Proximate causes of avian protandry differ between subspecies with contrasting migration challenges

Article *in* Behavioral Ecology · September 2015

DOI: 10.1093/beheco/arv160

Heiko Schmaljohann
Carl von Ossietzky Universität Oldenburg
94 PUBLICATIONS **2,127** CITATIONS

Christoph Manuel Meier
Swiss Ornithological Institute
19 PUBLICATIONS **867** CITATIONS

Debora Arlt
Swedish University of Agricultural Sciences
46 PUBLICATIONS **1,040** CITATIONS

Franz Bairlein
Institute of Avian Research
306 PUBLICATIONS **15,399** CITATIONS

Behavioral Ecology Advance Access published September 28, 2015

Behavioral Ecology

The official journal of the ISBE International Society for Behavioral Ecology

Behavioral Ecology (2015), 00(00), 1–11. doi:10.1093/beheco/arv160

Original Article

Proximate causes of avian protandry differ between subspecies with contrasting migration challenges

Heiko Schmaljohann,[a] Christoph Meier,[b] Debora Arlt,[c] Franz Bairlein,[a] Herman van Oosten,[d] Yolanda E. Morbey,[e] Susanne Åkesson,[f] Martin Buchmann,[g] Nikita Chernetsov,[h,i] Robert Desaever,[j] John Elliott,[k] Magnus Hellström,[l] Felix Liechti,[b] Aïda López,[m] John Middleton,[n] Ulf Ottosson,[f] Tomas Pärt,[c] Fernando Spina,[o] and Cas Eikenaar

[a]Institute of Avian Research "Vogelwarte Helgoland", An der Vogelwarte 21, Wilhelmshaven 26836, Germany, [b]Swiss Ornithological Institute, Seerose, 6204 Sempach, Switzerland, [c]Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 75007 Uppsala, Sweden, [d]Biosphere Science Foundation, Berkenlaan 71, 6721 CB Bennekom, The Netherlands, [e]Department of Biology, Western University, 1151 Richmond Street, London, Ontario N6A 5B7, Canada, [f]Department of Biology, Center for Animal Movement Research, Lund University, Lund SE-22362, Sweden, [g]Unterer Sand 12, 55596 Waldböckelheim, Germany, [h]Biological Station Rybachy, Zoological Institute of Russian Academy of Sciences, Rybachy 238535, Kaliningrad Region, Russia, [i]Department of Vertebrate Zoology, St. Petersburg State University, St. Petersburg 199034, Russia, [j]34 Helvetiastraat, 8670 Koksijde, Belgium, [k]Hilbre Bird Observatory, Wirral, UK, [l]Ottenby Bird Observatory, Pl 1500, SE-380 65 Degerhamn, Sweden, [m]Lista Bird Observatory, Fyrveien 6, 4563 Borhaug, Norway, [n]NW Norfolk Ringing Group, 8 Back Lane, Burnham Market, Norfolk PE31 8EY, UK, and [o]Istituto Nazionale per la Fauna Selvatica, via Ca' Fornacetta 9, I-40064 Ozzano Emilia (BO), Italy

Received 27 May 2015; revised 26 August 2015; accepted 5 September 2015.

In many migratory birds, males precede females during migration and arrival at the breeding sites. Three proximate mechanisms are proposed to explain this phenomenon of protandry: males 1) winter closer to breeding sites, 2) start spring migration earlier, and/or 3) migrate faster than females. So far, the relative contribution of these mechanisms to protandry is unknown. The present study investigated the importance of each of the 3 proximate mechanisms of protandry for a songbird migrant wintering in Africa, the northern wheatear (*Oenanthe oenanthe*). Two subspecies co-occur in Europe on migration, of which the *leucorhoa* northern wheatears breeding from Iceland to Canada have to cross the North Atlantic, whereas the nominate form breeding in Europe does not face any significant sea barrier. We show that the *leucorhoa* subspecies had a significantly higher degree of protandry at stopover sites across Europe than the *oenanthe* subspecies (−6 vs. −2 days). *Leucorhoa* northern wheatear's higher degree of protandry was associated with a larger age effect, in which old males preceded young males, and greater sex-specific differences in wing shape and refueling yielding higher migration speeds in males than females. In *oenanthe* northern wheatears, light-level geolocators revealed that males did not winter closer to the breeding sites or migrate faster than females, but initiated spring migration earlier. Our results demonstrate that the significance of the mechanisms causing protandry can differ between related taxa and highlight the importance of the advancement in male arrival date with age as a potential factor shaping the degree of protandry.

Key words: **arrival, breeding, migration, protandry, proximate causes, songbird.**

Address correspondence to H. Schmaljohann. E-mail: heiko.schmaljohann@ifv-vogelwarte.de.

INTRODUCTION

In seasonal breeders, it is a common pattern that males arrive at the site of reproduction earlier in the season than females. This sex-specific phenomenon concerning phenology is termed protandry (Morbey and Ydenberg 2001). Among several mutually nonexclusive ultimate causes, protandry is generally regarded as a strategy to maximize individual fitness (Kokko 1999; Morbey and Ydenberg 2001; Kokko et al. 2006). Less is known about the proximate, behavioral mechanisms underlying sex-specific timing, and how these might interact with environmental variability to affect phenology at ecological timescales. Such sex differences are important, as they will contribute to the overall response of species to shifting environmental seasonality due to climate change.

Many migratory birds show protandry both at breeding areas and at migratory stopover sites (Møller 1994; Rubolini et al. 2004; Tøttrup and Thorup 2008; Coppack and Pulido 2009; Saino et al. 2010). Three non-mutually exclusive, proximate mechanisms of protandry have received the most attention in birds (Table 1; Coppack and Pulido 2009). First, males could winter closer to breeding sites (i.e., latitudinal sex segregation). Assuming that males initiate migration at the same time as females, males would have shorter distances to travel and they would arrive earlier at stopover sites and breeding sites than females. Second, males could migrate earlier from wintering sites. With respect to departure from wintering sites, captive studies show that caged male songbirds start their nocturnal migratory activity earlier in spring than females (Coppack and Pulido 2009) even under constant photoperiod and environmental conditions (Maggini and Bairlein 2012). In the wild, the actual start of migration might be modified by environmental factors (Gwinner 1996; Marra et al. 1998) and sexes might differ in their response to these factors (Marra and Holmes 2001; Saino et al. 2004). Third, males could migrate faster than females, which could be realized by sex-specific airspeeds caused by sex-specific wing shapes (Hedenström and Pettersson 1986; Corman et al. 2014). Additionally, males might have a higher rate of fuel replenishment (fuel deposition) than females during stopover, which would result in shorter stopover duration and hence faster total speed of migration (Alerstam and Lindström 1990; Seewagen et al. 2013). As no study has jointly investigated these 3 mechanisms in a single species, the relative contribution of each of these proximate causes to the observed level of protandry is unclear (Coppack and Pulido 2009; Morbey et al. 2012; Seewagen et al. 2013). Moreover, theory is lagging, and the relative costs and benefits of these different mechanisms of protandry have not yet been worked out.

Here, our aim is to provide a comprehensive overview of the relevance of these 3 proximate mechanisms of protandry by using field data of a well-studied, long-distance insectivorous songbird migrant, the northern wheatear (*Oenanthe oenanthe*, wheatear hereafter). During spring and autumn, 2 wheatear subspecies co-occur in Western Europe. *O. o. oenanthe* (*oenanthe* wheatears hereafter) breeds in Europe but not Iceland. *O. o. leucorhoa* (*leucorhoa* wheatears hereafter) breeds in Iceland, Greenland, and eastern Canada (Figure 1). Both subspecies breed primarily in rocky tundra, but also use other open habitats (Cramp 1988). They winter sympatrically in the same habitat in Western Africa (Bairlein et al. 2012; Schmaljohann, Buchmann, et al. 2012). The main ecological differences between subspecies are their breeding ranges and their migratory challenges. In contrast to *oenanthe* wheatears, *leucorhoa* wheatears cross the North Atlantic (800–3400 km) to their Arctic breeding areas (Figure 1). With an estimated airspeed of 50 km/h (Bruderer and Boldt 2001), such distances correspond to nonstop flights of 16–68 h.

Initially, we estimated the degree of protandry for both subspecies based on ringing data at multiple stopover sites over an extensive spatiotemporal scale (Figure 1). For *oenanthe* wheatears only, we used light-level geolocation data to investigate the 3 proximate mechanisms of protandry. In addition, for both subspecies, we examined whether sex-specific differences in wing shape and rates of fuel deposition influenced the total speed of migration (Nilsson et al. 2013). We compared whether sex differences in wing shape and fueling rates matched the subspecies difference in protandry as observed at our stopover sites. In summary, we used capture data to estimate the degree of protandry in both subspecies, light-level geolocation data to assess the 3 proximate mechanisms in *oenanthe* wheatears, and finally, data on sex-specific wing shape and refueling rate to assess sex-specific migration speed in both subspecies (Table 1).

Table 1

Proximate causes of protandry in *oenanthe* and *leucorhoa* northern wheatears

Proximate cause	*Oenanthe o. oenanthe*	*Oenanthe o. leucorhoa*
Males winter closer to breeding sites	No (geolocation data)	No data
Males start spring migration earlier	Yes (geolocation data)	No data
Males migrate faster than females	No (geolocation data, wing shape, fuel deposition rate)	Yes (wing shape, fuel deposition rate)

Evidence for these mechanisms of protandry comes from the current study. Light-level geolocation data were available for *oenanthe* northern wheatears showing that males started spring migration significantly earlier than females. Data on wing shape and fuel deposition rate demonstrated only for *leucorhoa* northern wheatears that males migrate faster than females.

MATERIALS AND METHODS

Estimation of protandry in *leucorhoa* and *oenanthe* northern wheatear

At 16 study sites distributed over Europe (Figure 1), we estimated the degree of protandry by comparing arrival dates of males and females. Study sites included 6 breeding sites and 10 stopover sites where migrating wheatears of known subspecies were caught in spring (before 1 July) in the years from 1957 to 2014 (Figure 1; details of site-specific capture protocols are in Supplementary Table S1 and of individual ringing data in Table S2 in Supplementary Appendix S1). At stopover sites, migrants rest for a few days and replenish the fuel used during previous flights. Estimates of arrival dates based on captures are usually more precise at stopover sites than at breeding sites due to shorter stays at stopover sites than at the breeding areas. The degree of protandry measured on migration tends to be slightly lower than at breeding sites (details in Supplementary Table S5 in Supplementary Appendix S1). This difference could be explained by the mixing of populations (with different breeding times) at stopover and by mortality events after departure from stopover sites. “Arrival date” at stopover sites was approximated by “date of capture.” The stochastic bias between estimated “arrival date” and true arrival date depended on the actual trapping effort. As trapping effort was not related to subspecies or sex, the existing stochastic bias is mostly independent

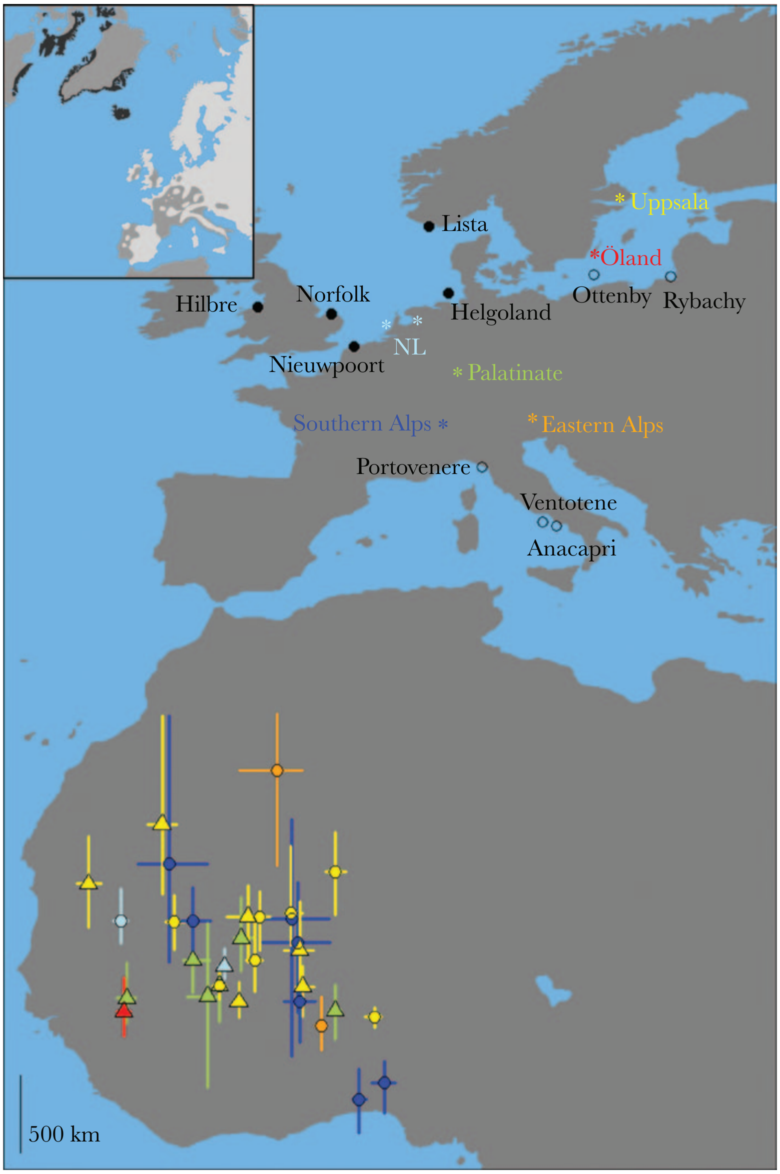

Figure 1

Study sites in Europe and estimated wintering sites in Africa. Asterisks show breeding sites. Dots indicate stopover sites where northern wheatears were trapped (open circle: only *oenanthe* subspecies; filled circles: *oenanthe* and *leucorhoa* subspecies). Anacapri: 13 years of data/402 individuals; Ventotene: 10/434; Portovenere: 11/434; Nieuwpoort: 29/1871; Hilbre: 32/303; Norfolk: 15/872; Helgoland: 11/1343; Ottenby: 21/115; Rybachy: 30/112; Lista: 24/511. Light-level geolocation data were available for 6 breeding sites of *oenanthe* northern wheatears (details in Table S4 in Supplementary Appendix S1). There are 2 breeding locations in close vicinity within the Netherlands. These 2 locations are treated as 1 breeding site. Estimated wintering locations are color coded by breeding site with males (triangles) and females (circles) shown separately. Error bars indicate the 25th and 75th quantile of estimated latitude and longitude. The map is a Mercator projection. Inset shows breeding distribution of *oenanthe* northern wheatears (light gray) and of *leucorhoa* Northern Wheatears (black) on a north polar stereographic projection map.

of subspecies and sex. We note that sex-specific stopover duration might lead to a higher likelihood of catching the longer staying sex later after arrival at a site.

Birds were sexed based on plumage (Svensson 1992). Males were aged as second calendar year (2 cy birds hereafter) or older (old birds hereafter) (Svensson 1992). As female wheatears cannot be aged in spring (Svensson 1992), we could not consider a potential age effect in females. Following established protocol, we used wing length, as maximum wing chord (Svensson 1992), to categorize birds to subspecies: males and females with wing lengths exceeding 102 and 99 mm, respectively, were assigned as *leucorhoa* wheatears, whereas those with wing lengths below 99 mm (males) and 96 mm (females) were assigned as *oenanthe* wheatears (Cramp 1988; Svensson 1992). Individuals with intermediate wing lengths were excluded because of uncertainty in subspecies classification. By this discrimination, relatively small-winged *leucorhoa* wheatears and, conversely, relatively large-winged *oenanthe* wheatears were systematically excluded. This, however, unlikely biased our analyses of arrival date or protandry. In subspecies-specific linear models with wing length, sex, their 2-way interaction, and stopover site as explanatory variables, neither wing length (*oenanthe*: 0.07 ± 0.20 mm [mean ± standard error {SE}], $n = 3615$, $P = 0.71$; *leucorhoa*:

−0.20 ± 0.15 mm, n = 2697, P = 0.18) nor the interaction (*oenanthe*: −0.23 ± 0.26, n = 3615, P = 0.39; *leucorhoa*: 0.13 ± 0.21, n = 2697, P = 0.53) had a significant effect on arrival date.

Light-level geolocation data in *oenanthe northern wheatear*

In *oenanthe* wheatears, departure from the wintering sites and "arrival date" at the breeding sites was approximated by analyzing light-level geolocation data from 31 geolocators attached to wheatears from 6 breeding sites (Figure 1; details of individual light-level data are in Supplementary Table S3 and details of deployment and light-level analyses are in Table S4 in Supplementary Appendix S1). Nineteen of these 31 were analyzed before to address different research questions (Schmaljohann, Buchmann, et al. 2012; Arlt et al. 2013; Van Oosten et al. 2014; Arlt et al. 2015). To make data from these different studies comparable, all data were (re-)analyzed following the same protocol (see Analysis details S1 in Supplementary Appendix S1). First, we used the light threshold method as described in Lisovski et al. (2012) to assign times closely associated with sunrise and sunset (sunrise and sunset times, hereafter). As a low light threshold generally is less susceptible to shading events (Lisovski et al. 2012), a threshold of 3 light units above the basic light level as recorded during the night was selected (details in Table S4 in Supplementary Appendix S1). On 30 days, our algorithm failed to assign an unambiguous sunrise or sunset time because some light was recorded >1 h from the closest sunrises and/or sunsets (Supplementary Table S4). As in other studies, for example Stutchbury et al. (2009), we manually selected the correct sunrise and/or sunset times. Second, we calibrated the data for sun elevation angle based on all light recorded while the individual bird was stationary and attending its breeding site. This analysis of geolocator data provided 2 estimates of the bird's position (latitude and longitude) per day throughout its annual cycle (Ekstrom 2004; Lisovski et al. 2012). Estimating positions from light-level data does not yield exact positions. Therefore, we reported the 25th, 50th, and 75th quantiles of the position for sites where a bird stayed at least 3 days (Fudickar et al. 2012; Lisovski et al. 2012). Inherently, latitude cannot be estimated on days around the equinoxes (Lisovski et al. 2012), and so we discarded 10 days before and 10 days after the equinoxes (cf. Lisovski et al. 2012). Third, departure date from the wintering site and arrival date at the breeding ground was determined. Based on single-location estimates of light-level geolocation data, it is difficult to discriminate between local movements and directional movements during migration due to the general noise in such data (Lisovski et al. 2012). Therefore, each track was divided into migratory and stationary phases. We did this by screening raw twilight times for changes in bird's movement behavior within a moving window across the whole season. The algorithm for this analysis was based on the R package "GeoLight" version 1.03 (Lisovski and Hahn 2012) and consisted of self-customized R functions (see Analysis details S1 in Supplementary Appendix S1). Dates of first and last sunrise or sunset at a stationary site were assumed to be arrival and departure dates for that site.

The individual wintering site was defined as that site where the bird spent most of its time within the period from October until February. This covered the longest non-migratory period during winter (Cramp 1988) and excluded equinoxes. We report the median, 25th, and 75th quantile for longitude and latitude of this site. Date of departure from the wintering site was defined as the day when the bird departed from the last site within 500 km north of the wintering site. A threshold of 500 km is about 2-fold to 3-fold the magnitude of the error range reported in latitude estimates from other light-level geolocator studies (Stutchbury et al. 2010; Fudickar et al. 2012; Lisovski et al. 2012) and a more conservative threshold than in Bächler et al. (2010). A bird that moved more than 500 km north without re-entering the 500-km radius of the wintering site had certainly left the wintering site and initiated spring migration (cf. Figure 1). Similarly, date of arrival at the breeding site was defined as the date at the first site closer than 500 km from its breeding site. We could not estimate departure date from the wintering site for 1 bird. Six geolocators stopped recording during migration. Their arrival dates at the breeding sites could not be estimated (details in Table S4 in Supplementary Appendix S1). Total migration distance was estimated as the great circle distance, that is, the shortest distance between 2 points on earth, between the individual's wintering site and breeding site. Migration speed was approximated as total migration distance divided by the time between departure from the wintering site and arrival at the breeding site.

Geolocators (manufactured by the Swiss Ornithological Institute [Switzerland], the British Antarctic Survey [UK], and Migration Technology [UK], details in Table S4 in Supplementary Appendix S1) were attached using an elastic leg loop harness. The total weight of devices did not exceed 5% of a bird's body mass as recommended by Kenward (2001), except for 4 individuals (maximum load 6.1% of body mass) (Arlt et al. 2013).

Wing shape in *leucorhoa* and *oenanthe northern wheatear*

Within a species, flying with more pointed wings increases airspeed and aspect ratio, but decreases drag, wing load, and flight maneuverability relative to flying with rounder wings (Lockwood et al. 1998; Pennycuick 2008). A pointed wing is indicated by a low wing pointedness index. This index is independent of wing length and body size (Lockwood et al. 1998). Here, we tested whether subspecies- and sex-specific differences in wing shape matched subspecies- and sex-specific differences in the degree of protandry. We considered data already published in Corman et al. (2014) and calculated wing pointedness index following Lockwood et al. (1998) for an additional 220 wheatears caught on Helgoland (54°11′N, 07°55′E, Germany) in spring 2014 (n_{total} = 560).

Fuel deposition rate in *leucorhoa* and *oenanthe northern wheatear*

To examine whether sex-specific differences in rates of fuel deposition during stopover might contribute to differences in migration speed and hence in the degree of protandry, we measured fueling rates under supplemental feeding conditions in both wheatear subspecies caught on migration. Wheatears are metabolically limited, and their food, that is, kelp fly larvae (Coelopidae), is regularly superabundant when kelp algae are washed onshore at coastal stopover sites (Dierschke et al. 2003). Fuel deposition rates are extremely difficult to estimate in free-flying birds (Schmaljohann et al. 2013) and are strongly influenced by environmental variation. Therefore, fuel deposition rate was determined in temporarily caged wheatears caught on Helgoland in spring 2010 (22 March–26 May) and 2014 (1 April–25 May). Wheatears responded very well to caging; on confinement, wheatears readily started eating and refueling. Birds were housed individually in common birdcages set up in a single indoor windowless room. All birds were released into the wild after 3 nights in captivity. Indoor temperature was constant at 20 °C throughout. During the 2010 season, the lights in the room were switched on at 08:00 h and off at 21:00 h CET, whereas in 2014, the room was lit from local sunrise (earliest: 05:18 h, latest: 06:56 h) to local sunset (earliest: 20:06 h, latest: 21:27 h). Food (mealworms *Tenebrio molitor*) and water were offered ad libitum during daytime from 08:00 h to 21:00 h in 2010 and from sunrise to 1 h before sunset in 2014. Wheatears were weighed to the nearest 0.1 g on a digital balance (WEDO Dig 2000, Germany) shortly after lights went on and before lights went off. Day of capture was treated as an acclimation phase, as birds were captured at different times during the day. Fuel deposition rate per day was estimated similarly to Lindström and Alerstam (1992) using lean body mass, but morning and not evening body mass was used to avoid the problem of undigested food influencing birds' body mass. Lean body mass was derived from wing length using a linear regression based on "lean" *oenanthe* and *leucorhoa* wheatears with fat scores <2 (Kaiser 1993) and muscle scores <2 (Bairlein 1994), that is, birds with little muscle and fat, captured on Helgoland in the years 1998–2002 and 2008:

$$\text{Lean body mass}_i(\text{g}) = 0.29\,\text{g} / \text{mm} \times \text{wing length}_i(\text{mm}) - 6.85\,\text{g} \quad (1)$$

(linear regression: n = 220, $F_{1,218}$ = 95.07, adj-R^2 = 0.30, P < 0.00001; after Schmaljohann and Naef-Daenzer 2011). We examined average individual daily fuel deposition rate, that is, the spontaneous reaction to food and water ad libitum, over a period of 2 days divided by the number of hours birds had access to food to correct for the different light regimes:

$$\begin{aligned}\text{Hourly fuel}&\\ \text{deposition rate}\,(\text{day}^{-1}\ \text{hour}^{-1}) = {}&(\text{body mass}_{i\,\text{3rd morning}}[\text{g}]\\ &-\text{body mass}_{i\,\text{1st morning}}[\text{g}])\\ &\times \text{lean body mass}_i^{-1}(\text{g})\\ &\times \Delta\text{time}^{-1}(\text{day}) \times \Delta\text{hours}_i^{-1}\end{aligned} \quad (2)$$

Variation of hourly fuel deposition rate was not significantly influenced by any of the 2-way or 3-way interactions with year (general linear model [GLM]: subspecies: −0.0018 ± 0.0024, t = −0.77, P = 0.44; sex: 0.0007 ± 0.0024, t = 0.30, P = 0.76; year: −0.0006 ± 0.00095, t = −0.64, P = 0.52; subspecies by sex: 0.0017 ± 0.0033, t = 0.5, P = 0.62; subspecies by year: 0.00007 ± 0.0014, t = 0.05, P = 0.96; sex by year: 0.00076 ± 0.0014, t = 0.5, P = 0.59; subspecies by sex and year: 0.0025 ± 0.0019, t = 1.3, P = 0.19; n = 258, reference category for subspecies is *oenanthe* wheatear and for sex is male). Therefore, data from both years were pooled.

Modeling the effect of fuel deposition rate on protandry in *leucorhoa* and *oenanthe northern wheatear*

If the sex differences in fueling rates contribute to observed protandry, we predict that sex differences in fueling rates should match the degree of protandry at specific stopover sites. To evaluate this prediction, we modeled the effect of a range of fuel deposition rates on total duration of migration. We assumed for simplicity a lean wheatear of 20 g with a migration distance of 4410 km (great circle distance between mean of estimated wintering sites in western Africa [15.6°N, 3.9°W] and Helgoland [54.2°N, 7.9°E]), an airspeed of 13 m/s (Bruderer and Boldt 2001), and no wind influence. Initial fuel load was set to 0.5 at the initiation of spring migration in Africa so that birds had a sufficiently high fuel load for crossing the Sahara. Body mass loss during the flight was defined as 1% of the actual body mass per hour (Schmaljohann, Fox, et al. 2012). Minimum fuel load for a nocturnal flight was arbitrarily set to 0.05 (cf. Delingat et al. 2006). If fuel load was lower than this threshold, the model bird performed a stopover until a threshold fuel load was reached. We let fuel load vary from 0.1 to 1.0 to see whether a threshold fuel load would influence the model outcome. For convenience, we chose a constant diurnal schedule and assumed that the model bird migrates the entire night and feeds the entire day, ignoring any search and settling costs (Schmaljohann, Fox, et al. 2012). That is, on each date, the model bird migrates for 10 h and feeds for 14 h (R-code in Supplementary Appendix S2).

Data analysis

All data were analyzed using the statistical software R 3.1.2 (R Core Team 2014).

For arrival dates of both subspecies of wheatears at stopover sites, models with date as a response variable were fitted using a normal error distribution. Linear mixed-effect models (GLMMs) were run with the R package "lme4" (Bates et al. 2015). Standard diagnostic plots showed that the model assumptions were not violated. For assessing the effect of subspecies, sex, and their 2-way interaction on arrival date at stopover sites, we allowed random intercepts per year and site and corresponding random slopes for each subspecies:

$$\begin{aligned}\text{Arrival date} = {}&\text{subspecies} + \text{sex} + (\text{subspecies} \times \text{sex})\\ &+ (1 + \text{subspecies} \mid \text{year}) + (1 + \text{subspecies} \mid \text{site})\end{aligned} \quad (3)$$

The effect of age (2 cy or older birds) on arrival date at stopover sites could only be modeled for males, as females cannot be reliable aged. Year and site were considered as random effects, and random slopes per subspecies were allowed:

$$\begin{aligned}\text{Arrival date} = {}&\text{subspecies} + \text{age} + (\text{subspecies} \times \text{age})\\ &+ (1 + \text{subspecies} \mid \text{year}) + (1 + \text{subspecies} \mid \text{site})\end{aligned} \quad (4)$$

We used the function "interactionMeans" from the R package "phia" (De Rosario-Martinez 2013) to visualize 2-way interactions and to estimate the adjusted means of the given factors of our linear mixed-effect models.

For analyzing arrival dates of *oenanthe* wheatears at their breeding sites using geolocator data, we considered sex, latitude of the breeding site, and their 2-way interaction because the degree of protandry might change with migration distance. We allowed random intercepts per year and per breeding site in a linear mixed-effect model:

$$\begin{aligned}\text{Arrival date} = {}&\text{sex} + \text{latitude of breeding site}\\ &+ (\text{sex} \times \text{latitude of breeding site})\\ &+ (1 \mid \text{year}) + (1 \mid \text{breeding site})\end{aligned} \quad (5)$$

As arrival date was right skewed and the residuals of the corresponding model were not normally distributed, we transformed the dependent variable, arrival date, by taking its inverse. The diagnostic plots of this linear mixed-effect model did not show violation of the model assumptions. The same transformation of the dependent variable was applied when modeling the initiation of spring migration and migration speed. In these models, sex was included as a fixed effect, and year and breeding site were allowed to have random intercepts:

$$\text{Dependent variable}_i = \text{sex} + (1 \mid \text{year}) + (1 \mid \text{breeding site}) \quad (6)$$

No transformation was required with longitude and latitude of wintering sites, migration distance, and duration of migration as dependent variables with the same fixed and random effects.

The spatial and temporal organization of bird migration gained from light-level geolocation data should be treated cautiously especially if movements occur in spring or autumn (Fudickar et al. 2012; Lisovski et al. 2012). This should be born in mind when interpreting results of models for arrival at the breeding sites, initiation of spring migration, and their derivatives should be treated cautiously.

Parameter estimates derived from linear models are given with SE; estimated means are given with standard deviation. For low sample sizes (n < 10), we give median and range (minimum–maximum).

RESULTS

Protandry at stopover in *leucorhoa* and *oenanthe* northern wheatear

Capture dates of wheatears at stopover sites were significantly affected by sex and the 2-way interaction between subspecies and sex, with a clear demonstration of protandry (Table 2). The degree of protandry was significantly higher in *leucorhoa* (−5.9 days) than in *oenanthe* wheatears (−2.3 days; Table 2, Figures 2 and 3a). In both subspecies, older males arrived significantly earlier at the stopover sites than 2 cy males. This effect was significantly stronger in *leucorhoa* (−4.3 days before 2 cy males) than in *oenanthe* wheatears (−1.1 days before 2 cy males; Table 3, Figures 2 and 3b). This age effect contributed significantly to the high degree of protandry in *leucorhoa* wheatears (Figures 2 and 3b).

Protandry at breeding areas in *oenanthe* northern wheatear

Oenanthe wheatears carrying a light-level geolocator were recaptured at the breeding site on average 30 ± 25 days (n = 25) after their arrival as estimated by light-level geolocation (details in Table S4 in Supplementary Appendix S1). Based on light-level geolocator data, male *oenanthe* wheatears arrived at breeding sites earlier than females (Table 4). The significant interaction between sex and latitude of the breeding site indicated that the degree of protandry decreased with increasing breeding latitude.

Spatiotemporal patterns during winter and migration in *oenanthe* northern wheatear

Location of wintering sites

In *oenanthe* wheatears, locations of wintering sites were slightly more to the west (3.3° ± 1.6°) in males compared with females (Table 5, Figure 1). A difference of 3.3° in longitude corresponded to a distance of 350 km at the average latitude (15.5°N ± 4.1°N) of wintering sites. We did not find latitudinal sex segregation (Table 5; Figure 1), nor did migration distance differ between sexes (Table 5).

Table 2

Results of a linear mixed-effect model investigating the effect of subspecies and sex on arrival date at stopover sites in Europe (Figure 1)

Fixed effects	Estimate ± SE	df	t	Significance
Subspecies	−4.3 ± 3.7	9	−1.17	$P = 0.27$
Sex	−5.9 ± 0.5	6248	−12.9	$P < 0.0001$
Subspecies × sex	3.6 ± 0.6	6261	5.9	$P < 0.0001$

We allowed random intercepts per year and site and corresponding random slopes for each subspecies. Estimated parameter values ± SE, df, and the corresponding t and P values are given for the fixed effects. The reference category for subspecies is *oenanthe* northern wheatear, and the reference category for sex is male.

Initiation of spring migration

In *oenanthe* wheatears, initiation of spring migration was significantly earlier in males than in females (M: 8 March ± 16 days, n = 14; F: 19 March ± 19 days, n = 16; Table 5). Initiation of spring migration was a good predictor of arrival date at breeding areas (linear regression, estimates: 0.636 ± 0.17, t = 3.8, P = 0.001, whole model: $F_{1,23}$ = 14.2, R^2 = 0.38, P = 0.001).

Speed and duration of migration

In *oenanthe* wheatears, the total duration of migration did not differ between males and females (Table 5). We found no sex differences in average migration speeds (M: 156 ± 62 km/day, n = 13; F: 118 ± 59 km/day, n = 12; Table 5).

Wing shape in *leucorhoa* and *oenanthe northern wheatear*

Leucorhoa wheatears had more pointed wings (i.e., a lower wing pointedness index) than *oenanthe* wheatears, and males had more pointed wings than females (GLM: *oenanthe*: 0.117 ± 0.013, t = 8.9, P < 0.0001; males: −0.041 ± 0.014, t = 2.98, P = 0.0030; 2-way interaction: −0.024 ± 0.019, t = −1.26, P = 0.21; whole model: $F_{4,556}$ = 43.6, R^2 = 0.19, P < 0.0001). In *leucorhoa* wheatears, the wing pointedness in males was significantly higher than in females (t-test: t = −3.14, degrees of freedom [df] = 251, P = 0.0019; M: 0.07 ± 0.09; F: 0.11 ± 0.11). This was not the case in *oenanthe* wheatears (t-test: t = −1.29, df = 231, P = 0.20).

Fuel deposition in *leucorhoa* and *oenanthe* northern wheatear

The hourly fuel deposition rate depended on the subspecies and sex (GLM: 2-way interaction: 0.0025 ± 0.001/h, t = −2.71, P = 0.007; whole model: $F_{3,254}$ = 15.3, R^2 = 0.15, P < 0.00001). Males had higher hourly fuel deposition rates in *leucorhoa* wheatears (t-test: t = −2.5, df = 81, P = 0.014; M: 0.0060 ± 0.0048/h, F: 0.0040 ± 0.0037/h) but not in *oenanthe* wheatears (t-test: t = 0.8, df = 132, P = 0.40). In males only, hourly fuel deposition rates was lower in *oenanthe* than in *leucorhoa* wheatears (GLM: *oenanthe:* −0.004 ± 0.0008/h, t = −5.1, P < 0.00001). In males, fuel deposition rate did not depend on age (P = 0.7) or the age by subspecies interaction (P = 0.9).

Our model of the effect of fuel deposition rate on total duration of migration demonstrated that with an increase in fuel deposition rate, total duration of migration decreases (Figure 4). Considering this model and sex-specific fuel deposition rates in *leucorhoa* wheatears (M: 0.006/h, F = 0.004/h), and a 14-h flight, males would precede females at arrival by 7.5 days (Figure 4). This degree of protandry was similar in magnitude to the estimated degree of protandry at stopover (Figures 2 and 3a). *Oenanthe* sexes did not significantly differ in their fuel deposition rates, and the predicted duration of migration greatly overlapped between the sexes. Different departure fuel loads had minimal effect on the total duration of migration (Figure 4).

DISCUSSION

Our light-level geolocation data show that in *oenanthe* wheatears, males departed about 14 days earlier from the wintering sites than females (Tables 1 and 5). Early initiation of spring migration by male *oenanthe* wheatears is consistent with the observation of

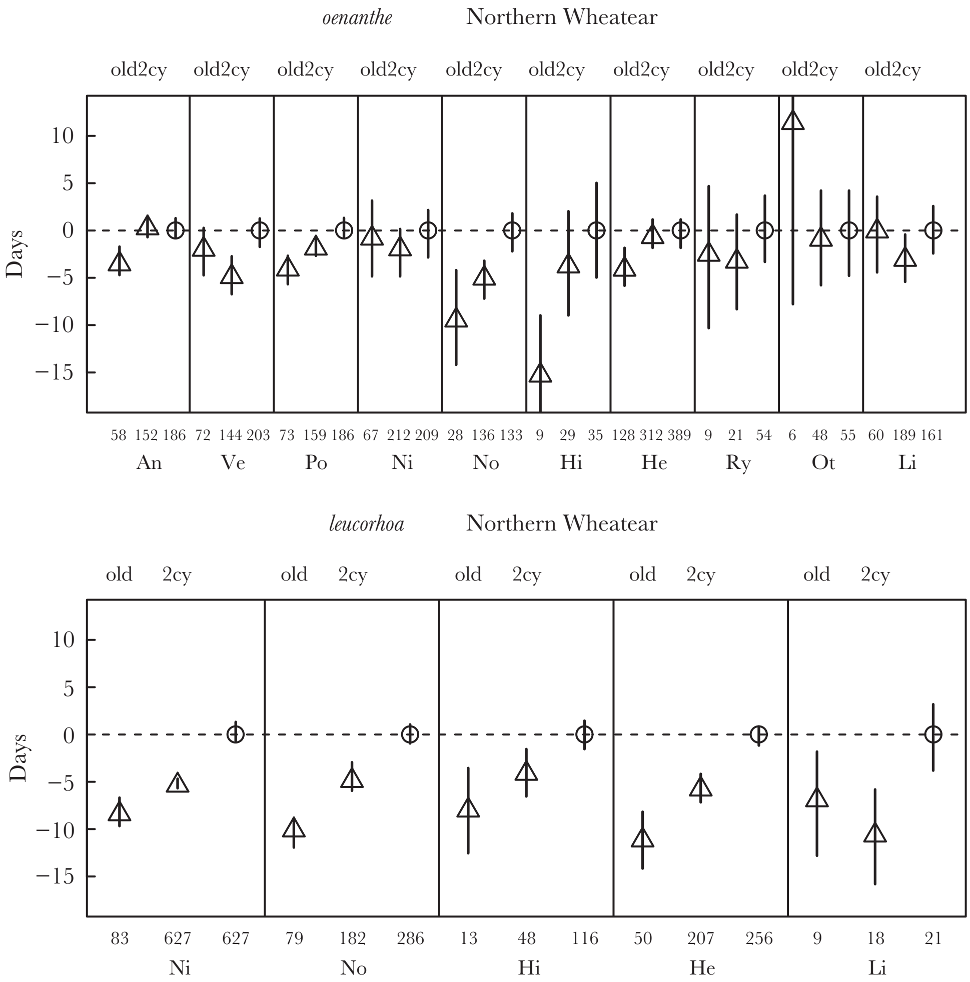

Figure 2

Arrival date at stopover sites (with 95% confidence interval) of old and 2 cy male northern wheatears relative to arrival date of female northern wheatears (set to 0). Males are indicated by triangles and females by circles. The upper panel shows data for *oenanthe* and the lower panel shows data for *leucorhoa* northern wheatears. Sample sizes are given below the boxes. Consider that sample size is low ($n < 10$) for some groups. Site abbreviations: An, Anacapri; Ve, Ventotene; Po, Portovenere; Ni, Nieuwpoort; No, Norfolk; Hi, Hilbre; He, Helgoland; Ry, Rybachy; Ot, Ottenby; and Li, Lista; for location of sites see Figure 1 (details in Table S1 in Supplementary Appendix S1).

protandry at stopover sites (−2.3 days). More generally, departure timing from wintering sites seems to be a good predictor for the arrival date at breeding sites, as in our *oenanthe* wheatears and other songbirds (Stanley et al. 2012; Tøttrup et al. 2012; Jahn et al. 2013). We lacked light-level geolocation data for *leucorhoa* wheatears. Thus, it remains unknown whether sex-specific differences in the onset of spring migration underlie protandry at stopover sites (−5.9 days) in *leucorhoa* wheatears. In common garden experiments, however, initiation of nocturnal migratory restlessness in spring was considerably earlier in males than in females both in *oenanthe* (36 days, $n_{\mathrm{M}} = 9$, $n_{\mathrm{F}} = 4$) and *leucorhoa* (16 days, $n_{\mathrm{M}} = 4$, $n_{\mathrm{F}} = 9$; $P = 0.002$). This indicates a sex-specific difference in the circannual rhythm that is consistent in both subspecies (Maggini and Bairlein 2012). If this were true under free-flying conditions, the endogenously controlled sex-specific start of spring migration would provide the basis for protandry in wheatears, in general. Sex-specific departure timing is not unique to wheatears. A sex difference in departure timing of similar magnitude was shown for western kingbirds (*Tyrannus verticalis*, 10.5 days), also based on light-level geolocator data (Jahn et al. 2013). Given the complementary evidence, sex-specific differences in the initiation of spring migration appear to be an important contributor to protandry in songbird migration.

In *oenanthe* wheatears, males did not winter closer to the breeding sites than females (Figure 1). This lack of latitudinal sex segregation has also been shown in barn swallows (*Hirundo rustica*) using geolocator data (Liechti et al. 2014). In Palearctic-African songbird migrants, the general assumption, based on single-snapshot records of individuals from various populations, is that there is no apparent latitudinal sexual segregation of wintering sites (Berthold 2001; Newton 2008). Hence, sex-specific wintering sites and migration distances, so far, seem unlikely to account for the general pattern of protandry in Palearctic-African songbird migrants, including wheatears (Table 5).

We found no indication that the total duration of migration or migration speed was sex specific in *oenanthe* wheatears based on geolocator data (Table 5). Similarly, our sex-specific estimates of wing shape and fuel deposition rates suggest that male and female *oenanthe* wheatears might not differ much in their migration speed. However, in *leucorhoa* wheatears, we observed sex differences in wing shape and fuel deposition rates, with males

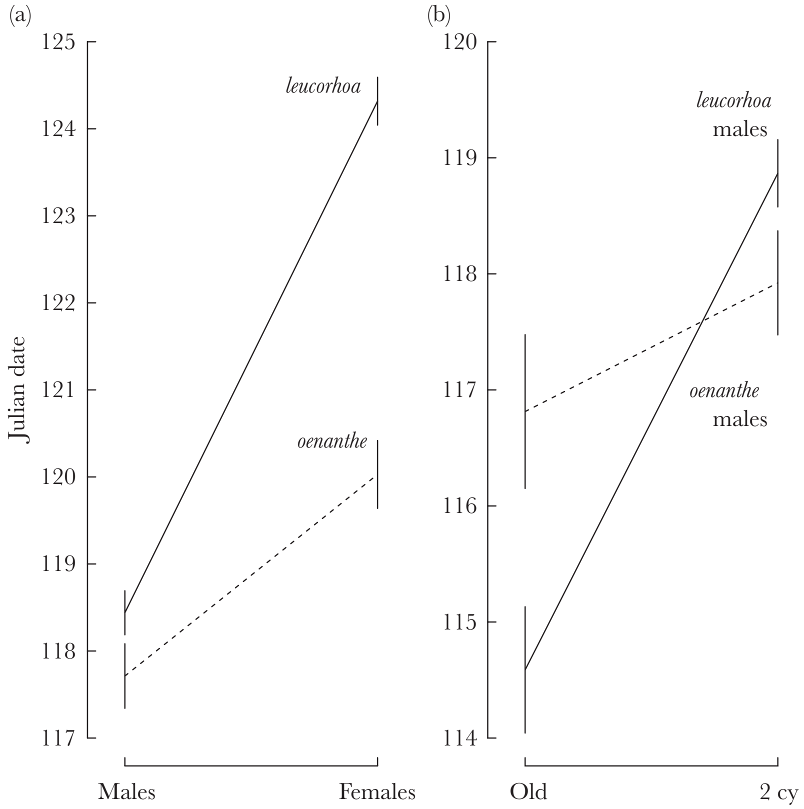

Figure 3
Arrival date (as Julian date) at stopover sites for (a) northern wheatears subspecies by sex and (b) male Northern Wheatears by age class. In (a), the significant interaction between subspecies and sex on arrival date indicates that male *leucorhoa* northern wheatears arrived significantly earlier than females (solid line) in comparison with the *oenanthe* northern wheatears (dashed line). In (b), the significant interaction between subspecies and age on arrival date indicates that old males contributed to the high degree of protandry in *leucorhoa* Northern Wheatears (solid line) more so than in *oenanthe* Northern Wheatears. Bars show SE.

Table 3
Results of a linear mixed-effect model investigating the effect of subspecies and age (old vs. 2 cy) on the arrival date of male northern wheatears at stopover sites in Europe (Figure 1)

Fixed effects	Estimate ± SE	df	t	Significance
Subspecies	-0.9 ± 4.0	9	−0.24	$P = 0.82$
Age	-4.3 ± 0.9	2193	−5.0	$P < 0.0001$
Subspecies × age	3.2 ± 1.1	2690	3.0	$P = 0.0026$

We allowed random intercepts per year and site and corresponding random slopes for each subspecies. Estimated parameter values ± SE, df, and the corresponding t and P values are given for the fixed effects. The reference category for subspecies is *oenanthe* northern wheatear, and the reference category for age is male older than 2 cy.

having more pointed wings and higher fuel deposition rates. In addition, our model showed that higher fuel deposition rates yield higher speeds of migration in males than in females, resulting in more protandry in *leucorhoa* wheatears. The predicted degree of protandry at stopover was fairly close to that observed in the field (observed: −6 days, predicted: about −8 days, Figure 4). We conclude that sex-specific migration speed is an important proximate cause of protandry in *leucorhoa* wheatears. Similarly, faster refueling in males than females has been found in some Nearctic warblers (Seewagen et al. 2013).

Table 4
Results of a linear mixed-effect model investigating the effect of sex, latitude of wintering site, and their 2-way interaction on arrival date, as estimated with light-level geolocation data for *oenanthe* northern wheatears, at several breeding sites in Europe (Figure 1)

Fixed effects	Estimate ± SE	df	t	Significance
Sex	0.015 ± 0.0036	2.4	4.2	$P = 0.038$
Latitude (°N)	$9.5 \times 10^{-5} \pm 4.6 \times 10^{-5}$	1.1	2.0	$P = 0.265$
Sex × latitude	$-2.5 \times 10^{-4} \pm 6.5 \times 10^{-5}$	3.0	−3.8	$P = 0.033$

We allowed random intercepts per year and breeding site. Estimated parameter values ± SE, df, the corresponding t and P values are given for the fixed effects. The dependent variable was transformed by taking its inverse. Reference category for sex is male.

Protandry at stopover sites was more pronounced in *leucorhoa* (−5.9 days), which is similar to the average degree found in birds (Morbey et al. 2012), than in *oenanthe* wheatears (−2.3 days; Figure 3a). The different selection pressures experienced during their contrasting migratory challenges might have optimized *leucorhoa* wheatear's migration in terms of low flight costs and a high rate of refueling (Corman et al. 2014) resulting in higher migration speed (200 km/day; Bairlein et al. 2012) than in *oenanthe* wheatears (150 km/day in our study). Our results show that migration speed is also sex specific, but only in *leucorhoa* wheatears. In contrast to

Table 5

Effect of sex (± SE) on 6 variables extracted from light-level geolocators in *oenanthe* northern wheatears

Dependent variable	Sex	df	t	Significance
Longitude of wintering site (°E)	-3.3 ± 1.6	29	−2.13	$P = 0.042$
Latitude of wintering site (°N)	-0.6 ± 1.5	17.5	−0.38	$P = 0.71$
Migration distance (km)	225 ± 204	27.5	1.11	$P = 0.28$
Initiation of spring migration (1/day)	0.003 ± 0.001	27.2	2.29	$P = 0.03$
Total duration of migration (days)	0.5 ± 6.2	22.6	0.08	$P = 0.94$
Migration speed (1/km/day)	$-8.8 \times 10^{-5} \pm 1.3 \times 10^{-3}$	21.4	−0.07	$P = 0.95$

In each linear mixed-effect model, sex was the independent variable (fixed factor), and year and breeding site were allowed to have random intercepts (random factors). Estimated parameter values ± SE, df, the corresponding t and P values are given for the effect of sex. Initiation of spring migration and migration speed were transformed by taking their inverse. Back-transformed estimate for initiation of spring migration was −14 days and for migration speed was −1.2 km/day.

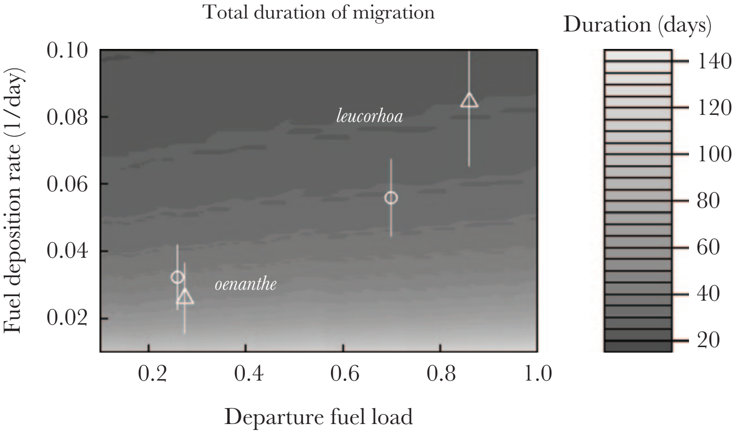

Figure 4

The effect of different fuel deposition rates (fdr) and departure fuel loads (dfl) on total duration of migration for a model northern wheatear migrating 4410 km from African wintering sites to Helgoland based on a simple migration model (see R-code in Supplementary Appendix S2). The total duration of migration is indicated in different shades of gray (scale on the right side), which go in increments of 5 days. Males are indicated by triangles and females by circles. Based on species-specific fdr, male *leucorhoa* northern wheatears are predicted to precede *leucorhoa* females by about 8 days, whereas there is no significant sex difference in the arrival time of *oenanthe* wheatears. Assumed fdr as estimated in both subspecies on Helgoland in this study (see Results for details): male *oenanthe*: fdr = 0.026/day, dfl = 0.26; female *oenanthe*: fdr = 0.032/day, dfl = 0.26; male *leucorhoa*: fdr = 0.085/day, dfl = 0.86; female *leucorhoa*: fdr = 0.055/day, dfl = 0.70. Note that male and female *oenanthe* northern wheatears do not differ significantly in their fdr and have the same dfl. They are shown next to each in order to see the corresponding 95% confidence interval.

oenanthe wheatears, flight costs were lower and rates of refueling were higher in male *leucorhoa* wheatears than in females. Additionally, *leucorhoa* males seem to minimize time spent on migration, whereas *leucorhoa* females optimize energy costs of migration resulting in lower total speeds of migration in females (Dierschke et al. 2005). Thus, sex-specific migration speed appears to contribute to protandry in *leucorhoa* but not in *oenanthe* wheatears. Perhaps *leucorhoa* males need a mechanism to catch up if wind conditions often delay crossing of the Atlantic Ocean, whereas for *oenanthe*, conditions may be more permissive for crossing the Mediterranean Sea.

Furthermore, *leucorhoa* males displayed a stronger age effect, whereby older *leucorhoa* individuals arrived consistently earlier than 2 cy individuals, than in *oenanthe* males (Figure 3b). The age effect contributed to the higher degree of protandry in *leucorhoa* than in *oenanthe* wheatears. Mechanistically, this advancement of arrival time with age could be attributable to learning (Sergio et al. 2014), whereby individuals improve their migration performance with age (Hake et al. 2003). From an evolutionary point of view, it may be that higher-quality, older males can better afford the extrinsic costs of early arrival. An alternative mechanism is selective disappearance, that is, selection acting on the timing of migration reduces phenotypic and genetic variances over life-history stages (van de Pol and Verhulst 2006).

Regardless of the proximate mechanisms involved, the fitness benefit of being earlier than competitors and females at breeding sites is presumably larger for *leucorhoa* wheatears than for the nominate wheatears. Currently, 7 ultimate causes of protandry are discussed (Morbey and Ydenberg 2001). Theoretical work highlights the importance of the mate opportunity hypothesis as the main ultimate cause of protandry in birds (Kokko et al. 2006). Therefore, we discuss here only this hypothesis in light of the subspecies differences in protandry. In the mate opportunity hypothesis, early males are assumed to maximize their mating opportunities. Due to competition for mating opportunities among males, the degree of protandry is predicted to increase with a more male-biased sex ratio, a higher rate of extrapair paternity, and when early arriving females are highly fecund (Morbey and Ydenberg 2001; Kokko et al. 2006). There is insufficient data on extrapair paternity (Currie et al. 1998; Kudernatsch et al. 2010) and sex ratios (Currie et al. 2000; Arlt and Pärt 2008) to assess their occurrence in wheatears, especially for *leucorhoa* wheatears. Field studies have, however, shown that early female wheatears have high fecundity, and early males have higher mating opportunities and more offspring than late males (Currie et al. 2000; Buchmann 2001; Pärt 2001; Öberg et al. 2014). This provides prerequisites for the mate opportunity hypothesis in our model species. Additional support for mate opportunity hypothesis comes from our observation that protandry was more pronounced in *leucorhoa* than in *oenanthe* wheatears. The advantages of early breeding might be stronger in *leucorhoa* wheatears, because they have a much shorter breeding season, only 1 brood, and lay no replacement clutches in comparison with *oenanthe* wheatears (Snow 1953; Cramp 1988; Conder 1989; Currie et al. 2000; Buchmann 2001). Hence, mating opportunities for late-arriving *leucorhoa* males are relatively fewer than for late-arriving *oenanthe* males. This might favor a higher intensity of sexual selection in *leucorhoa* wheatears.

Our results show that subspecies can differ in their degree of protandry during migration and in the underlying mechanisms of protandry. Furthermore, our data highlight the importance of the advancement in male arrival date with age as a potential contributor to protandry. Understanding the biological significance of each proximate cause on protandry is important to evaluate how changes in the environment may affect the temporal organization during the annual cycle (phenology) of migrants and to predict whether phenological shifts caused by climate change might affect species and sexes differentially (Hedlund et al. 2014). This may shed light on why and how strong adjustment to climate change is time constrained in migratory birds (Both and Visser 2001).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

FUNDING

H.S. is financed by the Deutsche Forschungsgemeinschaft (SCHM 2647/1-1). This work was partly supported by a Deutsche Forschungsgemeinschaft (BA 816/15-4) grant to F.B. D.A. and T.P. were financed by the Swedish Research Council VR. The geolocator development was partly financially supported by the Swiss Federal Office for Environment (UTF 254.08.08). S.Å. is financed by a research grant from the Swedish Research Council (621-2007-5930) and a Linnaeus grant (349-2007-8690) to CAnMove financed by the Swedish Research Council and Lund University. N.C. acknowledges research grant 1.37.149.2014 from St. Petersburg State University and support from the Zoological Institute RAS (registered research project no. 01201351182).

We thank many volunteers for their continuous support during field work. H. v.O. thanks PWN Watercompany and the National Forestry Service (Staatsbosbeheer) for access to their areas and continuous support. We thank J.E. Røer for providing wheatear data from Lista Bird Observatory. This is contribution no. 286 from Ottenby bird observatory. We thank 2 anonymous reviewers for their comments that significantly improved the manuscript.

Authors' contribution: H.S. and C.M. contributed equally to this work; H.S. designed research; H.S., C.M., and C.E. analyzed data; F.B. initiated the wheatear network; H.S., C.M., D.A., H.v.O., S.Å., F.B., M.B., F.L., U.O., and T.P. provided light-level geolocation data; H.S., S.Å., N.C., R.D., J.E., M.H., A.L., J.M., F.S., and C.E. provided ringing data; H.S., C.M., D.A., H.v.O., Y.E.M., and C.E. wrote the paper; all authors revised and contributed to the article.

Conflict of interests: We have no competing interests.

Ethical statement: Wheatears were tagged with light-level geolocators under license of the corresponding federal Ministries (Swiss bird banding licenses 3296, 3671, and 3672; under license of the Ministry for Agriculture, the Environment and Rural Areas, Rhineland Palatinate, Germany; under license of the Dutch Ministry of Economic Affairs; permission from the Swedish Bird Ringing Centre permits no. 509, and approval by the regional Swedish ethical committees permit Uppsala djurförsöksetiska nämnd Dnr C117/8 and Malmö/Lund djurförsöksetiska nämnd Dnr 112/09).

Data accessibility: All datasets supporting this article have been uploaded as part of the Supporting Information.

Handling editor: Marc Thery

REFERENCES

Alerstam T, Lindström Å. 1990. Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner E, editor. Bird migration: physiology and ecophysiology. Berlin (Germany): Springer-Verlag.

Arlt D, Low M, Pärt T. 2013. Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. PLoS One. 8:e82316.

Arlt D, Olsson P, Fox JW, Low M, Pärt T. 2015. Prolonged stopover duration characterises migration strategy and constraints of a long-distance migrant songbird. Anim Migr. 2:47–62.

Arlt D, Pärt T. 2008. Sex-biased dispersal: a result of a sex difference in breeding site availability. Am Nat. 171:844–850.

Bächler E, Hahn S, Schaub M, Arlettaz R, Jenni L, Fox JW, Afanasyev V, Liechti F. 2010. Year-round tracking of small trans-Saharan migrants using light-level geolocators. PLoS One. 5:e9566.

Bairlein F. 1994. Manual of field methods: European-African songbird migration network. Wilhelmshaven (Germany): Institut für Vogelforschung.

Bairlein F, Norris DR, Nagel R, Bulte M, Voigt CC, Fox JW, Hussell DJ, Schmaljohann H. 2012. Cross-hemisphere migration of a 25 g songbird. Biol Lett. 8:505–507.

Bates D, Maechler M, Bolker BM, Walker S. Forthcoming 2015. Fitting linear mixed-effects models using lme4. J Stat Software. Available from: http://arxiv.org/abs/1406.5823.

Berthold P. 2001. Bird migration: a general survey. 2nd ed. Oxford: Oxford University Press.

Both C, Visser ME. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature. 411:296–298.

Bruderer B, Boldt A. 2001. Flight characteristics of birds: I. radar measurements of speeds. Ibis. 143:178–204.

Buchmann M. 2001. Die Brutbiologie des Steinschmatzers (*Oenanthe oenanthe*) auf intensiv genutzten Flächen in Rheinland-Pfalz. Vogelwarte. 41:1–17.

Conder P. 1989. The wheatear. London: Christopher Helm.

Coppack T, Pulido F. 2009. Proximate control and adaptive potential of protandrous migration in birds. Integr Comp Biol. 49:493–506.

Corman AM, Bairlein F, Schmaljohann H. 2014. The nature of the migration route shapes physiological traits and aerodynamic properties in a migratory songbird. Behav Ecol Sociobiol. 68:391–402.

Cramp S. 1988. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic. Vol. 5. Oxford: Oxford University Press.

Currie DR, Burke T, Whitney RL, Thompson DBA. 1998. Male and female behaviour and extra-pair paternity in the wheatear. Anim Behav. 55:689–703.

Currie D, Thompson DBA, Burke T. 2000. Patterns of territory settlement and consequences for breeding success in the wheatear *Oenanthe oenanthe*. Ibis. 142:389–398.

Delingat J, Dierschke V, Schmaljohann H, Mendel B, Bairlein F. 2006. Optimal migration strategy by daily stopovers in a long distance migrating passerine: the northern wheatear (*Oenanthe oenanthe*). Ardea. 94:593–605.

Dierschke V, Delingat J, Schmaljohann H. 2003. Time allocation in migrating northern wheatears (*Oenanthe oenanthe*) during stopover: is refuelling limited by food availability or metabolically? J Ornithol. 144:33–44.

Dierschke V, Mendel B, Schmaljohann H. 2005. Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females? Behav Ecol Sociobiol. 57:470–480.

Ekstrom PA. 2004. An advance in geolocation by light. Mem Nat Inst Polar Res. 58:210–226.

Fudickar AM, Wikelski M, Partecke J. 2012. Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. Method Ecol Evol. 3:47–52.

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

Hake M, Kjellen N, Alerstam T. 2003. Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. Oikos. 103:385–396.

Hedenström A, Pettersson J. 1986. Differences in fat deposits and wing pointedness between male and female willow warblers caught on spring migration at Ottenby, SE Sweden. Ornis Scand. 17:182–185.

Hedlund JSU, Jakobsson S, Kullberg C, Fransson T. 2014. Long-term phenological shifts and intra-specific differences in migratory change in the willow warbler *Phylloscopus trochilus*. J Avian Biol. 46:97–106.

Jahn AE, Cuteo VR, Fox JW, Husak MS, Kim DH, Landoll DV, Ledezma JP, LePage HK, Levey DJ, Murphy MT, et al. 2013. Migration timing and wintering areas of three species of flycatchers (*Tyrannus*) breeding in the Great Plains of North America. Auk. 130:247–257.

Kaiser A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. J Field Ornithol. 64:246–255.

Kenward RE. 2001. A manual for wildlife radio tagging. London: Academic Press.

Kokko H. 1999. Competition for early arrival in birds. J Anim Ecol. 68:940–950.

Kokko H, Gunnarsson TG, Morrell LJ, Gill JA. 2006. Why do female migratory birds arrive later than males? J Anim Ecol. 75:1293–1303.

Kudernatsch D, Buchmann M, Fiedler W, Segelbacher G. 2010. Extrapair paternity in a German population of the northern wheatear (*Oenanthe oenanthe*). J Ornithol. 151:491–498.

Liechti F, Scandolara C, Rubolini D, Ambrosini R, Korner-Nievergelt F, Hahn S, Lardelli R, Romano M, Caprioli M, Romano A, et al. 2014. Timing of migration and residence areas during the non-breeding period of barn swallows *Hirundo rustica* in relation to sex and population. J Avian Biol. 45:1–12.

Lindström A, Alerstam T. 1992. Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. Am Nat. 140:477–491.

Lisovski S, Hahn S. 2012. GeoLight—processing and analysing light-based geolocator data in R. Meth Ecol Evol. 3:1055–1059.

Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW, Hahn S. 2012. Geolocation by light: accuracy and precision affected by environmental factors. Meth Ecol Evol. 3:603–612.

Lockwood R, Swaddle JP, Rayner JMV. 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. J Avian Biol. 29:273–292.

Maggini I, Bairlein F. 2012. Innate sex differences in the timing of spring migration in a songbird. PLoS One. 7:e31271.

Marra PP, Hobson KA, Holmes RT. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science. 282:1884–1886.

Marra PP, Holmes RT. 2001. Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. Auk. 118:92–104.

Møller AP. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. Behav Ecol Sociobiol. 35:115–122.

Morbey YE, Coppack TC, Pulido F. 2012. Adaptive hypotheses for protandry in arrival to breeding areas: a review of models and empirical tests. J Ornithol. S153:205–215.

Morbey YE, Ydenberg RC. 2001. Protandrous arrival timing to breeding areas: a review. Ecol Lett. 4:663–673.

Newton I. 2008. The migration ecology of birds. London: Academic Press.

Nilsson C, Klaassen RH, Alerstam T. 2013. Differences in speed and duration of bird migration between spring and autumn. Am Nat. 181:837–845.

Öberg M, Pärt T, Arlt D, Laugen AT, Low M. 2014. Decomposing the seasonal fitness decline. Oecologia. 174:139–150.

Van Oosten HH, Versluijs R, Van Wijk R. 2014. Migration routes and wintering areas of two Dutch northern wheatears *Oenanthe oenanthe* in the Sahel. Limosa. 87:168–173.

Pärt T. 2001. The effects of territory quality on age-dependent reproductive performance in the northern wheatear, *Oenanthe oenanthe*. Anim Behav. 62:379–388.

Pennycuick CJ. 2008. Modelling the flying bird. Amsterdam (The Netherlands): Elsevier.

van de Pol M, Verhulst S. 2006. Age-dependent traits: a new statistical model to separate within- and between- individual effects. Am Nat. 167:766–773.

R Core Team. 2014. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: http://www.R-project.org/.

De Rosario-Martinez H. 2013. Phia: post-hoc interaction analysis. R package version 01-5. Vienna (Austria): R Foundation for Statistical Computing. Available from: http://www.R-project.org/.

Rubolini D, Spina F, Saino N. 2004. Protandry and sexual dimorphism in trans-Saharan migratory birds. Behav Ecol. 15:592–601.

Saino N, Rubolini D, Serra L, Caprioli M, Morganti M, Ambrosini R, Spina F. 2010. Sex-related variation in migration phenology in relation to sexual dimorphism: a test of competing hypotheses for the evolution of protandry. J Evol Biol. 23:2054–2065.

Saino N, Szép T, Romano M, Rubolini D, Spina F, Møller AP. 2004. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. Ecol Lett. 7:21–25.

Schmaljohann H, Buchmann M, Fox JW, Bairlein F. 2012. Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. Behav Ecol Sociobiol. 66:915–922.

Schmaljohann H, Fox JW, Bairlein F. 2012. Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. Anim Behav. 84:623–640.

Schmaljohann H, Korner-Nievergelt F, Naef-Daenzer B, Nagel R, Maggini I, Bulte M, Bairlein F. 2013. Stopover optimization in a long-distance migrant: the role of fuel load and nocturnal take-off time in Alaskan northern wheatears (*Oenanthe oenanthe*). Front Zool. 10:26.

Schmaljohann H, Naef-Daenzer B. 2011. Body condition and wind support initiate shift in migratory direction and timing of nocturnal departure in a free flying songbird. J Anim Ecol. 80:1115–1122.

Seewagen CL, Guglielmo CC, Morbey YE. 2013. Stopover refueling rate underlies protandry and seasonal variation in migration timing of songbirds. Behav Ecol. 24:634–642.

Sergio F, Tanferna A, De Stephanis R, Jiménez LL, Blas J, Tavecchia G, Preatoni D, Hiraldo F. 2014. Individual improvements and selective mortality shape lifelong migratory performance. Nature. 515:410–413.

Snow DW. 1953. The migration of the Greenland wheatear. Ibis. 95:376–378.

Stanley CQ, MacPherson M, Fraser KC, McKinnon EA, Stutchbury BJ. 2012. Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. PLoS One. 7:e40688.

Stutchbury BJM, Gow EA, Done T, MacPherson M, Fox JW, Afanasyev V. 2010. Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. Proc Biol Sci. 278:131–137.

Stutchbury BJ, Tarof SA, Done T, Gow E, Kramer PM, Tautin J, Fox JW, Afanasyev V. 2009. Tracking long-distance songbird migration by using geolocators. Science. 323:896.

Svensson L. 1992. Identification guide to European passerines. 4th ed. Stockholm (Sweden): British Trust for Ornithology.

Tøttrup AP, Klaassen RH, Strandberg R, Thorup K, Kristensen MW, Jørgensen PS, Fox J, Afanasyev V, Rahbek C, Alerstam T. 2012. The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. Proc Biol Sci. 279:1008–1016.

Tøttrup AP, Thorup K. 2008. Sex-differentiated migration patterns, protandry and phenology in north European songbird populations. J Ornithol. 149:161–167.