Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world

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Migrants' responses to varying meteorological and magnetic conditions and their consequent costs in terms of energy and time are crucial for the understanding of the spatial principles guiding migration. Until now, studies of birds' phenotypic responses to environmental conditions and estimated costs of migration in terms of energy and time have focused on single sites and have rarely followed individuals along entire migration routes. We used individual-based light level geolocators to track birds' daily phenotypic responses to the environmental conditions experienced along a 30 000 km migration between Alaska and Africa. In autumn, departures of northern wheatears, Oenanthe oenanthe, were highly dependent on low temperatures and light winds but there was no such apparent dependence in spring. Migration was 1.4-times faster in spring than in autumn. There was an unexpected shift in the ratio of migration:stopover time towards less stopover time in spring, reducing spring's total energy costs for migration with respect to distance covered by nearly 50% in comparison to autumn. Despite strong changes in declination during migration, offering near-experimental conditions, birds did not navigate exclusively along any major compass course. In contrast to expectations, these high-Arctic migrants did not follow great circle routes; their hypothetical energetic benefit (ca. 20% for flying) might be insufficient and conditions for orientation too unfavourable to favour its evolution.
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Understanding the movement ecology of species requires a high spatiotemporal resolution of migration including the meteorological and magnetic conditions encountered en route (Alerstam 2006; Nathan et al. 2008; Shamoun-Baranes et al. 2010). We can now gather fundamental information about the spatiotemporal organization of migration in relation to weather (Bohrer et al. 2011), long-distance bird navigation (Alerstam 2006), and energy demands in respect of migrating and resting (Wikelski et al. 2003). Such analyses have been impossible for the entire migration route in small birds until the recent miniaturization of light level geolocators (hereafter geolocators; Stutchbury et al. 2009; Bächler et al. 2010; Tøttrup et al. 2011; Bairlein et al. 2012). Despite this, the accuracy of location fixes is limited by high latitudinal uncertainty during equinoxes often coinciding with migration periods (Stutchbury et al. 2009; Bächler et al. 2010; Tøttrup et al. 2011; Schmaljohann et al. 2012). Hence, movements with strong latitudinal components are less convenient to investigate than longitudinal movements (Hill 1994). East–west migration offers the opportunity to locate migratory routes and stopover sites on

a fairly accurate spatiotemporal scale. We took advantage of such a migration pattern as shown by the northern wheatear, Oenanthe oenanthe (hereafter wheatear), a small long-distance migratory songbird, migrating exclusively at night (Schmaljohann & Naef-Daenzer 2011), breeding in Alaska and wintering in eastern Africa, undertaking an annual migration circuit of about 30 000 km (Bairlein et al. 2012). With geolocators we tracked their migration at a high spatiotemporal resolution enabling us to investigate, coherently and for the first time, a songbird's movement ecology on a day-to-day basis in combination with meteorological and magnetic conditions en route. We addressed three main questions.

(1) How were these 15 000 km long migration trips organized in light of optimal migration theory (Alerstam & Lindström 1990)? Here we tested birds' daily phenotypic responses to the environmental conditions, publicly available via Movebank (Wikelski & Kays 2011; Kranstauber et al. 2011), along the entire migration route with respect to departure decisions, hypothesizing an importance of temperature and wind (Wikelski et al. 2003; Liechti 2006; Bauer et al. 2008) with possible seasonal differences (Tøttrup et al. 2011).

(2) Was the route of migration recognizable as a predetermin-able course? High-Arctic breeders with lengthy migration are thought to minimize their migration costs in terms of energy and time by migrating along great circle courses, that is, the shortest

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distance between two locations on earth (Alerstam & Pettersson 1991; Alerstam & Gudmundsson 1999; Alerstam et al. 2001). Here we investigated whether a high-Arctic breeding songbird follows a great circle course or whether other compass courses, such as constant magnetic, magnetoclinic or star compass (Kiepenheuer 1984; Muheim et al. 2003; Cochran et al. 2004), are predominantly used for navigation (Alerstam 2006).

(3) Was there a seasonal difference in time and energy costs between spring and autumn? Energy and time costs of migration have been only theoretically predicted (Hedenström & Alerstam 1997) or extrapolated (Wikelski et al. 2003). Here we modelled the total energy and time cost of migration for flying and resting by considering different physiological and aerodynamic approaches and the daily environmental conditions en route (Wikelski & Kays 2011; Kranstauber et al. 2011). We hypothesized a seasonal difference in both costs as migration is more time constrained in spring than in autumn.

By estimating these costs, verifying songbird migration along great circle courses and investigating birds' phenotypic responses to environmental conditions on a trip halfway around the world, we present the first coherent approach to studying movement ecology in a long-distance migratory songbird.

METHODS

General Procedure

Miniature stalked geolocators, Mk10S (1.2 g; Appendix Fig. A1), developed by the British Antarctic Survey (Cambridge, U.K.), were fitted to 15 adult female and 15 adult male wheatears breeding at Eagle Summit (65.6°N, 145.4°W, Alaska) in June 2009. Wheatears were caught with spring traps baited with mealworms, ringed and tagged under licence of the U.S. Fish and Wildlife Service (Federal Fish and Wildlife Permit: MB207892-0). Ringing and tagging lasted less than 2 min. Five birds returned in 2010, although one could not be caught and another had lost its geolocator. Data were downloaded from the three recaptured devices. We give sample size only if different from three. If not otherwise stated, mean ± SD are given.

Geolocator Compatibility

The geolocators were fitted using Rappole–Tipton style harnesses (Rappole & Tipton 1990) that were made from elastic silicone-rubber mixture (MVQ Arcus, http://www.arcus-shop.de/), and leg-loop length was adjusted individually to the wheatears (Naef-Daenzer 2007). If not removed, geolocators would eventually fall off, some after 1 year, others earlier (see above and e.g. Bächler et al. 2010; Schmaljohann et al. 2012).

The total attachment weighed 1.4 g. Because the lowest body mass of birds involved was 23.1 g (24.7 ± 1.9 g, $N = 30$), tag mass represented at maximum 6% (mean 5.7%) of the bird's body mass. The relative load was therefore similar to the suggested upper permissible load limit (Cochran 1980; Caccamise & Hedin 1985). Slightly higher loads than the 5% rule of thumb did not increase mortality rate in small birds (Naef-Daenzer et al. 2001). Only a little fat is stored during the breeding period, whereas on migration wheatears regularly increase their body mass by about 40–100% of their fat-free body mass (Dierschke et al. 2005). It seems, therefore, that wheatears are adapted to carrying high fuel loads.

Although tagging birds is invasive, no adverse effects have been found when transmitters are fitted appropriately (Naef-Daenzer et al. 2001; Rae et al. 2009), and the increase in flight costs is small (Irvine et al. 2007), although drag (Bowlin et al. 2010) and energy expenditure (Barron et al. 2010) increase. To estimate any direct effects of geolocators on wheatears, we attached dummy

geolocators to 12 birds of our indoor breeding population for half a year in 2008. Birds could fly freely. They adjusted their body mass seasonally to high values during migration periods but low values otherwise. Leg-loop harnesses still fitted well regardless of these natural changes in body mass. Birds did not differ in their flight behaviour from control birds, and did not show any damage to feathers or skin.

Although breeding site fidelity may be about 50% in wheatears, distances moved between years can be up to 4 km (Conder 1989; Currie et al. 2000; Arlt & Pärt 2008). In the Alaskan alpine tundra, distribution of snow-free patches has an important effect on breeding site selection. Temperature and wind define where alpine tundra is clear of snow and where soil humidity is sufficient to establish territories. In 2010 spring temperature was higher than in 2009 and only some breeding sites from 2009 were reoccupied, while other sites provided favourable breeding habitats in 2010 but not in 2009 (F. Bairlein & H. Schmaljohann, personal observations). This explained the relatively low recapture rate of 17%. In a wheatear breeding population at Iqaluit, Baffin Island (63.7°N, 68.5°W, Canada), none of 27 birds colour-ringed in 2009 returned in 2010. In 2011 two of 16 wheatears tagged with light level geolocators and two of 33 colour-ringed birds returned from 2010 (chi-square test: $\chi^2_1 = 0.47$, $P = 0.49$; Bairlein et al. 2012). It seems that site fidelity in the arctic-breeding populations is far lower than in well-studied populations in Europe. In a German breeding population, nine (45%) of 20 male wheatears attached with Mk 10S-geolocators in 2009 returned in 2010 (Schmaljohann et al. 2012), which was not significantly different to the natural return rate of 54% (58 of 107 males; chi-square test: $\chi^2_1 = 0.088$, $P = 0.77$) for this German population (Buchmann 2001; Schmaljohann et al. 2012). No adverse effect of the geolocators on arrival date, body condition, clutch size and hatching success could be detected in the German population (Schmaljohann et al. 2012). Hence, we feel confident that the 'low' recapture rate in the Alaskan birds is mainly caused by low fine-scale site fidelity. Furthermore, resighting probability of Alaskan wheatears that selected different hilltops for breeding in 2010 and 2009 is low in comparison to well-studied populations in easily surveyed habitats in Europe (F. Bairlein & H. Schmaljohann, personal observation).

Light Level Geolocator Data

Light data were processed with the programs provided by the British Antarctic Survey (BASTrak suite) and analysed using threshold light level geolocation (Stutchbury et al. 2009; Bächler et al. 2010; Tøttrup et al. 2011; Bairlein et al. 2012; Schmaljohann et al. 2012). Techniques employed for producing raw fixes and smoothed migration routes are given in the Appendix. A stopover was defined as staying more than two noon fixes at less than 1° longitude (Schmaljohann & Dierschke 2005; Fig. A2).

Total migration speed was defined as the migration distance between the breeding and wintering areas divided by the number of days required for migration including stopover days. We defined migration between two stopovers, including breeding and wintering areas, as one migration step. Altogether, the three birds provided 24 different migration steps in autumn and 13 in spring.

Nocturnal travel speed was calculated by assuming that all migratory movements occurred at night with no migratory movements occurring during stopover days (Tøttrup et al. 2011), and was estimated for each migration step separately as the distance between adjacent stopovers divided by the number of migratory nights. For seasonal comparisons we weighted nocturnal travel speed per migration step by the corresponding number of migratory nights with a generalized linear model (GLM) incorporating a binomial error distribution (for details see Appendix).

Phenotypic Responses to Meteorological Conditions

To characterize the meteorological conditions we downloaded surface temperature, surface wind speed, surface cloud cover and surface precipitation provided by the National Oceanic and Atmospheric Administration (NOAA, Boulder, CO, U.S.A.; http://www.cdc.noaa.gov/cdc/data.ncep.reanalysis.derived.html; Kalnay et al. 1996) for each bird and for each fix ($N_{bird\ A} = 173$, $N_{bird\ B} = 239$ and $N_{bird\ C} = 285$, including autumn and spring, and noon and midnight) via Movebank (Wikelski & Kays 2011; Kranstauber et al. 2011). Data from NOAA are available as a $2.58° \times 2.58°$ latitude−longitude grid. This corresponds to ground surface area cells of 120×120 km^2−290×290 km^2 for this study area. This is in the same order of magnitude as the general uncertainty of fixes of about $100-200$ km (Fudickar et al. 2011). Wind profit was estimated based on the direction towards the next stopover site with an assumed airspeed of 13 m/s (Bruderer & Boldt 2001), following Liechti et al. (1994):

$$
\begin{aligned}
\text{Wind profit(m/s)} = \text{airspeed(m/s)} \\
- \Big(\text{airspeed}^2 + \text{wind speed}^2 \\
- 2 \times \text{airspeed} \times \text{wind speed} \\
\times \cos(\text{wind direction} \\
- \text{direction to next stopover site})\Big)^{0.5} (\text{m/s})
\end{aligned}
\tag{1}
$$

Wind speed and wind direction were considered at five altitudinal pressure levels (surface, 1000 mb, 925 mb, 850 mb and 700 mb) corresponding to roughly five altitudinal levels (surface level, surface level to 445 m, 445−1145 m, 1145−2375 m and 2375−4000 m). We assumed birds flew within the air layer of highest wind profit at the location of the corresponding midnight fix (Schmaljohann et al. 2009; but see Mateos-Rodríguez & Liechti 2012). Results differed only slightly in comparison to migration in still air (see Appendix).

We incorporated the meteorological conditions experienced by the birds during the day and at night in a model to investigate departure decisions during autumn ($N_{autumn} = 480$) and spring migration ($N_{spring} = 217$) separately (Erni et al. 2002b; Jenni & Schaub 2003). We formulated the following generalized linear mixed models (GLMMs) with a binomial error distribution:

$$
\begin{aligned}
y_{ij} \sim\ & \text{surface temperature}_{ij} + \text{surface wind speed}_{ij} \\
& + \text{surface cloud cover}_{ij} + \text{surface precipitation}_{ij} \\
& + \text{best wind profit}_{ij} + \text{time of day}_{ij} + \text{residual error}_{ij}
\end{aligned}
\tag{2}
$$

The vector y_{ij} represents bird i's decision to depart or to stay during night j. The residual error contains the individual as a random effect allowing random intercepts for the three birds. Other effects are fixed and are included per day i and night i. Possible interactions were not significant. We simplified this model (see Appendix for details).

Compass Courses

We compared six major compass courses to wheatears' migration routes with, where appropriate, corresponding declination updated every 10 km: (1) constant magnetic course (Muheim et al. 2003), (2) constant magnetic course, but with daily recalibration of the bird's position and recalculation of the magnetic direction towards the wintering area (Cochran et al. 2004), (3) star compass course and (4) sun compass course compensating for the change in local time during migration, both having a constant geographical direction (both rhumb line) (Muheim et al. 2003), (5) sun compass course not compensating for the change in local time during migration (great circle course; Alerstam & Pettersson 1991; Alerstam & Gudmundsson 1999; Alerstam et al. 2001), and (6) magnetoclinic course with a constant specific angle of inclination (Kiepenheuer 1984; Fig. 1; see Appendix for details).

Energy Costs during Flight (migration)

Energy cost was estimated for each individual with an assumed body mass of 30 g, airspeed of 13 m/s (Bruderer & Boldt 2001) and individual wind profit for each migration step in relation to flight duration. Individual flight duration was estimated as migration
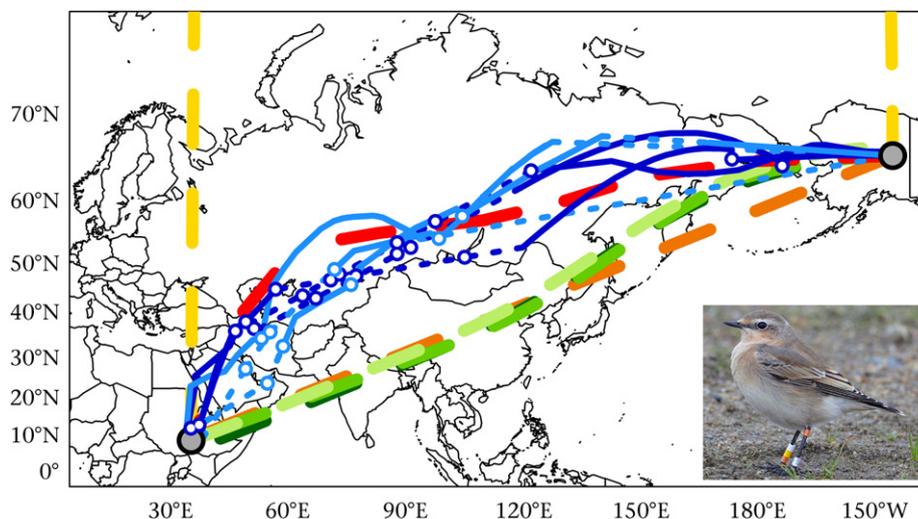

Figure 1. Geolocator tracks on a Mercator projection for three wheatears that bred in Alaska (65.6°N, 145.4°W, U.S.A.). Dark blue = autumn migration, light blue = spring migration; continuous lines = accurate tracks, dotted lines = presumed migration route but uncertain owing to (1) autumn equinox north of China, (2) 24 h daylight at high latitudes in spring and (3) one device failure on 1 May 2010. Blue dots with white centres indicate stopovers. Different orientation compass courses are indicated as thick dashed lines: yellow = great circle, orange = rhumb line, dark green = constant magnetic course, mid-green = constant magnetic course with daily recalibration in spring, light green = as latter but in autumn, red = magnetoclinic course. Inset: Alaskan wheatear.

distance/(airspeed + wind profit) for each migration step (see Appendix for details). We used three different types of model (see Appendix for details): (1) energy models, (2) an aerodynamic model and (3) a body mass model.

(1) The energy models used involved: (a) a wind tunnel study with rose-coloured starlings, *Sturnus roseus*, using doubly labelled water (Engel et al. 2006); (b) a field study with free-flying thrushes, *Catharus ustulatus* and *Catharus guttatus*, using doubly labelled water (Wikelski et al. 2003); (c) as (b) but with resting metabolic rate for wheatears; (d) the general dependence of energy costs on body mass (McWilliams et al. 2004); (e) a wind tunnel study with barn swallows, *Hirundo rustica*, using doubly labelled water (Schmidt-Wellenburg et al. 2007); and (f) a wind tunnel study with a single thrush nightingale, *Luscinia luscinia*, with body mass loss estimates (Klaassen et al. 2000; see Appendix for model details).

(2) The aerodynamic model was constructed according to the Flight program at sea level and at 3000 m above sea level (Pennycuick 2008; see Appendix for model details).

(3) The body mass model considered body mass loss during nocturnal flight, body mass loss on the ground during the night, body mass gain during the day and body mass loss during the day (see Appendix for model details).

If the models provided variation in parameters, we used these to choose randomly a value from the corresponding normal distribution. This procedure was repeated 100 times independently for each bird and model. Means and 95% confidence intervals are given (Fig. 2).

We finally compared the energy costs during flight of the energy model and the body mass model. Do to so, we converted body mass loss (g) into energy costs (kJ) by considering that the relevant fuel types of migrating birds are lipids and proteins of which lipids account for 90–95% and proteins for 5–10%. We further used energy equivalents of 37.6 kJ/g for fat and 5.3 kJ/g for protein, and took into account fat's water content of 5% and that of protein of 70% (Jenni & Jenni-Eiermann 1998).

Energy Costs on the Ground (stopover)

We divided energy costs on the ground into four different categories: (1) for the remaining time of the night after completing the nocturnal migratory flight, depending on the local night length and the average nocturnal flight duration per migration step, (2) during the day between two subsequent nocturnal migratory flights, (3) during the night, and (4) during a daytime stopover. These costs were modelled via wheatears' resting metabolic rate (energy model) and their body mass loss (body mass model). For both models we considered the corresponding local length of day and night (Fig. 3).

Regarding the energy model, we applied the dependency of resting metabolic rate on the related temperature, whereby temperature values were randomly chosen for each bird from their corresponding normal distributions per migration step or stopover. The resting metabolic rate of wheatears increases with decreasing temperature between $0\,°C$ and $25\,°C$ by $3.112\,(\pm 0.78) - 0.055\,(\pm 0.059) \times$ temperature $(kJ/(°C \times h))$ and is constant between $25\,°C$ and $30\,°C$ $(1.69 \pm 0.41\,(kJ/h)$; see Maggini 2009 and Appendix for details). We averaged the surface temperature considering the corresponding day (noon fix) and night (midnight fix) values
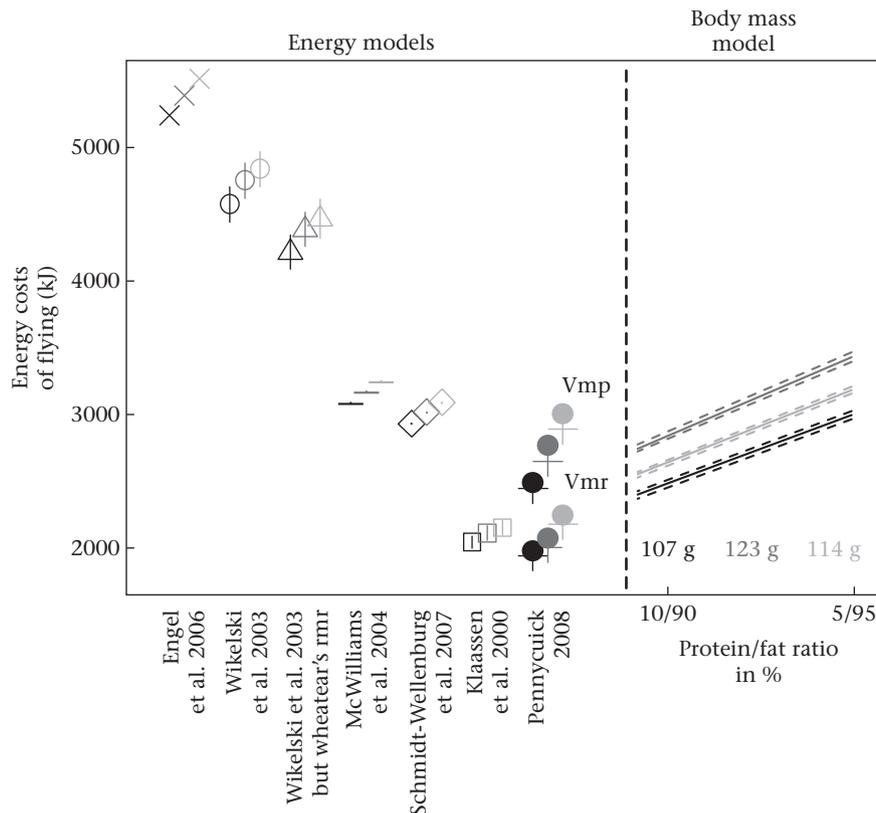

Figure 2. Energy costs for migratory flights based on the estimated flight duration taking into account wind conditions en route to migrate from the breeding to the wintering area; bird A: black; bird B: grey; bird C: light grey. Estimates were derived from six energy models (X: 17.57 kJ/h; O: 15.4 kJ/h; Δ: 14.19 kJ/h considering wheatear's resting metabolic rate (rmr; see Appendix); −: 10.34 kJ/h; ◇: 9.84 kJ/h; □: 6.88 kJ/h), an aerodynamic flight model (V_{mr}: maximum range speed; V_{mp}: minimum power speed; both at sea level (●) and 3000 m above sea level (+) with birds' specific values) and a body mass model. Individual body mass loss was converted into energy (kJ) over a range of fat:protein ratios from 10/90 to 5/95. Where appropriate, 95% confidence intervals are given.
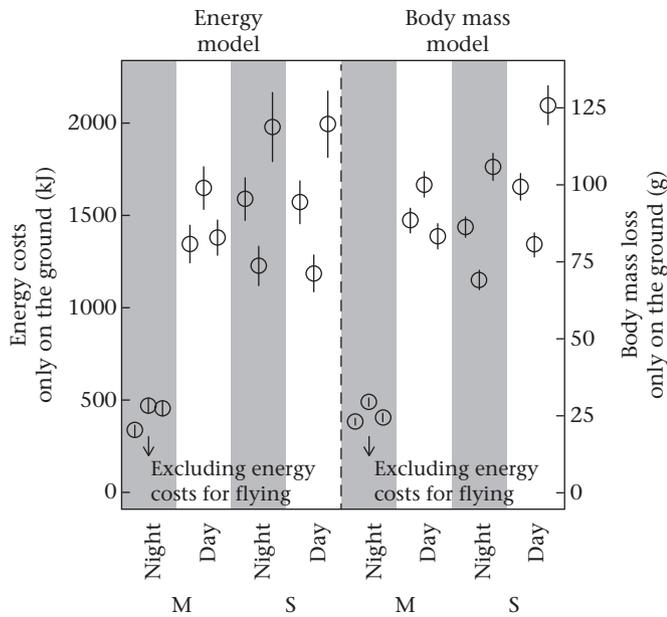
Figure 3. Energy costs only for the times when birds were on the ground in autumn. Migration (M) included the remaining time of the night after birds had performed their nocturnal migratory flights (not including the energy costs for flying; these are given in Fig. 2) and the days between the subsequent nocturnal migratory flights. Stopover (S) included nights and days of stopover. Estimates and 95% confidence intervals are given for the energy model considering the resting metabolic rate in relation to temperature and length of day and night and the body mass model considering the body mass loss in relation to length of day and night. From left to right: birds A, B, C. Nocturnal costs are highlighted in grey.

experienced during each stopover and each migration step for each bird separately. From the corresponding normal distributions we randomly assigned a diurnal and nocturnal temperature to each individual for each stopover and each migration step. These temperatures were used to estimate the energy costs on the ground in respect of the four categories via the resting metabolic rate. We probably underestimated the energy costs, because resting metabolic rates were estimated in captive birds.

Regarding the body mass model, the four categories of energy costs on the ground were incorporated into the model estimating body mass loss during flight (see above, Appendix, Supplementary material and Dierschke et al. 2005; Delingat et al. 2008, 2009). Estimates for energy costs on the ground are derived directly from this model.

Models were run 100 times per bird, each time applying randomly assigned values from the corresponding normal distributions.

RESULTS

Migration Strategy

Wheatears started migration between 18 and 20 August 2009, departing westwards, crossing the Bering Strait and continuing

Table 2
Stopover locations and durations for spring migration 2010

Spring	Stopover 1	Stopover 2	Stopover 3	Stopover 4
Bird A	19 Apr–23 Apr 34°N, 53°E			
Bird B	4 Apr–7 Apr 27°N, 49°E	10 Apr–16 Apr 36°N, 55°E	24 Apr–26 Apr 49°N, 72°E	1 May–7 May 54°N, 98°E
Bird C	31 Mar–5 Apr 23°N, 54°E	8 Apr–13 Apr 32°N, 58°E	16 Apr–23 Apr 49°N, 76°E	30 Apr–5 May 58°N, 104°E

west-southwesterly, covering distances of 4900 ± 400 km without a stopover for more than 2 days (Figs 1, A2). All birds circumvented the Himalaya and performed five stopovers lasting 4.5 ± 0.7 days (all shorter than 6 days, $N = 15$) before reaching the Caspian Sea, where they stopped for 24 ± 5 days prior to crossing the Arabian Desert (Table 1, Fig. A2). Wintering areas in eastern Africa were reached after about $14\,575 \pm 360$ km within 3 months (total migration speed: 160 ± 15 km/day). Birds initiated spring migration between 29 March and 8 April 2010, followed similar routes as in autumn (Fig. 1), had fewer but slightly longer stopovers (5.7 ± 1.5 days, $N = 9$) than in autumn (Wilcoxon test: $W = 32$, $N_{autumn} = 15$, $N_{spring} = 9$, $P = 0.03$, excluding the stopovers close to the Caspian Sea in autumn; Tables 1, 2, Fig. A2), and arrived at the breeding area around 24 May after $14\,274 \pm 541$ km (total migration speed: 257 ± 3 km/day, $N = 2$).

Nocturnal travel speed per migration step was higher in spring (weighted mean $\pm$ weighted SD $= 454 \pm 189$ km/night, $N_{migration\ steps} = 13$) than in autumn ($329 \pm 197$ km/night, $N_{migration\ steps} = 24$; GLM: $P = 0.015$; see Appendix for details). Bird A with a geolocator failure on 1 May 2010 covered about 4482 km during eight nights (23–30 April) resulting in a nocturnal travel speed of 560 km/night. Theoretically experienced best wind profit was higher in spring (1.4 ± 2.6 m/s, $N_{migration\ steps} = 13$) than in autumn ($-0.01 \pm 2.0$ m/s, $N_{migration\ steps} = 24$) although not significantly (GLM: $P = 0.086$; see Appendix for details).

Total flight time in spring in still air would be 305 h ($14\,277$ km/46.8 km/h) and 276 h ($14\,277$ km/(46.8 + 5) km/h) considering wind profit. This 30 h difference corresponds to an increase in the nocturnal travel speed of about 50 km/night (average of 30 migratory nights during spring and assuming an airspeed of 13 m/s), but is inadequate to explain a seasonal difference of 125 km/night.

We tested migrants' phenotypic responses to the meteorological conditions experienced during every day and night along the entire migration route in respect of their departure decision. In autumn, departure decision was supported significantly by lower surface temperature and lower surface wind speed, whereas birds chose to stop-over during higher surface temperatures and higher surface wind speed (GLMM: surface temperature: $P < 0.0001$; surface wind speed: $P = 0.015$; Fig. 4, see Appendix for details). None of the parameters considered played a significant role in spring (all parameters: $P > 0.3$). There was no seasonal difference in surface temperature (t test: $t_{110} = -1.15$, $P = 0.25$; all t tests unpaired and

Table 1
Stopover locations and durations for autumn migration 2009

| Autumn	Stopover 1	Stopover 2	Stopover 3	Stopover 4	Stopover 5	Stopover 6	Stopover 7	Stopover 8	Stopover 9
Bird A	6 Sep–10 Sep 64°N, 122°E	17 Sep–20 Sep 57°N, 98°E	22 Sep–26 Sep 53°N, 88°E	30 Sep–4 Oct 44°N, 63°E	6 Oct–11 Oct 44°N, 63°E	16 Oct–9 Nov 36°N, 46°E			
Bird B	28 Aug–30 Aug 64°N, 186°E	22 Sep–25 Sep 53°N, 91°E	25 Sep–28 Sep 52°N, 88°E	1 Oct–4 Oct 47°N, 76°E	10 Oct–14 Oct 43°N, 67°E	19 Oct–5 Nov 36°N, 51°E			
Bird C	18 Aug–22 Aug 66°N, 201°E	28 Aug–1 Sep 65°N, 173°E	19 Sep–22 Sep 51°N, 105°E	1 Oct–5 Oct 47°N, 77°E	7 Oct–10 Oct 47°N, 71°E	13 Oct–22 Oct 45°N, 57°E	23 Oct–9 Nov 38°N, 49°E	14 Nov–22 Nov 12°N, 37°E	24 Nov–1 Dec 11°N, 35°E
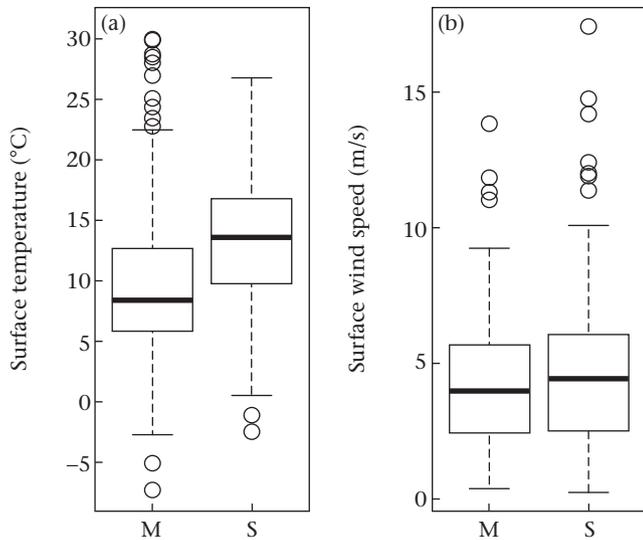
Figure 4. (a) Surface temperature and (b) surface wind speed of the day when birds decided to resume migration (M, $N = 211$) or to stop-over (S, $N = 269$) during autumn migration. Conditions at noon and midnight are given for each day along the migration route and for all three birds. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.
Difference between departure events: (a) $P < 0.0001$; (b) $P = 0.015$; see Results for further information.

two-tailed) and surface wind speed (t test: $t_{198} = -0.27$, $P = 0.79$) on the dates of stopover. On the dates of departure, surface temperature and wind speed differed significantly between autumn and spring (autumn: 9.8 ± 6.7 °C, $N = 211$; spring: 13.4 ± 10.1 °C, $N = 122$; t test: $t_{184} = -3.5$, $P = 0.0006$; autumn: 4.2 ± 2.3 m/s, $N = 211$; spring: 4.9 ± 2.6 m/s, $N = 122$; t test: $t_{229} = -2.3$, $P = 0.021$). This indicates a likely higher selectivity for lower surface temperature and lower wind speed for departure in autumn than in spring.

Orientation

Migration distances (autumn and spring) were on average 22% (2653 ± 400 km, $N = 6$) longer than the great circle course, 8% (1201 ± 455 km, $N = 6$) shorter than the rhumb line course and 7% (1070 ± 443 km, $N = 6$) shorter than the constant magnetic courses. Migration routes were distinctly different from all except the magnetoclinic course (645 ± 443 km, $N = 6$; Fig. 1).

Energy and Time Costs of Autumn Migration

In autumn, total energy costs for migratory flights varied between 2000 kJ and 5500 kJ (3448 ± 1222 kJ, $N_{models} = 8$,

considering only sea level values of the aerodynamic model; Fig. 2). Total energy costs for times on the ground (stopover) were 5085 kJ (Fig. 3, Table 3). According to the body mass model, birds lost 115 ± 6 g during the migratory flights, equivalent to 2570 ± 140 kJ and 3199 ± 173 kJ depending on the protein/fat ratio (10/90 and 5/95; Fig. 2). During stopover they lost 306 g (Fig. 3, Table 3).

In spring we could consider only $10\,753 \pm 2109$ km of migration (covering 37 ± 14 days; Fig. 1) costing, in terms of the energy model, on average 2331 ± 853 kJ ($N_{models} = 8$, considering only sea level values of the aerodynamic model) and during stopovers 1921 ± 895 kJ. According to the body mass model, spring migration cost 69 ± 17 g (equivalent to $1547-1926$ kJ depending on the protein/fat ratio) and stopover 106 ± 45 g.

The average ratio of the energy costs during flight and stopover ranged in autumn from 1:0.95 to 1:2.4 (models averaged 1:1.45, $N_{models} = 8$) and was 1:2.75 for the body mass model. In spring, the average ratio of the energy costs during flight and stopover ranged from 1:0.5 to 1:1.35 (models averaged: 1:0.8, $N_{models} = 8$) and was 1:1.45 for the body mass model, considering only spring migration for which fixes were available (Fig. 1).

The total energy costs (flight and stopover combined) relative to distance covered was significantly lower in spring (weighted mean $\pm$ weighted SD = 0.42 ± 0.11 kJ/km, $N_{migration\ steps} = 13$) than in autumn ($0.79 \pm 0.39$ kJ/km, $N_{migration\ steps} = 24$) assuming average energy costs during flight (McWilliams et al. 2004) and species' resting metabolic rate on the ground (GLMM: $P < 0.0001$). The same was true for the body mass model (spring: 0.019 ± 0.007 g/km; autumn: 0.043 ± 0.026 g/km; GLMM: $P < 0.0001$).

Assuming steady airspeed (13 m/s), no wind profit and an average energy cost during flight (Fig. 2; McWilliams et al. 2004), energy costs just for migratory flights were 22% (578 kJ) lower along the great circle course and 8%/4% (270 kJ/136 kJ) higher along the rhumb line/constant magnetic courses than along the actual route.

The ratio of time spent between migratory flight (306 ± 8 h) and being on the ground (1954 ± 305 h) in autumn was 1:6.35 and in spring 1:3.25.

DISCUSSION

Migration Strategy

Selection pressure will have strongly optimized the migration strategy of wheatears for migrating about 30 000 km a year. An important currency of the optimal migration strategy is the search and settling time, to locate food and to adapt physiologically to replenish energy expended, affecting fuel deposition and stopover duration (Alerstam & Lindström 1990). Covering several thousand kilometres without a longer stopover demonstrated a minimized search and settling time enabling wheatears to replenish their energy used during the previous migratory flight by the next

Table 3
Estimated energy costs for migratory flights and times when birds were on the ground for the energy model and the body mass model

| | Energy costs during migratory flights | Energy costs during times on the ground | | | | Σ Energy costs on the ground | Energy costs for migratory flights: times on the ground |
| | | Migration | | Stopover | | | |
		Night	Day	Night	Day		
Energy model (kJ)	3448 ± 1222	422 ± 72	1459 ± 166	1599 ± 376	1585 ± 404	5085	1: 1.5
Body mass model	115 ± 6	26 ± 3	91 ± 9	87 ± 18	102 ± 23	306	1: 2.7
(g)	2570 ± 140						
(kJ)*	3199 ± 173						
(kJ)†							

Mean and SD are given according to mean values displayed in Fig. 3. Estimated body mass loss during migratory flights was converted to kJ with an assumed lipid/protein ratio of 90/10 (*) and 95/5 (†) according to Jenni & Jenni-Eiermann (1998). Ratio of energy costs for migration and times on the ground (stopover) is given for both models.

morning (Fig. 1). This maximizes fuel deposition and equivalently speed of migration (Alerstam & Lindström 1990) explaining, at least in part, why the wheatear's total migration speed is at the songbirds' upper range of about 250 km/day for average seasonal values (Hall-Karlsson & Fransson 2008; Stutchbury et al. 2009; Bächler et al. 2010; Tøttrup et al. 2011; Schmaljohann et al. 2012). The seasonal difference in overall nocturnal travel speed could not be explained by variation in wind profit alone. Hence, birds either flew more hours per night (spring: 454 km/night:47 km/h ≈ 9.5 h/night; autumn: 330 km/night:47 km/h ≈ 7 h/night) or with a higher airspeed in spring than in autumn (Karlsson et al. 2012), for example when migrating at higher altitudes than in autumn (Schmaljohann & Liechti 2009).

Investigation of individual phenotypic responses to meteorological conditions encountered along 15 000 km revealed that autumn migration was significantly timed in relation to surface temperature and surface wind speed. Resuming migration at relatively low temperatures minimizes energy costs, because energy costs on the ground, the major cost of migration (Figs 2, 3), increase with decreasing temperature (Wikelski et al. 2003). Alternatively, a decrease in temperature indicates a change in air pressure and wind conditions often coinciding with departure decisions (Liechti 2006). Wheatears set off generally at low wind speed indicating favourable conditions for migration. Hence, two simple departure decision rules guided wheatears along their 15 000 km long migration route in autumn, as in, for example, dragonflies (Wikelski et al. 2006). This might suggest that there is an overall migration strategy at least in autumn, as none of the parameters tested was significant in spring.

Onset of autumn migration is restricted by the end of the postbreeding moult (Conder 1989). Because late arrival at the wintering area does not have any direct fitness consequences, birds can probably afford a slow and safe migration strategy with a higher selectivity in their departure decision than in spring. Onset of spring migration strictly depends on the photoperiod (Gwinner 1996) and the bird's innate program (Maggini & Bairlein 2012). In contrast to autumn, wheatears arriving late in Alaska during the brief Arctic summer will miss the short time window for successful reproduction and decrease their fitness (Kokko 1999). A simple, probably more risky, migration strategy with a rigid number of days for stopover and migration might be most likely to ensure prompt arrival at their breeding areas (Tables 1, 2; Erni et al. 2002a). We hypothesize that a stronger selection pressure towards a well-timed arrival at the breeding than at the wintering areas causes the seasonal differences in the migration strategies.

Orientation

High-Arctic breeding migrants are thought to select the shortest migratory route, that is, the great circle course, to the wintering areas in order to save time and energy (Alerstam & Pettersson 1991), as shown for some waders (Alerstam & Gudmundsson 1999; Alerstam et al. 2001) but not all (Gudmundsson 1994). In contrast to expectations (Alerstam et al. 2008), Alaskan wheatears did not migrate along such a course that would, hypothetically, cross the Arctic sea and ice for about 4500 km (Fig. 1). Possibly, the overall benefit of this great circle course is insufficient to favour its evolution because the energetic advantage (about 20% for the energy costs of flying) might be too low in comparison to the danger of the harsh climatic conditions. However, it is known that wheatears regularly cross large parts of the North Atlantic, which is as dangerous as the Arctic Sea, on migration (Bairlein et al. 2012). In addition to the unfavourable conditions, orientation performance while crossing the North Pole may be reduced because of the steep inclination angle, rapidly changing magnetic conditions and the lack of stars (Åkesson et al. 1995, 2001).

Migration routes coincided with the magnetoclinic course as in some other species (Kiepenheuer 1984; Liechti et al. 2012). This model cannot, however, explain the migration routes of very high-Arctic breeders, and it lacks an experimental background demonstrating that birds are able to sense the apparent angle of inclination (Kiepenheuer 1984; Alerstam & Gudmundsson 1999). The coincidence here is no proof that wheatears navigated using the apparent angle of inclination.

As no compass course seemed to be dominant over the other (Fig. 1), we generally believe that birds navigated by uniting the different compass mechanisms whose significance might shift geographically depending on the availability of their cues (Muheim et al. 2003; Alerstam 2006). The overall migration direction, including the southward shift at the Arabian Desert, may be endogenously controlled (Gwinner & Wiltschko 1978), and is likely to be triggered by external and internal cues (Schmaljohann & Naef-Daenzer 2011). We could not estimate how the navigational map learned during former migrations shaped the current migration routes (Thorup et al. 2007), because we tracked adult wheatears. Tracking the entire autumn migration of first-year birds would solve this problem. However, we also radiotracked the departure direction of 15 first-year wheatears from Wales, the most western point of mainland Alaska (66°N, 168°W). As they departed towards the southwest (233°; Rayleigh test: $R = 0.87$, $N = 15$, $P < 0.0001$; see Appendix for details) in August 2010, we can at least reject the possibility that these naïve birds did follow a great circle course. This indicates that the spatiotemporal departure from Alaska is at least partially endogenously controlled. The migration route might also be a relict of the post Late Pleistocene expansion of the wheatear's breeding range, as suggested for C. ustulatus, which has recently expanded into northwestern North America (Ruegg & Smith 2002).

Energy and Time Cost of Migration

Energy costs of migration (flight) above 4000 kJ seemed to be relatively high (Fig. 2), for example because rose-coloured starlings are diurnal migrants, migrating in flocks, but were flown in pairs (Engel et al. 2006). We believe that the total energy cost for autumn migration is divided between migratory flight (2630 ± 500 kJ, $N_{models} = 5$, all <4000 kJ in Fig. 2) and time on the ground (stopover) at a ratio close to 1:2 (energy models). This seems appropriate, as we probably underestimated the energy costs on the ground by applying resting metabolic rates of caged birds. This and the body mass model's (1:2.75) ratio are within the range of theoretical considerations (1:2; Hedenström & Alerstam 1997) and extrapolation of a field study (1:3.4; Wikelski et al. 2003). Likewise, the time ratio between migratory flights and stopover (1:6.35) in autumn was close to theoretical predictions (1:7; Hedenström & Alerstam 1997). In spring, the bias towards energy and time costs during stopover diminished in all models indicating that time for stopover was minimized, leading to an overall faster and energetically more economic migration with lower energy costs per migration unit in spring than in autumn. Although models considered migration distance, stopover time, local wind condition, temperature and length of the days on a daily basis along the entire migration route halfway around the world, we could not establish whether other costs, such as flight itself (higher airspeed) or stopover behaviour (higher feeding activity), differed between seasons. This, in combination with the low sample size, indicates the great need for movement ecology studies combining the spatiotemporal organization of migration with the environmental conditions encountered en route to verify our results.

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Supplementary Material

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Appendix

Light Level Geolocators

Analyses of light level geolocator data

The British Antarctic Survey (BAS) Mk10S geolocator measured light every minute and recorded the maximum value within each 10 min interval. Light data were processed with the programs provided by BAS (BASTrak suite). Programs were used as given in Fox (2010). Light data were corrected for clock drift. The program TransEdit2 provided by BAS was used to analyse the light data. For calibration, to identify the sun elevation corresponding to a particular light level threshold, data were gathered in an open habitat with a clear view (Helgoland, Germany; 54°11′N, 07°55′E) from 20 to 27 May 2009 as in Stutchbury et al. (2009). The light level threshold defining sunrise and sunset was set to 32 arbitrary data units as in Stutchbury et al. (2009) and, when we used the calibration data, this corresponded to our adopted sun elevation angle of $-5.0 \pm 0.45°$ for bird A, $-4.9 \pm 0.56°$ for bird B and $-4.8 \pm 0.59°$ for bird C. Longitudinal deviation from the reference site was $0.7 \pm 0.54°$ corresponding to 46 ± 35 km ($N = 39$) and latitudinal deviation was $0.4 \pm 0.34°$ corresponding to 47 ± 38 km ($N = 39$) from the given longitude of Helgoland.

All transitions were checked manually for obvious shading events during daytime and with the program TransEdit2 for lighting events during the night (Fox 2010). As the wheatears inhabit open habitats during breeding, migration and winter (Cramp 1988), shading problems are dramatically reduced in comparison with forest birds (Stutchbury et al. 2009; Fudickar et al. 2011). Sunrise and sunset light transitions showing obvious shading interference were rejected. Generally, we derived the migratory pathways between the breeding area, stopover sites and wintering areas directly from the fixes. No fixes could be estimated during 24 h daylight. Typically, about 2 weeks around equinoxes (22 September 2009, 20 March 2010) latitudinal data errors are so high that latitude cannot be considered (Fox 2010). During this time, analysis decisions as to whether a bird arrived at or departed from a stopover site relied on longitudinal data (Stutchbury et al. 2009; Bächler et al. 2010; Egevang et al. 2010; Tøttrup et al. 2011; Schmaljohann et al. 2012; Fig. A2). We did not consider latitude during autumn migration from 9 September until 16 October 2009 for bird A, from 15 September until 18 October for bird B, and from 13 September until 11 October 2009 for bird C. We applied different exclusion periods in this manner owing to individual differences in the uncertainty of latitude estimations (Figs A3, A4). During spring, the onset of migration occurred well after spring equinox and we considered all latitudinal data for bird A, latitudinal data from 6 April onwards for bird B, and from 8 April onwards for bird C.

In contrast to other studies, for example Stutchbury et al. (2009); Bächler et al. (2010); Tøttrup et al. (2011) and Schmaljohann et al. (2012), Alaskan wheatears have a large longitudinal component in their migratory route. As longitudinal uncertainties are usually much smaller and vary little with date or latitude in comparison to latitude uncertainties, stopover sites could be more accurately located than with geolocation studies in which latitude is most significant. This is also true, not just because of the inherent uncertainties in the threshold geolocation method, but also because uncertainties in light attenuation (e.g. clouds, topography, foliage) typically cause smaller errors in longitude than latitude (Hill 1994). Stopovers were defined as staying more than 2 days within 1° longitude based on

research with wheatears (Dierschke et al. 2005; Schmaljohann & Dierschke 2005; Schmaljohann & Naef-Daenzer 2011; Fig. A2).

Fixes during stopovers found to be on water were moved towards the nearest land. Stopovers and wintering areas were defined by kernel densities, as in Bächler et al. (2010), encompassing 75% of the maximum density. Kernel densities were calculated with kernelUD from the R package adehabitat using the ad hoc method for the estimation of the smoothing parameter and the bivariate normal kernel (R Development Core Team 2010). For stopovers with fewer than five fixes we calculated mean latitude, as did Stutchbury et al. (2009) for wintering areas. The cleaned data set of birds A, B and C contained 410, 486 and 483 fixes for the periods 18 August 2009 to 30 April 2010, 20 August 2009 to 23 May 2010 and 20 August 2009 to 24 May 2010 including departure from the breeding area until arrival at the breeding area. The low number of fixes from bird A's geolocator was due to premature failure on 1 May 2010. The other two collected light data until download on 5 July 2010.

Migration routes

To determine a likely migration route between stopover sites (including breeding area and wintering areas) we smoothed latitude data by local polynomial regression loess fitting with raw longitude data as the predictor (R Development Core Team 2010). Obvious latitudinal outliers, for example close to the equinoxes and those caused by light interference, were rejected (see above). Raw longitude data and the smoothed latitude estimations were used to indicate the smoothed migration routes (Fig. A3).

surface precipitation) for each fix (bird A: 173; bird B: 239; bird C: 285) but with the smoothed values for latitudes.

Day- and night length

Day- and night length were estimated by the function daylength from the R package geosphere for all locations. For stopovers we used the kernels' centres or means; for migration we identified the corresponding locations in the centre between the corresponding stopover sites. Our estimated daylength was slightly longer after departure from a stopover site but slightly shorter before arrival at the next stopover site. We defined migration between two stopovers (including breeding and wintering area) as one migration step. To estimate the time birds were on the ground during the nights of migration we calculated the product of the corresponding average night length per migration step and the number of nights, giving the total number of night hours. From this we subtracted the total flight duration (considering wind profit) for each migration step. The remaining time was divided by the number of nights per migration step indicating the average time birds stayed on the ground during the night after each nocturnal migratory flight.

Analysis of nocturnal travel speed

With a generalized linear mixed model incorporating a binomial error distribution we tested whether there was a statistical difference between the nocturnal travel speed in autumn and spring weighted by the number of nights per migration step, because precision of nocturnal travel speed estimation increases with number of migratory nights considered, with individual as

$$\text{Smoothed latitude} = \text{predict}(\text{loess}(\text{raw latitude data} \sim \text{raw longitude data}, \text{ data excluding latitudinal outliers}, \text{ span} = 1, \text{ degree} = 2), \text{ data including outliers})$$

$$(A1)$$

In doing so, the number of fixes concerning only the migration between the breeding and wintering areas increased from 128, 215, 267 to 173, 239 and 285 fixes for birds A, B and C. To indicate the deviation of raw latitudinal data from each migration route given its longitude data we calculated the shortest (great circle) distances from each raw fix (excluding outliers) to the estimated smoothed latitude of the corresponding longitude (Fig. A3). By using a smoothed line to indicate the migratory route, we probably underestimated the overall migration distance and migratory speed because, in doing so, we did not consider small-scale movements of the birds. Migration distances were calculated using great circle distances (R Development Core Team 2010) along the smooth lines between stopover sites.

Environmental Conditions

Meteorological data

For the description of the meteorological conditions encountered en route, we predicted the latitude of outlier fixes by their longitude based on the dependency of latitude on longitude (equation A1). If stopover sites were estimated by kernel densities (see above), kernel centres were used to describe the whereabouts of the birds during the stopover. If fewer fixes were available the mean of longitude and latitude were used. When latitude could not be estimated directly from fixes close to equinoxes, we set the stopover sites on the rhumb lines connecting trustworthy latitude estimations from the fixes (see dotted lines in Figs 1, A3, A4). Via Movebank (Wikelski & Kays 2011; Kranstauber et al. 2011) we downloaded the environmental data (surface temperature, surface wind speed, surface cloud cover and

a random factor (GLMM: parameter = 0.003, SE = 0.0008, $P = 0.0001$). As the estimate of the variance of the random effect was zero, the level of variability between the individuals was not strong enough to warrant incorporating the random effect in this model (Crawley 2005). Hence, we removed the random effect and calculated a GLM with a binomial error distribution (GLM: $P < 0.001$). Here the ratio of residual deviance to residual degrees of freedom was $227.36/35 = 6.5$ indicating that the model was overdispersed. To correct for overdispersion we calculated the same model with a quasibinomial error distribution and used an F test rather than a chi-square test to produce the analysis of deviance table. This reduced the significance from $P < 0.0001$ to $P = 0.015$.

Analysis of wind profit

The same procedure was applied for the analysis of seasonal differences in the wind profit starting with a GLMM with individual as a random factor and weighted by the number of nights per migration step (GLMM: parameter = 0.29, SE = 0.07, $P < 0.0001$). As the variance of the random effect size was zero, we applied a GLM with a binomial error distribution (GLM: $P < 0.0001$). Here the ratio of residual deviance to residual degrees of freedom was $227.36/35 = 6.5$ indicating that the model was overdispersed. To correct for overdispersion we calculated the same model with a quasibinomial error distribution and used an F test rather than a chi-square test to produce the analysis of deviance table. This reduced the significance to $P = 0.086$.

Wind profit at pressure levels of 850 mb and 700 mb was more favourable in spring (850 mb: 0.1 ± 4.5 m/s; 700 mb: 1.7 ± 3.8 m/s, $N = 122$) than in autumn (850 mb: -2.8 ± 4.4 m/s; 700 mb:

-0.3 ± 3.5 m/s, $N = 211$; Mann–Whitney U tests: $W > 3700$, $N_{spring} = 122$, $N_{autumn} = 211$, $P < 0.0001$) but not at the surface, 1000 mb, or 925 mb level (Mann–Whitney U tests: all $P > 0.12$).

Analysis of phenotypic responses to meteorological cues

We formulated the following GLMMs with a binomial error distribution:

$$y_{ij} \sim \text{surface temperature}_{ij} + \text{surface wind speed}_{ij}$$
$$+ \text{surface cloud cover}_{ij} + \text{surface precipitation}_{ij}$$
$$+ \text{best wind profit}_{ij} + \text{time of day}_{ij} + \text{residual error}_{ij} \quad (A2)$$

The vector y_{ij} represented bird i's decision to depart or to stay on night j. The residual error contained the individual as a random effect allowing random intercepts for the three birds. Other effects were fixed and included per day i and night i. We simplified this model stepwise (backwards) by removing the fixed effect with the highest P value. We also included possible interactions.

Autumn migration. The number of fixes considered was 480 (bird A: 129; bird B: 156; bird C: 195). In the first model we included possible interactions between (1) surface temperature and time of day, (2) surface wind speed and best wind profit and (3) surface cloud cover and precipitation.

$$y_{ij} \sim \text{surface temperature}_{ij} + \text{surface wind speed}_{ij}$$
$$+ \text{surface cloud cover}_{ij} + \text{precipitation}_{ij} + \text{best wind profit}_{ij}$$
$$+ \text{time of day}_{ij} + \text{surface temperature}_{ij} \times \text{time of day}_{ij}$$
$$+ \text{surface wind speed}_{ij} \times \text{best wind profit}_{ij}$$
$$+ \text{surface cloud cover}_{ij} \times \text{precipitation}_{ij} + \text{residual error}_{ij}$$
$$(A3)$$

No interactions were statistically significant ($P > 0.14$) and were therefore removed. Afterwards parameters with the highest nonsignificant P value were omitted. Parameters with a significant P value were not removed. For model 2 all interactions were removed; for model 3 precipitation was removed; for model 4 surface cloud cover was removed; for model 5 time of day was removed; for model 6 best wind profit was removed. Model 6 was the final model with surface temperature (parameter $= -0.09$, SE $= 0.017$, $P < 0.0001$) and surface wind speed (parameter $= -0.09$, SE $= 0.039$, $P = 0.015$) both having a negative coefficient. For a comparison of models see Table A1.

The long stopovers, with relative warm conditions, in the vicinity of the Caspian Sea/Arabian Desert might bias the analysis of autumn data. To test their influence on our results, we ran the same model (model 6) but excluded data from these stopovers close to the Caspian Sea. The overall result did not change (surface temperature: $P = 0.002$; surface wind speed: $P = 0.040$).

Spring migration. The number of fixes considered was 217 (bird A: 44; bird B: 83; bird C: 90). No parameter and no interaction were significant in any of the models (all $P > 0.38$).

Orientation and Compass Courses

Compass courses

(1) Constant magnetic course: we simulated the wheatear's autumn (spring) migration by starting from the breeding area (wintering area) towards 246° (66°). Every 10 km we considered the declination experienced and corrected the flight route accordingly. Declination was estimated by the magneticDeclination function from the R package oce (R Development Core Team 2010).

The seasonal difference in the constant magnetic course was minimal and therefore not shown.

(2) Constant magnetic course, but with daily recalibration of the bird's position and recalculation of the magnetic direction towards the wintering (breeding) area, if birds went off course owing to declination (Cochran et al. 2004): we calculated this as in (1) but after each nocturnal flight of 330 km in autumn (454 km in spring) we let birds recalibrate their position. Accordingly, we recalculated from the birds' current position the migration direction towards the migratory goal. During the subsequent migratory nocturnal flight birds migrated towards this direction but the migration route was altered by the declination experienced en route. As average nocturnal migration distances differed between seasons, the corresponding migration routes were not identical (Fig. 1).

(3) Star compass course and (4) sun compass course compensating for the change in local time during migration both with a constant geographical direction (Muheim et al. 2003): the rhumb line course between the breeding and wintering area was estimated with the bearingRhumb function from the R package geosphere (R Development Core Team 2010).

(5) Sun compass course not compensating for the change in local time during migration (great circle course; Alerstam & Pettersson 1991; Alerstam & Gudmundsson 1999; Alerstam et al. 2001, 2008): the great circle course between the breeding and wintering areas was estimated with the greatCircle function from the R package geosphere (R Development Core Team 2010).

(6) Magnetoclinic course with a constant specific angle of dip: this was estimated following Kiepenheuer (1984).

Radiotracking of first-year wheatears at Wales, western Alaska, in autumn

During autumn migration in 2010 (11–31 August) H.S. carried out a stopover ecology study at Wales (65.61°N, 168.10°W, Alaska). Wheatears were caught and tagged with radiotransmitters constructed by the Swiss Ornithological Institute in cooperation with the University of Applied Sciences Bern, Switzerland (Naef-Daenzer et al. 2005). Departure directions were radiotracked using Yagi 3EL2 hand-held antennas (Vårgårda, Sweden) in combination with YAESU FT-290RII receivers and corrected for local declination ($+11.19°$). Detection range of the radiotransmitters was about 12–15 km. For further information about the radiotracking technique see Schmaljohann et al. (2011) and Schmaljohann & Naef-Daenzer (2011). Wheatears were caught, ringed and tagged there under licence of the U.S. Fish and Wildlife Service (Federal Fish and Wildlife Permit: MB207892-0).

Cost of Migration

Estimation of variables

To estimate the energy costs for migration (flying) we applied different energy models, an aerodynamic model and a body mass model. Flight duration was considered in hours. Based on mean and SD of the parameters considered (see below) we randomly chose a value from the corresponding normal distribution. This procedure was repeated 100 times for each model and each bird. The appropriate variation was used to determine the 95% confidence interval (Figs 2, 3, A5).

Migratory body mass

For some models the birds' body mass was required. As there is an innate circannual change in the body mass with high values during migration and rather low values otherwise (Maggini & Bairlein 2012), we had to assume a certain body mass for migration, as we could not weigh birds en route. During a field study in Wales (65.61°N, 168.10°W, Alaska, see above) we estimated wheatears' departure

body mass from this westernmost point of Alaska prior to the crossing of the Bering Strait. Mealworms offered ad libitum in bowls with balances underneath were used to determine departure body mass (including only body mass measurements 2 h before sunset on the evening of departure) of individually colour-ringed wheatears. For more information about the method see Schmaljohann & Dierschke (2005). Average body mass at departure was 30.7 ± 2.95 g ($N = 29$). Using this, we assumed a body mass for migration of 30 g. Our results clearly demonstrated here that wheatears did not seem to have a long search and settling time, as each bird migrated several thousand kilometres without a longer stopover (Figs 1, A2). Hence, we are confident that the assumed migratory body mass of 30 g is an appropriate seasonal average also for times when birds resumed migration after only a short rest.

Basis of modelling

We divided migration into different migration steps ($N_{autumn} = 24$, $N_{spring} = 13$). For each migration step we estimated the hypothetical flight duration as the total distance between the adjacent stopover sites divided by the wheatear's airspeed of 13 m/s (Bruderer & Boldt 2001). To incorporate the effect of wind we added to the bird's airspeed the average of the best wind profit per night along the corresponding migration step. In Fig. A5 and Tables A2–A4 we also provide results for migration in still air. We modelled the energy costs during flight as the flight duration times the specific energy costs of the model. The total energetic cost for flying was the sum of the flight costs of all single migration steps. Total energy costs of migration were calculated only for autumn because fixes were lacking for spring migration, but we made relative comparisons between seasons.

Energy costs during flight

Energy models. (1) Based on a wind tunnel study with rose-coloured starlings, energy cost during flight was estimated with doubly labelled water as a function of body mass: $0.741 \times$ body mass$^{0.554}$ (W) with body mass in g (Engel et al. 2006). This is equivalent to 17.568 kJ/h × flight duration (h) for a 30 g wheatear.

(2) A field study with free-flying thrushes, *C. ustulatus* and *C. guttatus*, employing doubly labelled water, revealed an energy cost during flight of $(2.92 (\pm 0.375) + 12.5 (\pm 2.1))$ kJ/h × flight duration (h) (Wikelski et al. 2003). As the body mass of these thrushes, 30 g, was similar to the assumed body mass of wheatears during migration, we did not correct for body mass.

(3) We also combined the results from the thrush study (Wikelski et al. 2003) with our own measurements of the resting metabolic rate of wheatears: $(1.69 (\pm 0.41) + 12.5 (\pm 2.1))$ kJ/h × flight duration (h) (for details see below).

(4) Based on a general dependence of energy cost on body mass, $10^{1.780} \times$ body mass$^{0.868}$ (W) with body mass in kg (McWilliams

body mass of this thrush nightingale varied between 26 g and 30 g during the experiment. We applied this equation to our birds without correcting for body mass.

Aerodynamic model. We applied the aerodynamic flight model from Pennycuick (2008). Values differing from the default values of the Flight program are listed below. In spring 2010 we measured wing length following Svensson (1992), wing area and wing span of 200 wheatears stopping over on Helgoland (54.18°N, 7.92°E, Germany). The latter two were significantly related to wing length (linear regression of wing span with wing length: $R^2 = 0.91$, $F_{1,198} = 1892$, $P < 0.0001$; linear regression of wing area with wing length: $R^2 = 0.75$, $F_{1,197} = 592.2$, $P < 0.0001$). We estimated wing span (bird A: 29.4 cm; bird B: 30.0 cm; bird C: 29.0 cm) and wing area (bird A: 0.0128 m^2; bird B: 0.0133 m^2; bird C: 0.0125 m^2) from the wing length. We assumed a body mass of 30 g for each bird at the beginning of each nocturnal migratory flight. The corresponding fat fraction was 0.19 for bird A, 0.17 for bird B and 0.203 for bird C following Pennycuick (2008). Wheatears have a bounding flight style (Bruderer & Boldt 2001) with a bounding value of 0.53 and a wing beat frequency of around 14.55 Hz (Bruderer et al. 2010). The latter gives support to the similar values suggested by the Flight program (14.8–15.1 Hz) that we used.

We used (1) the 'Migration calculation' and (2) the 'Power Curve calculation' to estimate the energy cost of migratory flights according to the Flight program. (1) The 'Migration calculation' is a time-marching computation that considers the decrease in body mass over time. Here we considered for each bird the overall migration distance covered during each nocturnal migratory flight as the total migration distance divided by the number of migratory nights and considered the bird's seasonal average wind profit. The corresponding energy cost per nocturnal migratory flight was then multiplied by the number of migratory nights (Table A2). In the Results section of this paper we showed only results from the 'Power Curve calculation' (see below) because their ranges include the estimates following the 'Migration calculation' (Tables A2–A4).

(2) The 'Power Curve calculation' is a performance snapshot at one particular value of the mass and in this respect is unlike the 'Migration calculation' (Pennycuick 2008). One could estimate, however, the possible range of energy costs for migratory flights. When a bird migrates, its airspeed is between the minimum power speed (V_{mp}) and the maximum range speed (V_{mr}; Pennycuick 2008). We estimated these two speeds at sea level (Table A3) and at 3000 m above sea level (Table A4) where the lower air density results in higher airspeed (Pennycuick 2001, 2008; Schmaljohann & Liechti 2009). Based on the chemical power estimates given by the program we calculated the energy cost during flight for migration as:

$$\text{Total energy cost}_{i,j}(\text{kJ}) = \text{chemical power}_{i,j}(\text{W}) \cdot (\text{total migration distance}_i(\text{km})/\text{groundspeed}_i(\text{km/h})) \times 3.6 \qquad (\text{A4})$$

et al. 2004), energy costs for flying are about 10.34 kJ/h × flight duration (h) for a 30 g wheatear.

(5) Based on a wind tunnel study with barn swallows, energy cost during flight estimated with doubly labelled water is a function of body mass, $0.38 \times$ body mass$^{0.58}$ (W) with body mass in g (Schmidt-Wellenburg et al. 2007), and for a 30 g wheatear the energy cost is 9.85 kJ/h × flight duration (h).

(6) A wind tunnel study with a single thrush nightingale, based on the estimation of body mass loss, estimated an energy cost of $6.876 (\pm 0.667)$ kJ/h × flight duration (h) (Klaassen et al. 2000). The

with bird *i*'s specific specification, including size, fat fraction, migration distance and wind profit, and chemical power estimates *j* in respect to minimum power speed (V_{mp}) and maximum range speed (V_{mr}). Ground speed equals airspeed plus wind profit.

Estimates for the energy cost of flight for the migration distance in spring only for which fixes were available at sea level are as follows.

(1) Considering wind profit: bird A (8987 km): total energy with $V_{mp} = 1525$ kJ, total energy with $V_{mr} = 1214$ kJ; bird B (10 183 km): total energy with $V_{mp} = 1993$ kJ, total energy with $V_{mr} = 1491$ kJ;

bird C (13 088 km): total energy with $V_{mp} = 2646$ kJ, total energy with $V_{mr} = 1984$ kJ.

(2) In still air conditions: bird A (8987 km): total energy with $V_{mp} = 1750$ kJ, total energy with $V_{mr} = 1322$ kJ; bird B (10 183 km): total energy with $V_{mp} = 1972$ kJ, total energy with $V_{mr} = 1482$ kJ; bird C (13 088 km): total energy with $V_{mp} = 2563$ kJ, total energy with $V_{mr} = 1947$ kJ.

Body mass model. Following Delingat et al. (2008) we assumed that wheatears lose about $1 \pm 0.48\%$ of their actual body mass during a 1 h flight based on Nisbet (1963); Hussell & Lambert (1980); Kvist et al. (1998) and Klaassen et al. (2000). For this model we had to consider the body mass change during the nocturnal flight, the time on the ground during the nights after the nocturnal flights, during the next day and during stopovers (night and day; Dierschke et al. 2005; Delingat et al. 2006, 2009). This resulted in a more complex model. We provide the full R code and detailed explanations about how we modelled body mass loss during flight and on the ground on a day-to-night basis in the Supplementary material. The models were run with each bird 100 times to estimate individual variation for the energy costs during flight. Estimates for migration in still air are given in Fig. A5.

Energy costs on the ground (stopover)
Energy model. Dependence of resting metabolic rate on temperature (range 0–30 °C) was determined by a common garden experiment with captive wheatears. Under licence we collected young wheatears from nests in Germany, Norway and Iceland. Birds were hand-raised at the Institute of Avian Research, Germany, and kept indoors in individual cages on a lighting scheme of 14:10 h light:dark until 6 weeks of age when they were shifted to 12:12 h. Lowest body mass in healthy birds was taken as proxy of lean body mass. Metabolic rate was measured as nocturnal deep resting metabolic rate at 30 °C, 25 °C, 20 °C, 15 °C, 10 °C, 5 °C and 0 °C by using an open circuit respirometry approach following Withers (1977); see Scheiffarth & Bairlein (1998) and Maggini (2009) for further details. Birds were neither moulting nor nocturnally active.

Resting metabolic rate did not differ significantly at 25 °C (1.75 ± 0.47 kJ/h, 95%CI: 1.42–2.08, $N = 10$) and 30 °C (1.67 ± 0.39 kJ/h, 95%CI: 1.51–1.82, $N = 26$; t test, two-tailed: $F = 0.313$, $P = 0.579$). Thus, we pooled these data as a proxy of the resting metabolic rate within the thermoneutral zone (1.69 ± 0.41 kJ/h, $N = 36$). Below 25 °C resting metabolic rate increased by 0.055 ± 0.0585 kJ/°C with an intercept of 3.11 ± 0.78 kJ (linear regression: $F_{2,135} = 149$, $P < 0.001$).

Body mass model. The cornerstones of the model are body mass loss during flight (see above), body mass loss on the ground during the night ($0.4 \pm 0.28\%$ of the current body mass per h; Delingat et al. 2009), body mass gain during the day ($1.0 \pm 0.512\%$ of the current body mass per h; Dierschke et al. 2005) and body mass loss during the day ($0.4 \pm 0.28\%$ of the current body mass per h; Delingat et al. 2009). The full R code is given in the Supplementary material explaining how the four different categories of energy costs on the ground were estimated. All estimates of body mass gain and loss were derived from our own stopover ecology field studies with wheatears (Dierschke et al. 2005; Schmaljohann & Dierschke 2005; Delingat et al. 2006, 2009).

Costs of migration in still air
We give here energy and time costs for migration in still air: Total energy costs for autumn migratory flights varied between 2100 kJ and 5500 kJ (3509 ± 1241 kJ, $N_{models} = 8$ considering only sea level values of the aerodynamic model; Fig. A5). Total energy costs for times on the ground (stopover) were 5081 kJ. According to the body

mass model birds lost 112 ± 3 g during the migratory flights in autumn, which is equivalent to 2511 ± 67 kJ and 3126 ± 84 kJ depending on the protein/fat ratio (10/90 and 5/95; Fig. A5). During stopovers they lost 309 ± 29 g. In spring we could consider only $10\,753 \pm 2109$ km of migration, covering 37 ± 14 days costing in terms of migration 2585 ± 916 kJ (range 1590–4040, $N_{models} = 8$ considering only sea level values of the aerodynamic model) and stopovers 1895 ± 905 kJ (energy model). In respect of the body mass model migration cost 68 ± 18 g, equivalent to 1524–1898 kJ depending on the protein/fat ratio) and stopovers cost 104 ± 46 g. The average ratio of the energy costs during flight and (stopover) times on the ground ranged in autumn from 1:0.93 to 1:2.4 (models' average: 1:1.45, $N_{models} = 8$) and was 1:2.75 for the body mass model, and in spring 1:0.475 to 1:1.2 (models' average: 1:0.73) and was 1:1.4 for the body mass model. The total energy cost for migration relative to distance covered was significantly lower in spring (weighted mean = 0.44 kJ/km, weighted SD = 0.11 and weighted mean = 0.019 g/km, weighted SD = 0.007, $N_{migration\ step} = 13$) than in autumn (weighted mean = 0.80 kJ/km, weighted SD = 0.40 and weighted mean = 0.043 g/km, weighted SD = 0.026, $N_{migration\ step} = 24$; energy model: assuming a medium energy cost during flight (McWilliams et al. 2004) and species' resting metabolic rate and body mass model (all GLMMs: $P < 0.0001$).

The ratio of time spent between migratory flight (311 ± 8 h) and being on the ground (1949 ± 305 h) was 1:6.35 in autumn and 1:2.75 in spring, when considering only spring migration for which fixes were available (Fig. 1).

Comparison of total energy costs of migration relative to distance during autumn and spring
We could not estimate total energy costs during spring, because of one geolocator failure and of two birds migrating so far north that no fixes were derived for 7 and 10 days. Hence, we compared the energy costs relative to the distance covered for the energy (resting metabolic rate + McWilliams et al. 2004 estimates) and body mass models. In both models the total energy costs per migration distance were defined as the sum of energy costs (1) for nocturnal migratory flights, (2) on the ground for the remaining time of the migratory night, (3) on the ground during the day between migratory flights, (4) on the ground during nights of stopover, and (5) on the ground during days of stopover divided by migration distance. We formulated the following GLMMs with a binomial error distribution:

$$y_i \sim \text{total cost of migration relative to distance}_i$$
$$+ \text{residual error}_{ij} \qquad (A5)$$

The vector y_i represented season (autumn versus spring). The residual error contained the individual as a random effect allowing random intercepts for the three birds. Each model was estimated by considering individual wind profit and migration under still air conditions.

Energy model. (1) Total cost of migration relative to distance considering wind profit: parameter = -9.38, SE = 1.18, $P < 0.001$.

(2) Total cost of migration relative to distance under still air conditions: parameter = -8.12, SE = 1.08, $P < 0.001$.

Body mass model. (1) Total cost of migration relative to distance considering wind profit: parameter = -165.02, SE = 20.01, $P < 0.001$.

(2) Total cost of migration relative to distance under still air conditions: parameter = -158.98, SE = 19.50, $P < 0.001$.
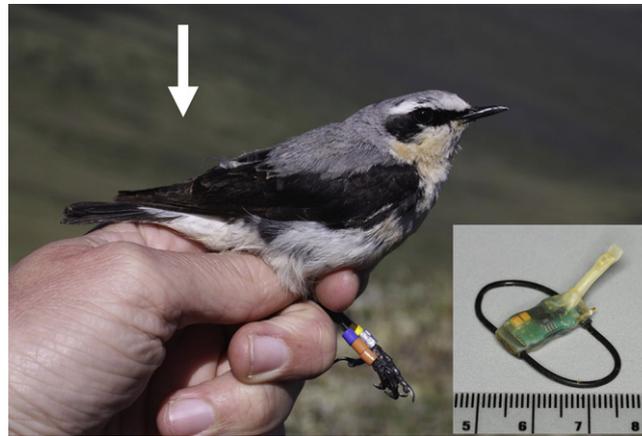
Figure A1. Male Alaskan wheatear, *Oenanthe oenanthe* (bird B) with light level geolocator (arrow) attached via Rappole–Tipton style harness on 25 June 2009, Eagle Summit (65.6°N, 145.4°W, Alaska). Photo: Heiko Schmaljohann. Inset: light level geolocator, Mk10S (1.2 g, with 13 mm sensor stalk at 30° angle to the horizontal), from British Antarctic Survey with elastic silicone-rubber O-ring. Photo: Rolf Nagel.
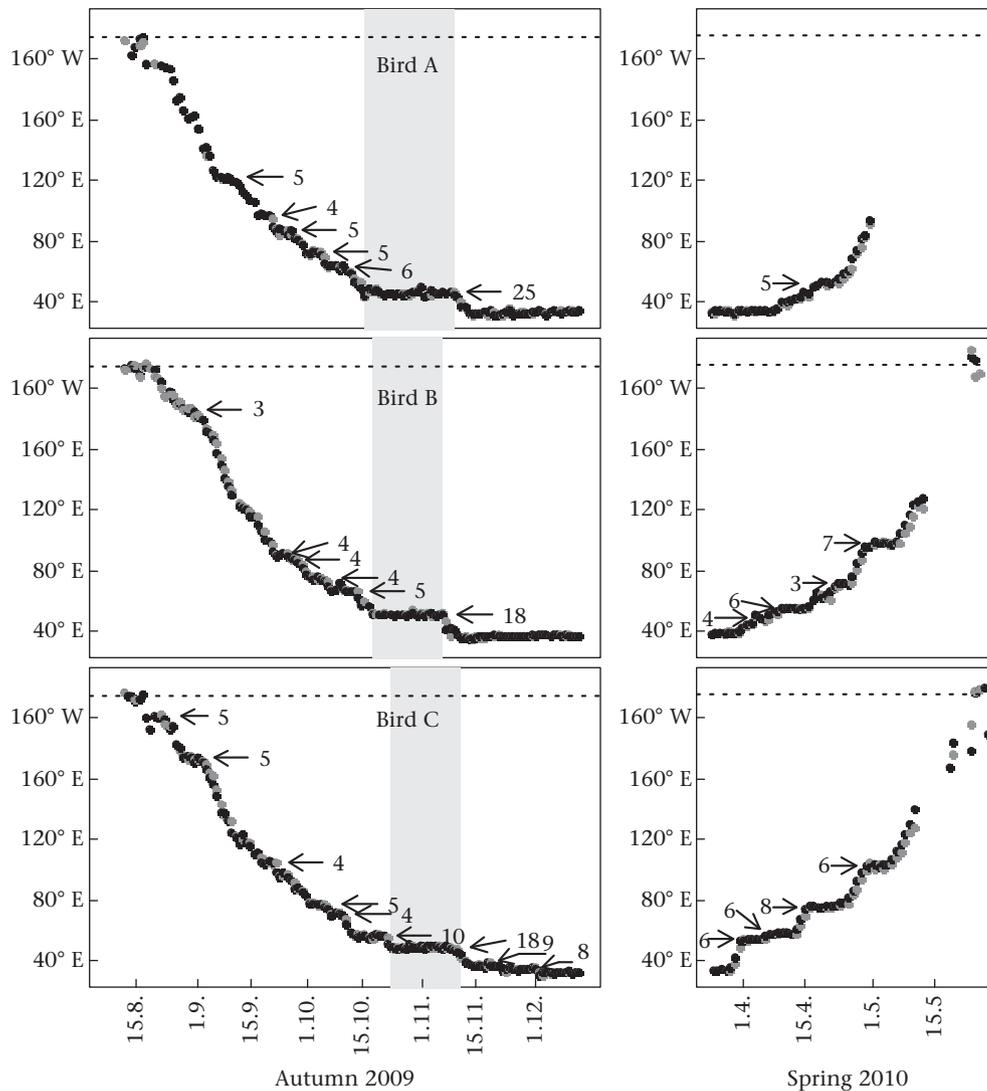
Figure A2. All raw (unsmoothed) longitudinal fixes of two male (A, B) and one female (C) wheatears, breeding at Eagle Summit in Alaska, for autumn and spring migrations. Dotted black line indicates breeding site longitude. Black = midnight fixes, grey = noon fixes. Stopovers were defined as more than two noon fixes within 1° of longitude and are indicated by arrows. Black numbers indicate the corresponding stopover duration in days as number of noon fixes. Shaded areas indicate stopover at the Caspian Sea prior to crossing of the Arabian Desert. Longitudinal data for bird A are shown until geolocator failure on 1 May 2010. Bird B migrated for 10 days and bird C for 7 days north of the 70° latitude where, owing to 24 h daylight, no fixes were derived.

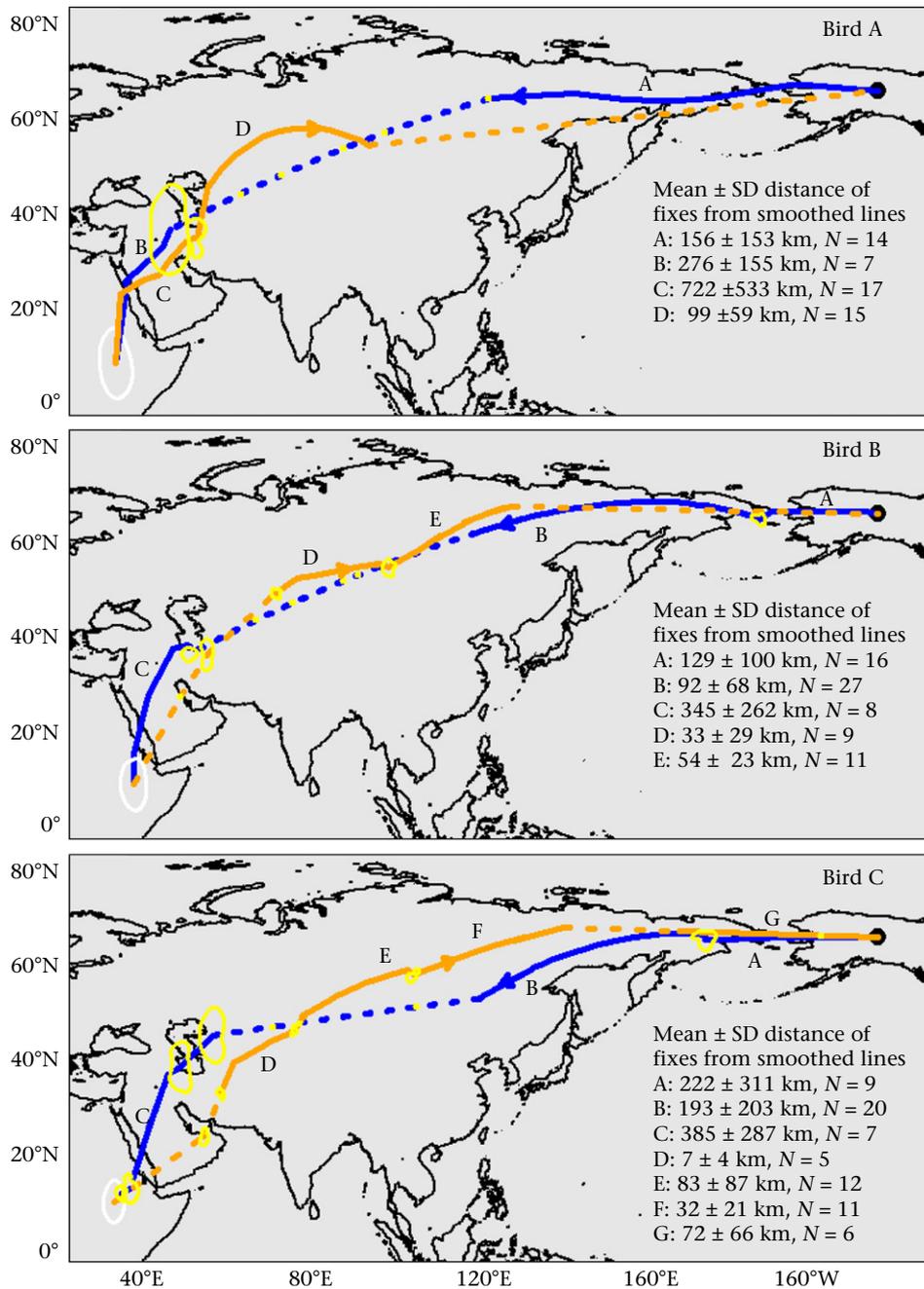**Figure A3.** Interpolated migration routes with stopover sites for birds A, B and C. Blue = autumn migration (mid-August to mid-November 2009), orange = spring migration (end March to mid-May 2010), yellow contour lines = stopovers with five or more fixes, yellow dots = stopovers with fewer than five fixes, white contour = wintering area. Density contour reflects 75% kernel density. Dotted lines between stopover sites indicate rejection of data owing to high uncertainty in latitude estimations (equinoxes or light interference) or 24 h daylight. Data logger of bird A failed during spring migration on 1 May 2010; the last known fix is hypothetically joined with the breeding area. Latitude data were smoothed by local polynomial regression fitting with raw longitude data as the predictor. Raw longitude data and the smoothed latitude estimations were used to indicate the smoothed migratory routes. Continuous lines between stopover sites and/or breeding or wintering areas indicate highly accurate tracks. Accuracy of these was estimated for each section as mean ± SD distance (km) of the original fixes to the smoothed line and the number of fixes considered.

Mean ± SD distance of
fixes from smoothed lines
A: 156 ± 153 km, N = 14
B: 276 ± 155 km, N = 7
C: 722 ± 533 km, N = 17
D: 99 ± 59 km, N = 15

Mean ± SD distance of
fixes from smoothed lines
A: 129 ± 100 km, N = 16
B: 92 ±68 km, N = 27
C: 345 ± 262 km, N = 8
D: 33 ± 29 km, N = 9
E: 54 ±23 km, N = 11

Mean ± SD distance of
fixes from smoothed lines
A: 222 ± 311 km, N = 9
B: 193 ± 203 km, N = 20
C: 385 ± 287 km, N = 7
D: 7 ± 4 km, N = 5
E: 83 ± 87 km, N = 12
F: 32 ± 21 km, N = 11
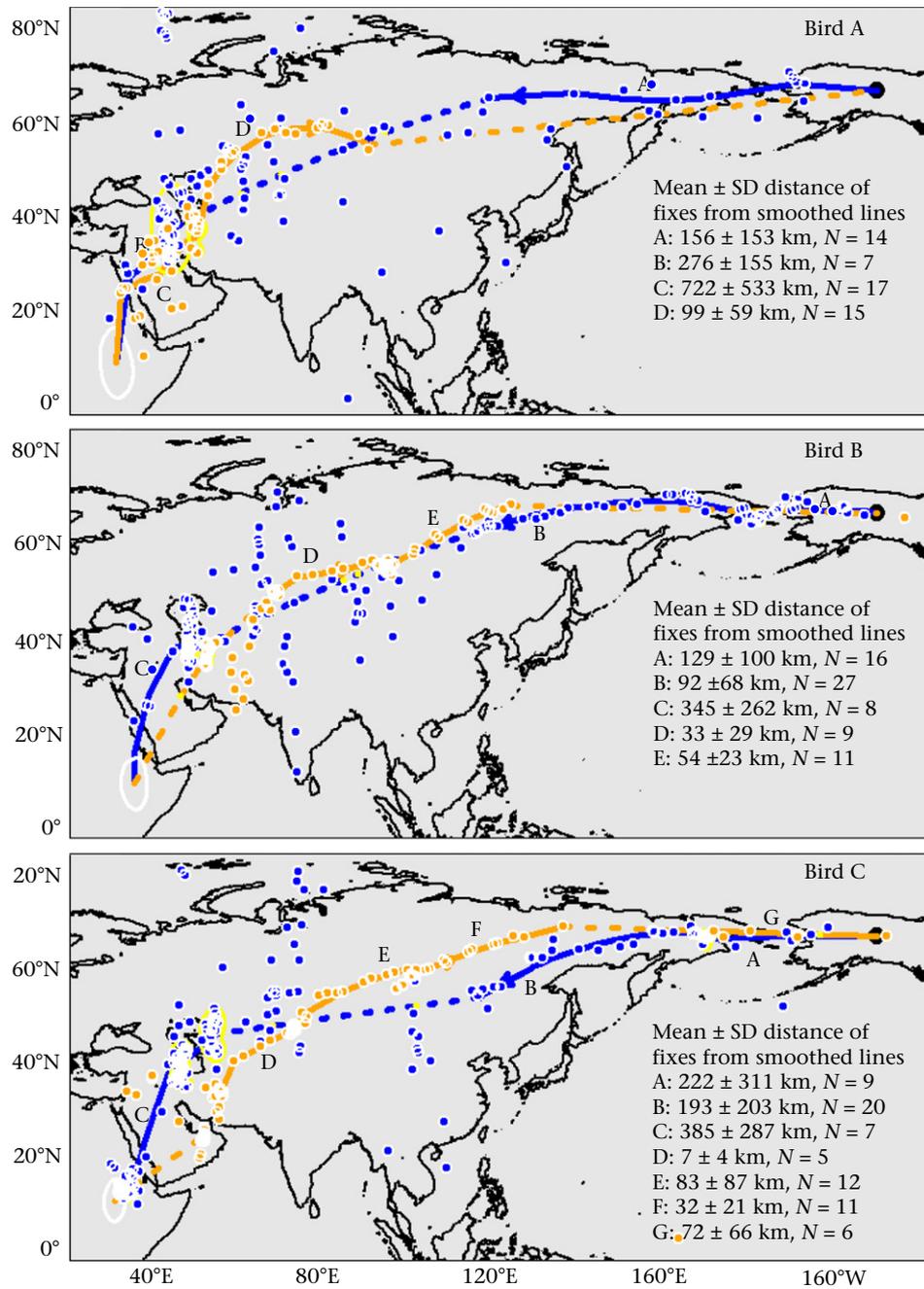G: 72 ± 66 km, N = 6

Figure A4. As Fig. A3 but raw fixes (blue = autumn, orange = spring, both encircled in white) are given for migration periods.
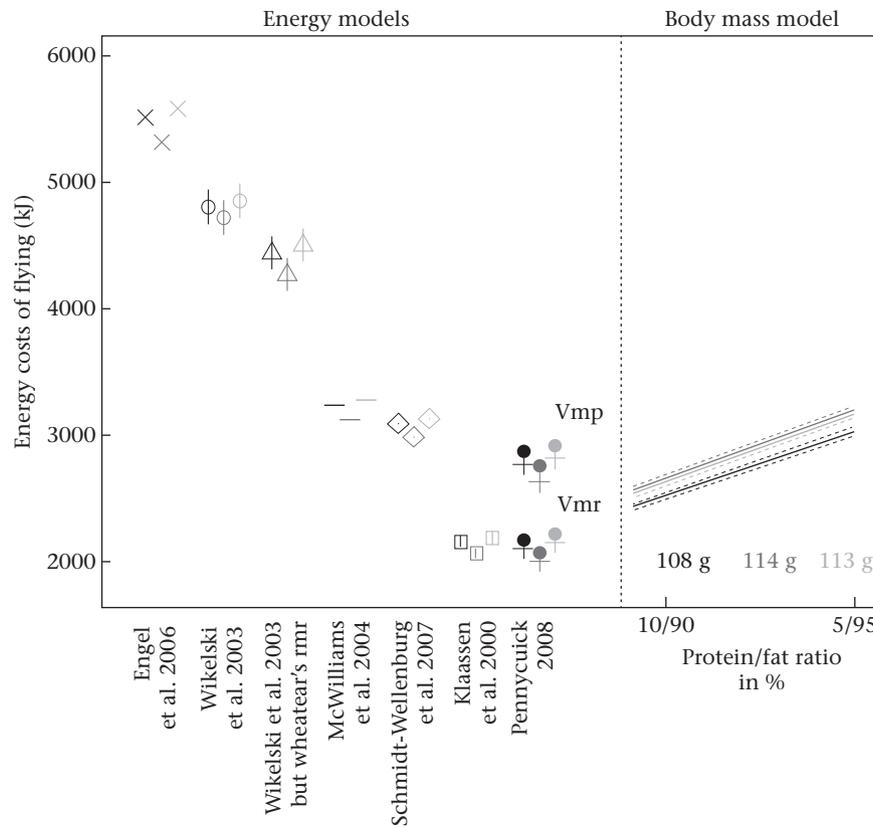
Figure A5. Total energy costs for migratory flights based on the estimated flight duration in still air from the breeding to the wintering area; bird A: black; bird B: grey; bird C: light grey. Estimates were derived from six energy models (X: 17.57 kJ/h; O: 15.4 kJ/h; Δ: 14.19 kJ/h considering wheatear's resting metabolic rate (rmr; see Appendix); −: 10.34 kJ/h; ◇: 9.84 kJ/h; □: 6.88 kJ/h), an aerodynamic flight model (V_{mr}: maximum range speed; V_{mp}: minimum power speed; both at sea level (●) and 3000 m above sea level (+) with birds' specific values) and a body mass model. Individual body mass loss was converted into energy (kJ) over a range of fat:protein ratios from 10:90 to 5:95. Where appropriate, 95% confidence intervals are given. Body mass shown in the figure refers to body mass loss for migratory flights; values in grey give the body mass loss for migration in still air.

Table A1
Comparison of models

	df	AIC	BIC	logLik	χ	Pr(>χ)	ΔAIC
Model 6	4	623.95	640.64	−307.97			
Model 5	5	624.58	645.45	−307.29	1.3682	0.2421	0.63
Model 4	6	626.07	651.11	−307.04	0.5101	0.4751	2.12
Model 3	7	627.81	657.03	−306.90	0.2603	0.6099	3.86
Model 2	8	629.76	663.15	−306.88	0.0521	0.8195	5.81
Model 1	11	632.96	678.87	−305.48	2.8001	0.4235	9.01

Table A2
Migration calculation (time-marching computation) with the Flight program (Pennycuick 2008)

	Bird A Autumn/spring	Bird B Autumn/spring	Bird C Autumn/spring
Total migration distance (km)	14 686/14 822	14 176/13 741	14 871/14 260
Average flight distance per migration night not considering wind profit (km)	358/473	302/407	330/485
Fuel burned (kJ) per average flight distance per migration night in still air	53.8/69.1	45.0/60	50.0/71.4
Fat; protein (kJ)	51.5; 2.7/65.7; 3.4	42.8; 2.2/57.0; 3.0	47.5; 2.5/67.8; 3.5
Total energy for flying in still air (kJ)	**2206/2165**	**2115/2026**	**2250/2102**
Overall wind profit during autumn migration (km/h)	1.4/3.1	−1.0/1.1	−0.3/1.6
Actual flight distance per migration night considering wind profit (km)	323/382	327/375	338/432
Fuel burned (kJ) per average flight distance per migration night considering wind profit	49.2/57.0	49.1/55.6	51.2/64.3
Fat; protein (kJ)	46.8; 2.43/54.2; 2.8	46.7; 2.4/52.8; 2.8	487; 2.5/61.1; 3.2
Total energy for flying considering wind profit (kJ)	**2237/2212**	**2129/2037**	**2253/2122**
3000 m above sea level			
Fuel burned (kJ) per average flight distance per migration night in still air	51.6/67.3	43.6/57.8	48.0/69.0
Fat; protein (kJ)	49.0; 2.5/64.0; 3.3	41.5; 2.1/55.0; 2.9	45.6; 2.4/65.6; 3.4
Total energy for flying in still air (kJ)	**2118/2113**	**2047/1952**	**2163/2029**
Fuel burned (kJ) per average flight distance per migration night considering wind profit	47.3/55.2	47.1/53.6	49.4/61.8
Fat; protein (kJ)	44.9; 2.3/52.5; 2.7	44.8; 2.3/50.9; 2.6	47.0; 2.4/58.7; 3.1
Total energy for flying considering wind profit (kJ)	**2151/2136**	**2042/1964**	**2173/2040**

Energy cost estimates during flight are given in bold for autumn and spring migration in still air and considering wind profit.

Table A3
Power Curve calculation with the Flight program (Pennycuick 2008) at sea level

	Bird A Autumn/spring	Bird B Autumn/spring	Bird C Autumn/spring
V_{mp} chemical power (W)	1.85	1.82	1.88
V_{mr} chemical power (W)	2.31	2.27	2.35
V_{mp} (m/s)	9.5	9.4	9.6
V_{mr} (m/s)	15.7	15.6	15.8
Total migration distance (km)	14 686/14 822	14 176/13 741	14 871/14 260
Total energy V_{mp} in still air (kJ)	**2860/2886**	**2745/2660**	**2912/2793**
Total energy V_{mr} in still air (kJ)	**2161/2181**	**2063/1999**	**2212/2121**
Overall wind profit during autumn migration (km/h)	1.4/3.1	−0.1/1.1	−0.3/1.6
Total energy V_{mp} considering wind profit (kJ)	**2493/2176**	**2774/2382**	**3006/2394**
Total energy V_{mr} considering wind profit (kJ)	**1984/1821**	**2076/1868**	**2255/1926**

Energy costs during flight on migration are given in bold for minimum power speed (V_{mp}) and maximum range speed (V_{mr}) each in still air and when considering wind profit.

Table A4
Power Curve calculation with the Flight program (Pennycuick 2008) at 3000 m above sea level

	Bird A Autumn/spring	Bird B Autumn/spring	Bird C Autumn/spring
V_{mp} chemical power (W)	2.07	2.02	2.10
V_{mr} chemical power (W)	2.57	2.52	2.61
V_{mp} (m/s)	11.0	10.9	11.1
V_{mr} (m/s)	18.0	17.9	18.1
Total migration distance (km)	14 686/14 822	14 176/13 741	14 871/14 260
Total energy V_{mp} in still air (kJ)	**2764/2789**	**2627/2546**	**2813/2698**
Total energy V_{mr} in still air (kJ)	**2097/2116**	**1996/1934**	**2144/2056**
Overall wind profit during autumn migration (km/h)	1.4/3.1	−0.1/1.1	−0.3/1.6
Total energy V_{mp} considering wind profit (kJ)	**2452/2176**	**2651/2313**	**2892/2358**
Total energy V_{mr} considering wind profit (kJ)	**1946/1805**	**2007/1822**	**2181/1889**

Energy costs during flight on migration are given in bold for minimum power speed (V_{mp}) and maximum range speed (V_{mr}) each in still air and when considering wind profit.