than did birds in the late replicates ($F_{9,216} = 0.01$, $p < 0.05$), while there were no effects of year ($F_{1,24} = 0.01$, $p = 0.9$), the two replicates were treated separately. In the early replicate, experimental birds experiencing the magnetic treatment increased more in body mass than did control birds (table 2). Experimental birds increased by 8.5 ± 0.6 g (mean ± s.e.) (32% body-mass increase) from day 1 to day 11, whereas control birds increased by 4.9 ± 0.5 g (19% body-mass increase) (figure 2a). However, in the late replicate the body mass of both experimental and control birds increased substantially (mean ± s.e. increase in body mass from day 1 to day 11 for experimental birds: 8.5 ± 1.0 g (34% body-mass increase); for control birds: 8.4 ± 0.7 g (32% body-mass increase); figure 2b). Furthermore, measurements of the pectoral muscle of the thrush nightingales in 2001 revealed that the muscle area increased with increasing wing load (effect of day; table 3) and that there was a difference in pectoral-muscle change between the two replicates. The late replicate increased more in muscle area from day 1 to day 11 than did the early replicate, resulting in a higher muscle ratio at the end of the experiment (table 3; figure 3).

4. DISCUSSION

Data from the two successive years show that control birds experiencing the ambient magnetic field in southeast Sweden had higher fuel loads as the season progressed (early replicates versus late replicates). Furthermore, in the early replicates, control birds showed a lower fuel deposition than did birds experiencing a magnetic treat-

Table 1. Wing length, initial body mass and total increase in body mass.

(Mean ± s.e. wing length, initial body mass and total increase in body mass during the study for the two years and treatments; the two replicates are combined.)

year	treatment	wing length (mm)	initial body mass (g)	total increase in body mass (g) day 1–day 11
2000	control	89.4 ± 0.8	23.5 ± 0.3	6.4 ± 1.0
2000	experiment	88.7 ± 0.7	22.9 ± 0.4	8.6 ± 0.7
2001	control	90.2 ± 0.6	22.9 ± 0.5	6.8 ± 0.8
2001	experiment	90.5 ± 0.6	22.9 ± 0.3	8.4 ± 0.9

Table 2. Increase in body mass from day 1.

(Statistics from ANOVAs for early and late replicates, respectively. Factors: 1, treatment; 2, year; 3, day (repeated measurement factor with 10 levels; day 2–11); and the subsequent interactions.)

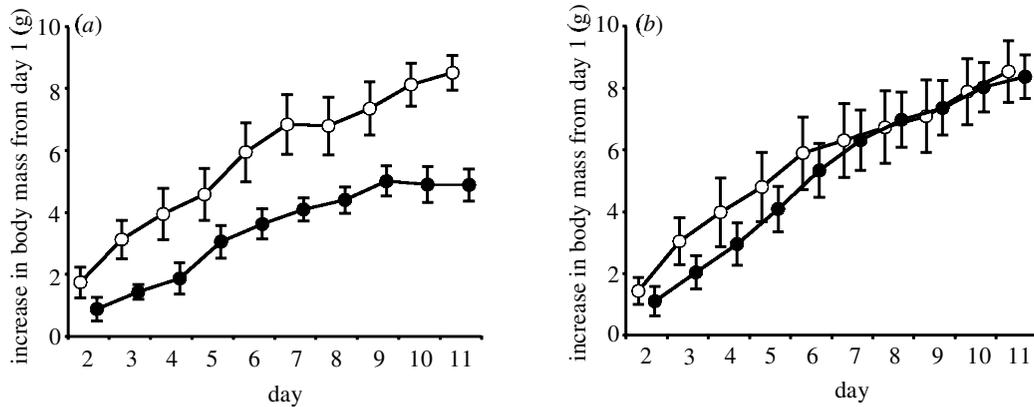| factor	d.f. effect, d.f. error	early replicate F	p	late replicate F	p
1	1, 12	8.1	0.015	0.1	0.8
2	1, 12	0.1	0.7	0.1	0.7
3	9, 108	50.0	< 0.001	72.1	< 0.001
1 × 2	1, 12	0.3	0.6	1.0	0.3
1 × 3	9, 108	2.3	0.02	0.8	0.6
2 × 3	9, 108	0.6	0.8	0.8	0.6

Figure 2. The effect of magnetic field and time of season on migratory fuelling. Mean (± s.e.) body-mass increase from day 1 for experimental (open circles) and control (filled circles) birds in the (a) early and (b) late replicates. Data points are shifted to increase readability.

Table 3. Muscle area and muscle ratio in 2001.

(Statistics from ANOVAs for muscle area and muscle ratio, respectively. Factors: 1, replicate; 2, treatment; 3, day (repeated measurement factor with two levels; day 1 and day 11); and the subsequent interactions.)

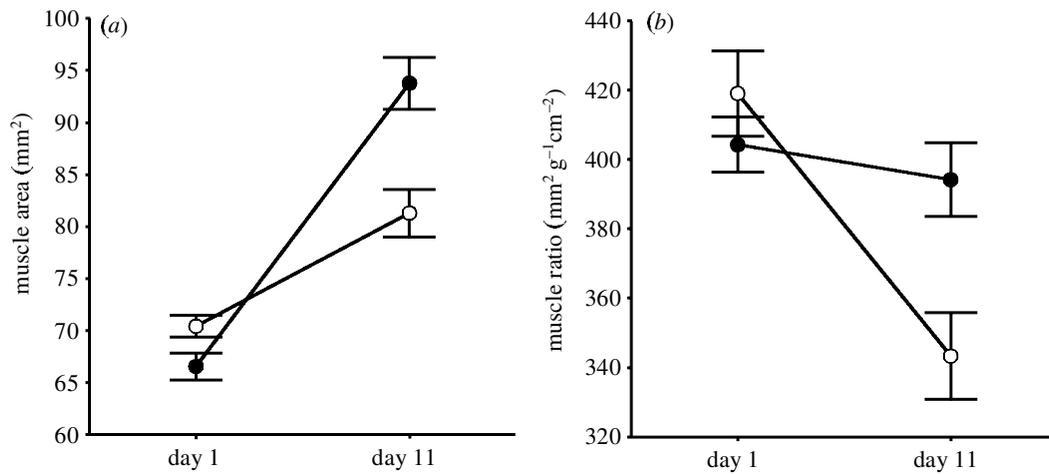| factor	d.f. effect, d.f. error	muscle area F	p	muscle ratio F	p
1	1, 12	3.8	0.08	1.4	0.3
2	1, 12	0.2	0.6	0.09	0.8
3	1, 12	215.9	< 0.001	63.2	< 0.001
1 × 2	1, 12	1.7	0.2	0.9	0.4
1 × 3	1, 12	39.8	< 0.001	37.0	< 0.001
2 × 3	1, 12	0.1	0.8	3.2	0.1

Figure 3. Change in (*a*) muscle area and (*b*) muscle ratio for the two replicates in 2001. Early replicates are represented by open circles; late replicates are represented by filled circles.

ment, thus verifying the conclusion of Fransson *et al.* (2001) that first-year thrush nightingales can use information from the Earth's magnetic field in fuelling decisions. In the late replicates, control birds and birds experiencing a magnetic treatment showed equally high fuel depositions. We believe that since birds increase their fuel load late in the season when they were more time constrained (Dänhardt & Lindström 2001) the effect of the magnetic treatment on fuel deposition is concealed. The responses to the magnetic treatment are indistinguishable in early and late birds, indicating that the extensive fuelling in the magnetic treatment is not affected by the endogenous time programme. It could be argued that thrush nightingales experiencing the magnetic field of northern Egypt should accumulate higher fuel loads than control birds late in the season. However, owing to constraints in our experimental set-up (for example the simulated fast migration and short stopover periods) we cannot expect to observe levels of fuel loads that totally resemble natural patterns.

A prerequisite for birds to use geomagnetic information as a cue to accumulate extensive fuel loads during migration is the ability to detect small changes in the magnetic field. In fact, the bobolink (*Dolichonyx oryzivorus*), a long-distance migrant, has been shown to detect changes as small as 200 nT (Semm & Beason 1990). This is to be compared with the difference in total intensity between southeast Sweden and northern Egypt, which is 7600 nT. Furthermore, for the ability to use magnetic cues in making decisions about extensive refuelling to evolve, the magnetic information has to be reliable. The magnetic field varies predictably across most of the earth (Åkesson 1996), and is also reasonably stable over time; for example, the change in the total intensity of the magnetic field in northern Egypt has been 15 nT per year during the last century (International Association of Geomagnetism and Aeronomy 2000; see also Lohmann *et al.* 2001).

The non-random pattern of Danish, Swedish and Finnish ringing recoveries of autumn-migrating thrush nightingales (figure 1) cannot be explained by extensive hunting in this particular area, since hunting for small birds takes place in large parts of the Mediterranean area. Non-random patterns are also found in other trans-Saharan migrants. Recoveries of barred warblers (*Sylvia nisoria*)

are, for example, found only in a restricted area in Syria and Lebanon, while blackcaps (*Sylvia atricapilla*) are only found in Cyprus and Lebanon (Swedish Museum of Natural History 1960–1998). As suggested by Thorup & Rabøl (2001), the observed geographical concentration in species-specific migratory patterns indicates that first-time migrants use some external cues in addition to the clock-and-compass system. One such important cue for locating species-specific stopover sites, for example prior to crossing the Sahara desert, may be magnetic information, as indicated by Beck & Wiltschko (1988), Fransson *et al.* (2001), Fischer *et al.* (2003) and this study.

Natural selection in favour of birds locating the right area and making the right fuelling decisions in front of large ecological barriers is probably strong. However, whether the effect shown in our study is triggered by a simple latitudinal change, is an evolved response to a magnetic field in a specific area, or is a result of the birds using a bicoordinate magnetic map that permits continuous navigation, which has been suggested for sea turtles (*Caretta caretta*) (Lohmann *et al.* 2001) and newts (*Notophthalamus viridescens*) (Fischer *et al.* 2001), remains to be investigated.

This study provides further evidence that birds increase their flight-muscle size as wing load increases during migratory fuelling (cf. Fry *et al.* 1972; Dietz *et al.* 1999; Battley *et al.* 2000; Lindström *et al.* 2000). However, our study indicates that the extent of flight-muscle enlargement is not simply a function of increasing wing load, since thrush nightingales in the late replicate increased more in flight-muscle size than birds in the early replicate. Consequently, the ratio of flight-muscle area to body mass was reduced in early birds during the experiment while late birds had the same muscle ratio throughout the experiment. Thus, the endogenous time programme seems to be important for extensive flight-muscle increase within the migratory period (see also Dietz *et al.* 1999). The underlying reason for the seasonal effect on flight-muscle increase remains to be investigated.

In conclusion, our results indicate that thrush nightingales trapped late in the season adjust their fuelling decisions to a time constraint resulting in a faster accumulation of both fat and muscle tissue. As suggested by Jenni & Schaub (2003), early migrants may be more risk-

sensitive than late migrants, which may take a higher risk in order to increase their migration speed. The results also support the suggestion by Jenni & Schaub (2003) that fuel deposition is controlled by the endogenous time pro-gramme in late migrating birds while early birds might be more affected by environmental factors. Yet, to traverse large barriers successfully, magnetic cues may prove cru-cial and, as shown in this study, override the fuelling decisions based on an endogenous time programme.

REFERENCES

Able, K. P. 1993 Orientation cues used by migratory birds: a review of cue-conflict experiments. *Trends Ecol. Evol.* **8**, 367–371.

Åkesson, S. 1996 Geomagnetic map used for long-distance migration? *Trends Ecol. Evol.* **11**, 398–400.

Alerstam, T. 1990 *Bird migration*. Cambridge University Press.

Alerstam, T. & Lindström, Å. 1990 Optimal bird migration: the relative importance of time, energy, and safety. In *Bird migration: the physiology and ecophysiology* (ed. E. Gwinner), pp. 331–351. Berlin: Springer.

Battley, P. F., Piersma, T., Dietz, M. W., Tang, S., Dekinga, A. & Hulsman, K. 2000 Empirical evidence for differential organ reductions during trans-oceanic bird flight. *Proc. R. Soc. Lond.* B **267**, 191–195. (DOI 10.1098/rspb.2000.0986.)

Bauchinger, U. & Biebach, H. 1998 The role of protein during migration in passerine birds. *Biol. Conserv. Fauna* **102**, 299–305.

Bauchinger, U. & Biebach, H. 2001 Differential catabolism of muscle protein in garden warblers (*Sylvia borin*): flight and leg muscle act as a protein source during long-distance migration. *J. Comp. Physiol.* B **171**, 293–301.

Beck, W. & Wiltschko, W. 1988 Magnetic factors control the migratory direction of pied flycatchers (*Ficedula hypoleuca* Pallas). In *Acta XIX Congr. Intern. Ornithol.*, vol. 2 (ed. H. Ouellet), pp. 1955–1962. Ottawa, Ontario: University of Ottawa Press.

Berthold, P. 1996 *Control of bird migration*. London: Chap-man & Hall.

Berthold, P., Querner, U. & Schlenker, R. 1990 *Die Mönch-grasmücke Sylvia atricapilla*. Wittenberg Lutherstadt: Die neue Brehm-Bücherei.

Blem, C. R. 1980 The energetics of migration. In *Animal migration, orientation and navigation* (ed. S. A. Gautreaux Jr), pp. 125–218. Toronto: Academic Press.

Dänhardt, J. & Lindström, Å. 2001 Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. *Anim. Behav.* **62**, 235–243.

Dietz, M. W., Piersma, T. & Dekinga, A. 1999 Body-building without power training: endogenously regulated pectoral muscle hypertrophy in confined shorebirds. *J. Exp. Biol.* **202**, 2831–2837.

Fischer, J. H., Freake, M. J., Borland, S. C. & Phillips, J. B. 2001 Evidence for the use of magnetic map information by an amphibian. *Anim. Behav.* **62**, 1–10.

Fischer, J. H., Munro, U. & Phillips, J. B. 2003 Magnetic navi-gation by an avian migrant? In *Avian migration* (ed. P. Ber-thold, E. Gwinner & E. Sonnenschein). Heidelberg: Springer.

Fransson, T., Jakobsson, S., Johansson, P., Kullberg, C., Lind, J. & Vallin, A. 2001 Bird migration—magnetic cues trigger extensive refuelling. *Nature* **414**, 35–36.

Fry, C. H., Ash, J. S. & Ferguson-Lees, I. J. 1970 Spring weights of some Palearctic migrants at Lake Chad. *Ibis* **112**, 58–82.

Fry, C. H., Ferguson-Lees, I. J. & Dowsett, R. J. 1972 Flight muscle hypertrophy and ecophysiological variation of yellow wagtail *Motacilla flava* races at Lake Chad. *J. Zool.* (*Lond.*) **167**, 293–306.

Gwinner, E. 1996 Circadian and circannual programmes in avian migration. *J. Exp. Biol.* **199**, 39–48.

International Association of Geomagnetism and Aeronomy 2000 Division V, working group 8. International geomag-netic reference field 2000. *Geophys. J. Int.* **141**, 259–262.

Jenni, L. & Jenni-Eiermann, S. 1998 Fuel supply and meta-bolic constraints in migrating birds. *J. Avian Biol.* **29**, 521–528.

Jenni, L. & Schaub, M. 2003 Behavioural and physiological reactions to environmental variation in bird migration: a review. In *Avian migration* (ed. P. Berthold, E. Gwinner & E. Sonnenschein). Heidelberg: Springer.

Kullberg, C., Fransson, T. & Jakobsson, S. 1996 Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). *Proc. R. Soc. Lond.* B **263**, 619–624.

Lindström, Å., Kvist, A., Piersma, T., Dekinga, A. & Dietz, M. W. 2000 Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting and fuelling. *J. Exp. Biol.* **203**, 913–919.

Lohmann, K. J. & Lohmann, C. M. F. 1994 Detection of mag-netic inclination angle by sea turtles: a possible mechanism for determining latitude. *J. Exp. Biol.* **194**, 23–32.

Lohmann, K. J., Cain, S. D., Dodge, S. A. & Lohmann, C. M. F. 2001 Regional magnetic field as navigational mark-ers for sea turtles. *Science* **294**, 364–366.

Pennycuick, C. J. 1989 *Bird flight performance. A practical calcu-lation manual*. Oxford University Press.

Pettersson, J. & Hasselquist, D. 1985 Fat deposition and migration capacity of robins *Erithacus rubecula* and goldcrest *Regulus regulus* at Ottenby, Sweden. *Ringing Migration* **6**, 66–76.

Piersma, T. 1998 Phenotypic flexibility during migration: opti-mization of organ size contingent on the risk and rewards of fueling and flight? *J. Avian Biol.* **29**, 511–520.

Schaub, M. & Jenni, L. 2000 Fuel deposition of three passerine bird species along the migration route. *Oecologia* **122**, 306–317.

Selman, R. G. & Houston, D. C. 1996 A technique for meas-uring lean pectoral muscle mass in live small birds. *Ibis* **138**, 348–350.

Semm, P. & Beason, R. C. 1990 Responses to small magnetic variations by trigeminal system of the bobolink. *Brain Res. Bull.* **25**, 735–740.

Swedish Museum of Natural History 1960–1998 *Annual reports of Swedish bird ringing*. Stockholm, Sweden: Bird Ringing Centre.

Thorup, K. & Rabøl, J. 2001 The orientation system and migration pattern of long-distance migrants: conflict between model predictions and observed patterns. *J. Avian Biol.* **32**, 111–119.

Wiltschko, W. & Wiltschko, R. 1992 Migratory orientation: magnetic compass orientation of garden warblers (*Sylvia borin*) after simulated crossing of the magnetic equator. *Eth-ology* **91**, 70–74.

Wiltschko, R. & Wiltschko, W. 1995 *Magnetic orientation in animals*. Berlin: Springer.

Wiltschko, W., Munro, U., Ford, H. & Wiltschko, R. 1993 Red light disrupts magnetic orientation of migratory birds. *Nature* **364**, 525–527.