

Can wheatears weather the Atlantic? Modeling nonstop trans-Atlantic flights of a small migratory songbird

Authors: Bulte, Marc, McLaren, James D., Bairlein, Franz, Bouten, Willem, Schmaljohann, Heiko, et al.

Source: The Auk, 131(3) : 363-370

Published By: American Ornithological Society

URL: <https://doi.org/10.1642/AUK-13-233.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



RESEARCH ARTICLE

Can wheatears weather the Atlantic? Modeling nonstop trans-Atlantic flights of a small migratory songbird

Marc Bulte,^{1*} James D. McLaren,^{2*} Franz Bairlein,¹ Willem Bouten,² Heiko Schmaljohann,¹ and Judy Shamoun-Baranes²

¹ Institute of Avian Research, Wilhelmshaven, Germany

² Computational Geo Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands

* Corresponding authors: Marc Bulte, marc.bulte@ifv-vogelwarte.de; James D. McLaren, j.d.mclaren@uva.nl; these authors contributed equally to the manuscript

Received March 27, 2014; Accepted April 6, 2014; Published July 2, 2014

ABSTRACT

Oceans represent extreme ecological barriers for land birds. Yet the Northern Wheatear (*Oenanthe oenanthe leucorhoa*), a 25-g songbird, negotiates the North Atlantic Ocean twice yearly between Canadian natal and sub-Saharan wintering grounds. Each autumn, these migrants appear to have 2 options: (1) a detour via Greenland, Iceland, and/or Europe to reduce the extent of open-ocean flights or (2) an astonishing nonstop flight of 4,000–5,000 km without resting opportunities between eastern Canada and northwestern Africa. We assessed the feasibility and reliability of nonstop trans-Atlantic migration of Northern Wheatears from Canada to Africa using an individual-based model incorporating flight costs and autumnal wind data from 1979 to 2011. Prevalent wind conditions were supportive of nonstop migration, especially at high altitudes and when winds at departure were favorable. For modeled individuals with high fuel loads, flying at altitudes of ~3,000 m, successful nonstop trans-Atlantic flights reached Africa on 62% of departure days. On 24% of unsuccessful departure days, individuals could have first stopped in Europe before continuing to Africa. Durations of successful flights varied between 31 and 68 hr, with significantly shorter flights after mid-September. It remains unclear whether natural selection might favor nonstop ocean crossings by *O. o. leucorhoa* between North America and Africa, but we conclude that reliably supportive winds en route and potentially huge time savings render it a feasible migration strategy.

Keywords: ecological barrier, individual-based model, nonstop migration, North Atlantic Ocean, Northern Wheatear, songbird, wind

Oenanthe oenanthe leucorhoa peut-il résister à l'Atlantique? Modéliser les vols transatlantiques sans escale d'un petit oiseau chanteur migrateur

RÉSUMÉ

Les océans représentent des barrières écologiques extrêmes pour les oiseaux terrestres. Pourtant, *Oenanthe oenanthe leucorhoa*, un oiseau chanteur de 25 g, traverse l'océan Atlantique Nord deux fois par année entre son aire natale canadienne et son quartier d'hivernage subsaharien. Chaque automne, ces migrants semblent avoir 2 options: (1) un détour via le Groenland, l'Islande ou l'Europe pour réduire l'ampleur des vols au-dessus de l'océan ou (2) un étonnant vol sans escale de 4,000–5,000 km sans possibilité de se reposer entre l'est du Canada et le nord-ouest de l'Afrique. Nous avons évalué la faisabilité et la fiabilité de la migration transatlantique sans escale d'*O. o. leucorhoa* du Canada vers l'Afrique en utilisant un modèle basé sur l'individu qui incorpore les coûts du vol et des données de vent de 1979 à 2011. Les conditions de vent dominants favorisaient la migration sans escale, particulièrement à de hautes altitudes et lorsque les vents étaient favorables au moment du départ. Pour les individus modélisés ayant une charge calorique élevée et volant à des altitudes de ~3,000 m, les vols transatlantiques sans escale ont atteint l'Afrique lors de 62% des jours de départ. Lors de 24% des jours de départ non réussis, les individus ont possiblement arrêté en Europe avant de continuer vers l'Afrique. La durée des vols réussis a varié entre 31 et 68 h, avec des vols significativement plus courts après la mi-septembre. Il n'est pas clair si la sélection naturelle peut favoriser les traversées océaniques sans escale entre l'Amérique du Nord et l'Afrique par *O. o. leucorhoa*, mais nous concluons que les vents favorables fiables lors de la traversée et possiblement une grande économie de temps en font une stratégie de migration possible.

Mots-clés: barrière écologique, modèle basé sur l'individu, migration sans escale, océan Atlantique Nord, *Oenanthe oenanthe leucorhoa*, oiseau chanteur, vent

INTRODUCTION

Oceans represent ecological barriers to terrestrial birds because they impede range expansion and/or migratory movements (Alerstam 1990). Nonetheless, migrant land birds may cross such barriers to shorten migration distances or exploit beneficial winds (Alerstam 2001). Only one migrant land bird, the Northern Wheatear (*Oenanthe oenanthe leucorhoa*; hereafter “wheatear”), regularly negotiates the Atlantic Ocean to migrate between the New World and Africa (Bairlein et al. 2012). The 4,000–5,000 km barrier between its Nearctic breeding grounds (Godfrey 1986) and sub-Saharan wintering grounds in western Africa has led to many discussions regarding this subspecies’ migration routes. Given that wheatears are seen regularly on the west coast of Europe, even east of Britain, in spring and autumn (Dierschke et al. 2011, Corman et al. 2014), a detour via Europe to reduce the sea-barrier distance seems reasonable and was suggested by Williamson (1958) and Alerstam (2001). Supporting evidence is given by one Canadian wheatear recently tracked with a light-level geolocator crossing, most likely southern Greenland and continuing via Europe toward its African wintering area (Bairlein et al. 2012). However, regular observations of wheatears on isolated Atlantic islands off the shore of Africa (e.g., Hooker 1958, Clarke 1999) raise the exciting possibility that wheatears can take advantage of prevailing westerlies to cross the Atlantic Ocean nonstop to northwestern Africa. Indirect evidence of nonstop wheatear flights was found on Selvagem Grande, an island 350 km off the coast of Morocco. Early-fall arrivals of wheatears on the island were negatively correlated with the arrival of several species of trans-Saharan songbird (hereafter “passerine”) migrants from continental Europe (Thorup et al. 2006). Their asynchrony with Western Palearctic migration, and emaciated condition compared with the normally high fuel loads of migrating continental Northern Wheatears (*O. o. oenanthe*), suggested a possible nonstop flight across the North Atlantic Ocean (Thorup et al. 2006). Similar circumstantial evidence indicates that some Neotropical migrants, including Blackpoll Warblers (*Setophaga striata*), fly nonstop along the Western Atlantic Ocean to the Caribbean or South America (Nisbet et al. 1995, Baird 1999). These warblers were thought to be highly dependent on favorable wind conditions and high fuel loads as well (Baird 1999). Such extensive nonstop ocean crossings (of $\leq 11,000$ km) by terrestrial birds have otherwise been confirmed only for several wader species (see, e.g., Gill et al. 2009, Minton et al. 2011, Battley et al. 2012, Johnson et al. 2012).

According to flight range estimates based on departure fuel loads (DFLs; i.e. fuel mass in relation to lean body mass), wheatears with DFLs >1.3 could fly nonstop from

Greenland to western Africa (4,200 km) in still air (Delingat et al. 2008). Theoretically, tailwinds of $\sim 5 \text{ m s}^{-1}$ would reduce their DFL required to arrive nonstop down to 1.0. Wheatears are known to accumulate DFLs >1.0 during migration, when they have to cross large bodies of water (Dierschke et al. 2005, Schmaljohann and Naef-Daenzer 2011). Furthermore, they select favorable wind conditions before attempting barrier crossings in spring (Schmaljohann and Naef-Daenzer 2011). However, these studies did not consider crosswinds, varying wind conditions en route, or the effects of fuel loss on airspeed (cf. Pennycuik 2008). Hence, it remains unknown whether the wind systems over the North Atlantic Ocean are favorable and reliable enough to allow for an evolutionarily stable nonstop migration strategy.

We examined the feasibility and reliability of wind-assisted nonstop ocean crossings of wheatears using a dynamic individual-based model together with spatiotemporal wind data. Specifically, we assessed the effects of flight altitude, departure fuel load, and wind conditions on arrival success and flight duration. This is the first study of simulated migration incorporating inter- and intra-annual variation in wind conditions at multiple altitudes as well as variation in airspeed in relation to fuel load. We chose the Canadian population of wheatears because their hypothesized nonstop flight would be the longest known nonstop migration route among all passerines, and most likely impossible without consistent wind support (Delingat et al. 2008).

METHODS

To simulate nonstop migratory ocean crossings of wheatears from Canada to Africa given realistic wind conditions, we used a spatially explicit individual-based model (following McLaren et al. 2012) together with wind data at pressure levels of 925, 850, and 700 mb or approximately 800, 1,500, and 3,000 m above mean sea level, respectively. It seems that most open-ocean bird migration, including that by passerines, takes place between these altitudes (Richardson 1976, Williams and Williams 1990). To establish whether a nonstop crossing directly to Africa was possible, we considered migration based on navigation between the closest possible locations between the Canadian and African ranges, southeast Newfoundland, Canada (47°N , 53°W), and southern Morocco (28°N , 13°W), separated by a great-circle distance (i.e. the shortest distance between 2 locations on Earth) of 4,055 km. We note that although the highest concentrations of wheatears breeding in the New World are found in Greenland and Canadian Arctic islands (Godfrey 1986), their range has recently expanded south along the Labrador coast and, occasionally, Newfoundland (Mactavish and Linegar 2002), and there are even

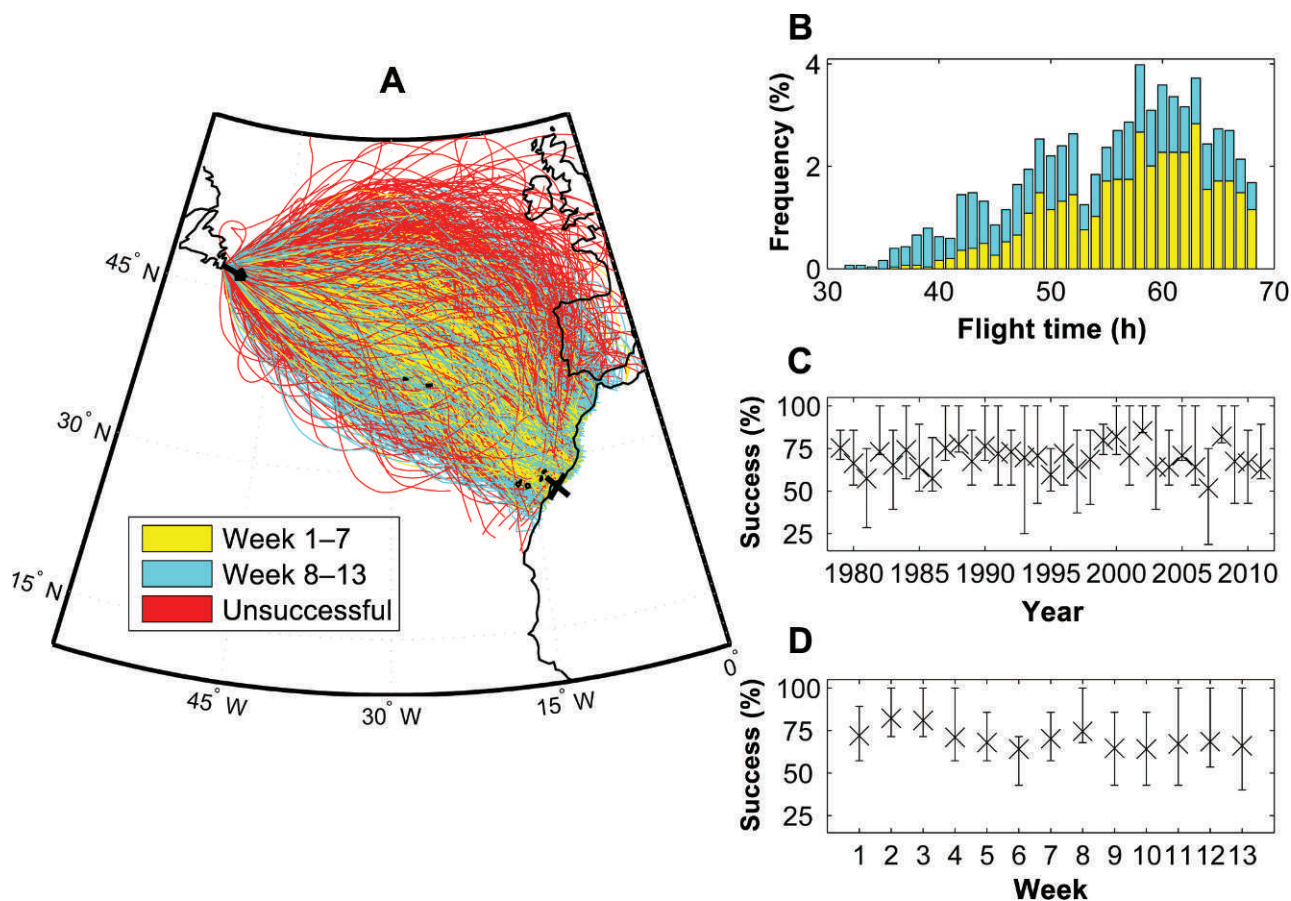


FIGURE 1. (A) Trajectories of successful (yellow: weeks 1–7; blue: weeks 8–13; $n = 1,887$) and unsuccessful (red, $n = 1,149$) modeled Northern Wheatears with a departure fuel load of 1.0 flying at 700 mb, during August–October, 1979–2011. The arrow indicates the initial great-circle heading between the departure point in Newfoundland (47°N, 53°W) and the goal location (X) on the Moroccan coast (28°N, 13°W). (B) Frequency (%) of flight duration (hr), among successful migrants (yellow: weeks 1–7; blue: weeks 8–13). (C) Mean annual arrival success, \bar{X} (%), with upper and lower quartiles among weeks per year. (D) Mean weekly arrival success, \bar{X} (%), with upper and lower quartiles among years per week.

suggestions of historical breeding along the Gulf of St. Lawrence (Comeau 1923).

Wind data in a modeled domain of 60–0°W and 10–60°N (see Figure 1A) were derived by linear interpolation of global NCEP/NCAR reanalysis data (Kalnay et al. 1996) onto a 0.5° spatial grid with hourly temporal resolution. Simulations were run with daily departures at 1 hr past civil dusk (Schmaljohann and Naef-Daenzer 2011, Schmaljohann et al. 2013), from August 1 to October 28, 1979–2011 (Koes 1995). For each of these dates, we simulated attempted nonstop migration by modeled wheatears (hereafter “individuals”) flying at each pressure level and with DFL “steps” of 0.1–1.4 in increments of 0.1. Simulated ocean crossings were considered successful if individuals reached the coast of Africa, and unsuccessful if individuals depleted their fuel loads before reaching Africa or left the modeled domain. Because we were only interested in nonstop flight to Africa, simulated birds did not stop outside of Africa, either on any islands or on the

coast of Europe. We also determined the proportion of departure days on which individuals with DFLs of 1.0 would have been able to make landfall in Europe before continuing migration to Africa.

Simulated trajectories and fuel loads were updated hourly according to behavioral rules and flight mechanics, following McLaren et al. (2012) and Pennycuik (2008). Individuals were assumed to navigate by recalibrating their preferred direction at dawn and dusk (Cochran et al. 2004), to coincide with orthodromes (great-circle routes) between the current and goal locations, as suggested for Arctic passerines (Alerstam et al. 2008). We further assumed flight at fixed pressure levels at maximum-range airspeeds, i.e. speeds that minimize transport costs (total energy loss), including metabolic costs per unit distance, in relation to the moving air; see Pennycuik 2008. Maximum-range airspeed depends on both exogenous factors (e.g., air density) and endogenous factors (notably fuel load and body morphology). We estimated body morphology from

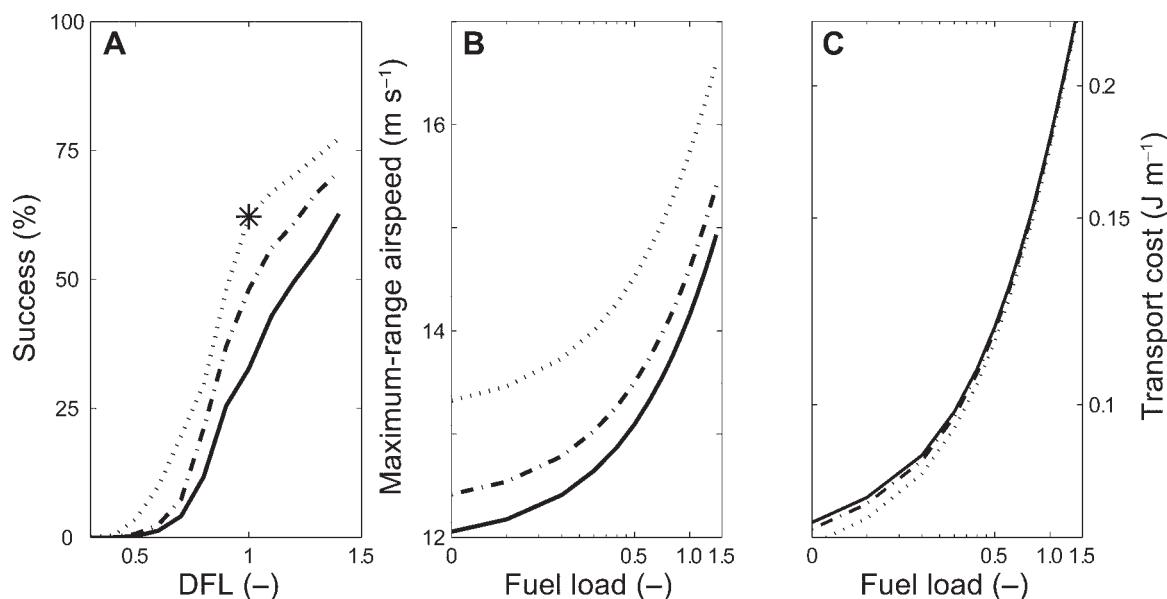


FIGURE 2. (A) Arrival success (%) over all departure dates as a function of departure fuel load (DFL) and (B) maximum-range airspeeds (m s^{-1}) and (C) transport cost (J m^{-1}) as a function of current fuel load, for flight at 925 mb (solid lines), 850 mb (dot-dashed lines), and 700 mb (dashed lines). The asterisk represents the default case depicted in Figure 1A–1D.

field measurements and allometric equations (wing length was set to 103 mm, resulting in an estimated wing span of 0.302 m and lean body mass of 23.0 g; see Schmaljohann et al. 2012). Birds can adjust their airspeed and/or heading in relation to the moving air to compensate for crosswinds and enhance ground speeds (Liechti 1995, Alerstam 2011, Kemp et al. 2012). However, because winds from opposite sides might be encountered farther on, offsetting the initial drift, it might be energetically favorable to refrain from reacting to wind constantly. Because birds may have difficulty assessing drift at sea (Alerstam and Pettersson 1976) and full drift is proposed to be close to optimal in broad-front migration (Alerstam 2011), locations were updated assuming that individuals fully drifted with the wind (i.e. did not adjust their heading or airspeed to compensate instantaneously for incident winds). Note that by recalibrating their preferred directions at dawn and dusk, individuals effectively compensated for wind drift a posteriori. Fuel loads were also updated at hourly time steps, assuming that protein sources provided 5% of energy used, which meant that protein comprised 27% of fuel loads by weight (Jenni and Jenni-Eiermann 1998).

The proportion of successfully arriving individuals (hereafter “arrival success”) was calculated from the individual-based model simulations per year, departure week (13 wk, from August 1–October 28), altitude (pressure level) of flight, and each DFL “step.” To separate the altitudinal effects of air density and wind on arrival success, we first assessed the effect of pressure level on flight in terms of transport cost and flight range in the absence of wind. Then, for the pressure level resulting in

highest overall arrival success and DFLs of 1.0, we analyzed flight duration and arrival success in relation to wind conditions on departure and en route. We quantified wind conditions as follows: (1) tailwind component and drift angle in relation to the initial preferred direction on departure, and (2) mean tailwind support and crosswind component en route (i.e. the mean wind-speed component parallel and perpendicular to the preferred direction at each time step; see, e.g., Kemp et al. 2012). Finally, we estimated the weekly incidence of favorable winds at departure (i.e. those producing the highest arrival success). For this, we calculated the number of days a migrant would have to wait for a given minimal tailwind support and maximal drift on departure.

To test the robustness of results to orientation strategy, we also determined the success rate of individuals with DFLs of 1.0 orienting along loxodromic as opposed to great-circle headings (see Schmaljohann et al. 2012), based on (1) twice-daily recalibration of preferred direction as above and (2) a fixed endogenous heading between the start and goal locations, 107° clockwise from north (Mouritsen 2003, McLaren et al. 2012).

RESULTS

With each simulated DFL, arrival success was highest at 700 mb (~3,000 m above mean sea level), and results are primarily summarized for this pressure level. On 62% of the departure days, individuals with DFLs of 1.0 flying at 700 mb arrived successfully in Africa. This DFL corresponds to a flight range of 3,691 km in the absence of

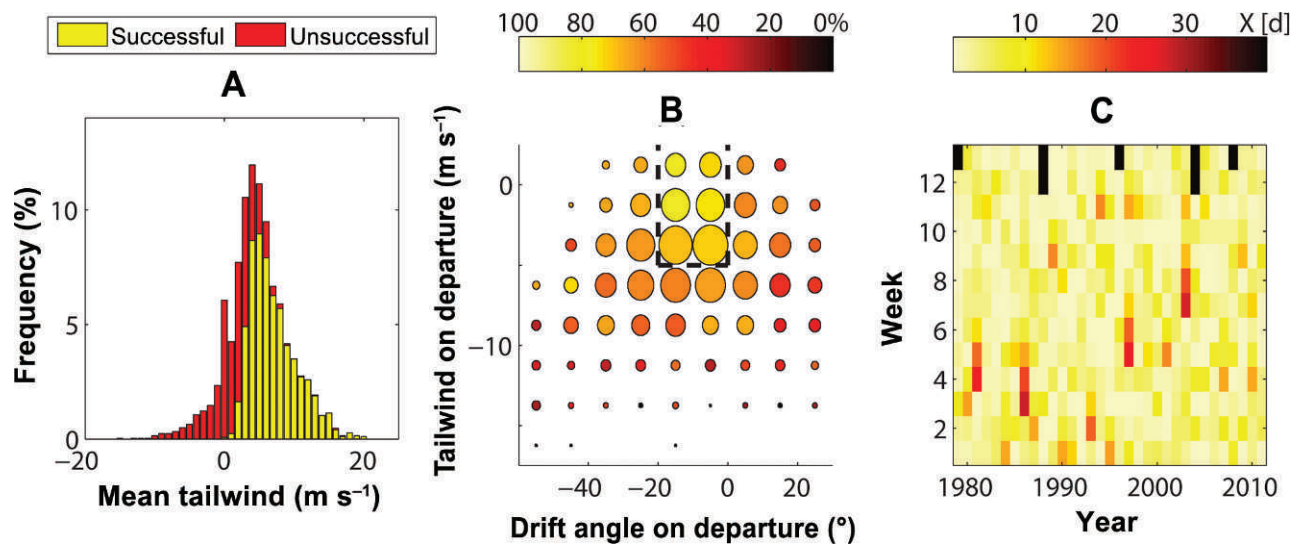


FIGURE 3. Effect of wind on modeled Northern Wheatears with a departure fuel load of 1.0 flying at 700 mb. **(A)** Frequency (%) of successful (yellow) and unsuccessful (red) migrants as a function of mean tailwind support (see text). **(B)** Arrival success (%), shown as colors, as a function of tailwind (m s⁻¹) and drift angle (°) on departure, with circle size proportional to the frequency of wind conditions on departure, considering all years and departure days. **(C)** Incidence of “favorable” winds (see text), contained within the dashed lines in B, depicting number of days before favorable winds occurred from each week (starting August 1) and year, with black cells (marked by X in the legend) indicating no more favorable winds that season.

wind, indicating the importance of wind assistance in successfully making the 4,055-km trip from Newfoundland to Africa. Trajectories of successful and unsuccessful individuals (Figure 1A) drifted generally northeast and occasionally southeast from the initially east–southeast great-circle heading (107°) by winds encountered en route. Individuals with DFLs of 1.0 flew over Europe (where they did not stop) on 10% of total departure days (1% of the “successful” and 24% of the “unsuccessful” departure days). There was no discernible difference in arrival success between early and late departures (weeks 1–7 vs. weeks 8–13, i.e. before and after September 19). Flight durations among successful individuals (Figure 1B) ranged from 31 to 68 hr (lower, median, and upper quartiles were 50, 58, and 63 hr, respectively); thus, migrants could reach Africa in <3 days of nonstop flight. After 68 hr, fuel loads were depleted and simulations stopped. Flight durations after week 7 (mean ± SD, 53 ± 9 hr, $n = 863$) were significantly shorter ($t = 13.3$, $P < 0.0001$) than beforehand (mean ± SD, 58 ± 7 hr, $n = 1,174$), with 77% of the flights lasting <48 hr occurring in weeks 8–13. Figure 1C, 1D depicts mean arrival success among years (range: 57–82%) and among weeks (range: 71–86%). Therefore, mean weekly and yearly success always exceeded 50%, with marginally more variation among years (SD 10%) than among weeks (SD 6%; $F = 0.4$, $df = 12$ and 32 , $P = 0.07$).

Arrival success increased with decreasing pressure level (i.e. increased with altitude), and increased strongly with DFL, especially between 0.5 and 1.0 (Figure 2A). Although maximum-range airspeed increased with altitude and fuel

load (Figure 2B), transport cost (Jm⁻¹) was only marginally lower at the higher altitudes (Figure 2C). This resulted in little difference in flight ranges between pressure levels (e.g., for DFL = 1.0, 3,458 km, 3,575 km, and 3,691 km at 925 mb, 850 mb, and 700 mb, respectively). Tailwind support varied more strongly with pressure level than did mean crosswind. For DFLs of 1.0, mean tailwind support (including unsuccessful individuals) at 925, 850, and 700 mb was 1.6, 3.1, and 4.9 m s⁻¹, respectively, whereas mean crosswinds were -2.4, -2.4, and -3.9 m s⁻¹, respectively (negative values indicating counterclockwise drift).

Arrival success was also strongly related to wind conditions at departure and to mean tailwind support. Among individuals with DFL of 1.0 flying at 700 mb (Figure 3A, 3B), no individuals arrived successfully when mean tailwind support was negative (which occurred on 11% of departure days in the modeled period), whereas 85% arrived successfully when mean tailwind support exceeded 3 m s⁻¹. In Figure 3B, we illustrate the relationship between wind on departure and arrival success. Tailwinds on departure at 700 mb were very common (on 93% of days, ranging 81–98% over years), typically strong (median 9.9 m s⁻¹, ranging 6.3–12.7 m s⁻¹ over years), and usually resulted in counterclockwise drift (negative values in Figure 3B). Mean crosswind was virtually identical among successfully arriving and unsuccessful individuals (both -3.9 m s⁻¹). With counterclockwise drift of ≤20° and tailwinds >10 m s⁻¹ on departure (i.e. “favorable” winds; area defined by the dashed line in Figure 3B), arrival success was enhanced from 62% to 75%.

Figure 3C depicts the number of days a migrant would have to wait before these favorable wind conditions occurred from the beginning of each week, with median and mean durations of 3 and 4.5 days, respectively (range: 1–28 days).

The great-circle and loxodromic distances differed by merely 32 km along this route. Arrival success with either orientation based on loxodromic navigation (mean over departure days = 68%) and with endogenous headings rather than navigation (mean = 63%) was rather similar to the default case (mean = 62%).

DISCUSSION

The majority of modeled wheatears reached northwestern Africa in <3 days of nonstop flight across the North Atlantic Ocean. Interannual stability of arrival success (Figure 1D) indicated that this 4,000-km nonstop ocean crossing might be an annually feasible migration option for wheatears of Canadian origin. One wheatear with a geolocator departed from Iqaluit, Canada, and flew for 2.5–3 days nonstop (Bairlein et al. 2012) across the North Atlantic to Europe, which strengthens the evidence for the feasibility of nonstop migration to Africa.

For a given DFL, arrival success of the modeled wheatears depended strongly on flight altitude. Given the similarity in both transport cost (Figure 2C) and mean crosswind between pressure levels, the fact that arrival success was highest with flight at 700 mb (Figure 2A) was therefore chiefly attributable to mean tailwind support (Figure 3A, 3B). Our results therefore reinforce conclusions from earlier studies that wind support is crucial to migration along over-ocean routes (cf. Felicísimo et al. 2008, Shamoun-Baranes and van Gasteren 2011, Yamaguchi et al. 2012).

More generally, although our assumption of maximum-range airspeed(s) enhanced flight ranges, our model is, otherwise, conservative in assessing the feasibility of nonstop crossings. In particular, we did not allow modeled individuals to select appropriate wind conditions on departure (Figure 3B; Schmaljohann and Naef-Daenzer 2011), adjust their general phenology in relation to seasonal wind conditions (Figure 3C), select optimal flight altitudes (Figure 2A; Schmaljohann et al. 2009), or adjust airspeed to tailwind or crosswind components (Liechti 1995). Furthermore, the drag and induced-power components we used (following Pennycuick 2008) have recently been assessed as overconservative for small avian migrants (Pennycuick et al. 2013). This implies that similar or even longer nonstop migration by landbird migrants may be feasible, including nonstop flights of 3,250–4,000 km by Blackpoll Warblers to South America from eastern North America (Nisbet et al. 1995, Alerstam 2001) or by wheatears reaching Africa directly from Greenland (Thor-

up et al. 2006, Delingat et al. 2008). Nonstop flights from Greenland and Arctic Canada will presumably be more challenging than Newfoundland departures, given that prevailing southwesterly winds will have lower tailwind and higher crosswind components in relation to the goal direction.

Given the arrival success in the present study, we conclude that migrating 4,000 km nonstop across the North Atlantic Ocean in autumn may be a feasible migration strategy for wheatears of Canadian origin. The migration phenology of *O. o. leucorhoa* in general remains unclear, for example why the birds observed on Selvagem Grande arrived earlier in the season than most fall recoveries in Europe (Thorup et al. 2006). In the model, survival of migration depended strongly on the initial fuel load and wind conditions en route. Because passerines preparing to embark on barrier crossings have the general ability to select for high fuel loads at departure (e.g., Schaub et al. 2008), as well as for favorable departure days (Schmaljohann and Naef-Daenzer 2011) and flight altitudes (Schmaljohann et al. 2009), the nonstop Atlantic crossing may be a faster and less energy-consuming migration alternative than the detour via Greenland and Europe. This is mainly due to the fact that the overall time and energy cost of stopovers exceeds that of flight. For example, using geolocator data of Alaskan Northern Wheatears (*O. o. oenanthe*) along entire migration routes (15,000 km), the estimated ratio of overall stopover to flight time expenditure was between 3:1 and 6:1, and the estimated ratio of overall stopover to flight energy expenditure was between 2:1 and 3:1 (Schmaljohann et al. 2012; also see Hedenström and Ålerstam 1997, Wikelski et al. 2003).

If a simple strategy based on wind support and navigation (or endogenous headings) can make nonstop trans-Atlantic crossings possible, the ocean may function more as a migratory corridor (i.e. chosen route) rather than a barrier for these birds, as long as wind conditions are supportive. However, determining whether selection should indeed favor the nonstop migration strategy would require a detailed comparison of both migration strategies regarding survival rate and reproduction success (Maynard Smith 1982), which was not in the scope of the present study.

Nevertheless, our results show, for the first time, that supportive wind systems can be sufficiently reliable to allow for successful barrier crossings over several decades. An alternative strategy to nonstop migration or migration with an obligatory stopover might be a bet-hedging strategy (e.g., whereby wheatears fly toward Africa but, if needed, make a stopover en route depending on wind conditions and on fuel load; see, e.g., Shamoun-Baranes et al. 2010). The efficacy of this possibility is supported by the fact that 24% of the unsuccessful individuals with DFLs of

1.0 could have stopped over in Europe en route. Fall ring recoveries of *O. o. leucorhoa* from Europe are consistent with both the bet-hedging and the obligatory stopover strategy. With a bet-hedging strategy, atmospheric conditions will determine, to a large extent, whether individual birds make a direct crossing to Africa or a detour via Europe.

ACKNOWLEDGMENTS

NCEP reanalysis data were provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from <http://www.esrl.noaa.gov/psd/>. This work was supported by the Deutsche Forschungsgemeinschaft (BA 816/15-4) and facilitated by infrastructures for e-science, developed with the support of the NLeSC (<http://www.esciencecenter.com>) and LifeWatch, carried out on the Dutch national e-infrastructure with support of SURF Foundation. H.S. was financed by the German Research Foundation (SCHM 2647/1-1). We thank M. T. Murphy, K. Thorup, A. Tsvey, and two anonymous reviewers for their helpful comments and suggestions.

LITERATURE CITED

- Alerstam, T. (1990). Bird Migration. Cambridge University Press, Cambridge, UK.
- Alerstam, T. (2001). Detours in bird migration. *Journal of Theoretical Biology* 209:319–331.
- Alerstam, T. (2011). Optimal bird migration revisited. *Journal of Ornithology* 152 (Supplement 1):5–23.
- Alerstam, T., J. Bäckman, R. Strandberg, G. A. Gudmundsson, A. Hedenström, S. A. Henningsson, H. Karlsson, and M. Rosén (2008). Great-circle migration of Arctic passerines. *The Auk* 125:831–838.
- Alerstam, T., and S.-G. Pettersson (1976). Do birds use waves for orientation when migrating across the sea? *Nature* 259:205–207.
- Baird, J. (1999). Returning to the tropics: The epic autumn flight of the Blackpoll Warbler. In *Gatherings of Angels: Migrating Birds and Their Ecology* (K. P. Able, Editor). Cornell University Press, Ithaca, NY, USA.
- Bairlein, F., D. R. Norris, R. Nagel, M. Bulte, C. C. Voigt, J. W. Fox, D. J. T. Hussell, and H. Schmaljohann (2012). Cross-hemisphere migration of a 25 g songbird. *Biology Letters* 8:505–507.
- Battley, P. F., N. Warnock, T. L. Tibbitts, R. E. Gill, Jr., T. Piersma, C. J. Hassell, D. C. Douglas, D. M. Mulcahy, B. D. Gartrell, R. Schuckard, D. S. Melville, and A. C. Riegen (2012). Contrasting extreme long-distance migration patterns in Bar-tailed Godwits *Limosa lapponica*. *Journal of Avian Biology* 43:21–32.
- Clarke, T. (1999). Autumn 1998 on the Azores. *Birding World* 12: 205–212.
- Cochran, W. W., H. Mouritsen, and M. Wikelski (2004). Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science* 304:405–408.
- Comeau, N. A. (1923). Wheatear at Godbout, Quebec. *The Auk* 40:544–545.
- Corman, A.-M., F. Bairlein, and H. Schmaljohann (2014). The nature of the migration route shapes physiological traits and aerodynamic properties in a migratory songbird. *Behavioral Ecology and Sociobiology* 68:391–402.
- Delingat, J., F. Bairlein, and A. Hedenström (2008). Obligatory barrier crossing and adaptive fuel management in migratory birds: The case of the Atlantic crossing in Northern Wheatears (*Oenanthe oenanthe*). *Behavioral Ecology and Sociobiology* 62:1069–1078.
- Dierschke, J., V. Dierschke, K. Hüppop, O. Hüppop, and K. F. Jachmann (2011). Die Vogelwelt der Insel Helgoland. OAG Helgoland, Helgoland, Germany.
- Dierschke, V., B. Mendel, and H. Schmaljohann (2005). Differential timing of spring migration in Northern Wheatears *Oenanthe oenanthe*: Hurried males or weak females? *Behavioral Ecology and Sociobiology* 57:470–480.
- Felícísimo, Á. M., J. Muñoz, and J. González-Solis (2008). Ocean surface winds drive dynamics of transoceanic aerial movements. *PLoS ONE* 3:2928.
- Gill, R. E., Jr., T. L. Tibbitts, D. C. Douglas, C. M. Handel, D. M. Mulcahy, J. C. Gottschalck, N. Warnock, B. J. McCaffery, P. F. Battley, and T. Piersma (2009). Extreme endurance flights by landbirds crossing the Pacific Ocean: Ecological corridor rather than barrier? *Proceedings of the Royal Society of London, Series B* 276:447–457.
- Godfrey, W. E. (1986). *The Birds of Canada*, revised ed. National Museum of Natural Sciences, Ottawa, Ontario, Canada.
- Hedenström, A., and T. Alerstam (1997). Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. *Journal of Theoretical Biology* 189:227–234.
- Hooker, T. (1958). Birds seen on the eastern Canary island of Fuerteventura. *Ibis* 100:446–449.
- Jenni, L., and S. Jenni-Eiermann (1998). Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology* 29:521–528.
- Johnson, O. W., L. Fielding, J. P. Fisher, R. S. Gold, R. H. Goodwill, A. E. Bruner, J. F. Furey, P. A. Brusseau, N. H. Brusseau, P. M. Johnson, J. Jukema, L. L. Prince, et al. (2012). New insight concerning transoceanic migratory pathways of Pacific Golden-Plovers *Pluvialis fulva*: The Japan stopover and other linkages as revealed by geolocators. *Wader Study Group Bulletin* 119:1–8.
- Kalnay, E., M. Kanamitsu, R. Kistler, W. Collins, D. Deaven, L. Gandin, M. Iredell, S. Saha, G. White, J. Woollen, Y. Zhu, A. Leetmaa, and R. Reynolds (1996). The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society* 77:437–471.
- Kemp, M. U., J. Shamoun-Baranes, E. E. van Loon, J. D. McLaren, A. M. Dokter, and W. Bouten (2012). Quantifying flow-assistance and implications for movement research. *Journal of Theoretical Biology* 308:56–67.
- Koes, R. F. (1995). The Northern Wheatear in Canada. *Birders Journal* 4:21–28.
- Liechti, F. (1995). Modelling optimal heading and airspeed of migrating birds in relation to energy expenditure and wind influence. *Journal of Avian Biology* 26:330–336.
- Mactavish, B., and P. Linegar (2002). Northern Wheatear: Breeding range extension in Newfoundland. *Birders Journal* 10:299–301.
- Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge University Press, Cambridge, UK.

- McLaren, J. D., J. Shamoun-Baranes, and W. Bouten (2012). Wind selectivity and partial compensation for wind drift among nocturnally migrating passerines. *Behavioral Ecology* 23: 1089–1101.
- Minton, C., K. Gosbell, P. Johns, M. Christie, M. Klaassen, C. Hassell, A. Boyle, R. Jessop, and J. Fox (2011). Geolocator studies on Ruddy Turnstones *Arenaria interpres* and Greater Sandplovers *Charadrius leschenaultii* in the East Asian–Australasia Flyway reveal widely different migration strategies. *Wader Study Group Bulletin* 118:87–96.
- Mouritsen, H. (2003). Spatiotemporal orientation strategies of long-distance migrants. In *Avian Migration* (P. Berthold, E. Gwinner, and E. Sonnenschein, Editors). Springer, Berlin, Germany.
- Nisbet, I. C. T., D. B. McNair, W. Post, and T. C. Williams (1995). Transoceanic migration of the Blackpoll Warbler: Summary of scientific evidence and response to criticisms by Murray. *Journal of Field Ornithology* 66:612–622.
- Pennycuik, C. J. (2008). *Modelling the Flying Bird*. Academic Press, London, UK.
- Pennycuik, C. J., S. Åkesson, and A. Hedenström (2013). Air speeds of migrating birds observed by ornithodolite and compared with predictions from flight theory. *Journal of the Royal Society Interface* 10:20130419.
- Richardson, W. J. (1976). Autumn migration over Puerto Rico and the Western Atlantic: A radar study. *Ibis* 118:309–332.
- Schaub, M., L. Jenni, and F. Bairlein (2008). Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. *Behavioral Ecology* 19:657–666.
- Schmaljohann, H., J. W. Fox, and F. Bairlein (2012). Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. *Animal Behaviour* 84:623–640.
- Schmaljohann, H., F. Korner-Nievergelt, B. Naef-Daenzer, R. Nagel, I. Maggini, M. Bulte, and F. Bairlein (2013). Stopover optimization in a long-distance migrant: The role of fuel load and nocturnal take-off time in Alaskan Northern Wheatears (*Oenanthe oenanthe*). *Frontiers in Zoology* 10:26.
- Schmaljohann, H., F. Liechti, and B. Bruderer (2009). Trans-Sahara migrants select flight altitudes to minimize energy costs rather than water loss. *Behavioral Ecology and Sociobiology* 63:1609–1619.
- Schmaljohann, H., and B. Naef-Daenzer (2011). Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird. *Journal of Animal Ecology* 80:1115–1122.
- Shamoun-Baranes, J., J. Leyrer, E. van Loon, P. Bocher, F. Robin, F. Meunier, and T. Piersma (2010). Stochastic atmospheric assistance and the use of emergency staging sites by migrants. *Proceedings of the Royal Society of London, Series B* 277:1505–1511.
- Shamoun-Baranes, J., and H. van Gasteren (2011). Atmospheric conditions facilitate mass migration events across the North Sea. *Animal Behaviour* 81:691–704.
- Thorup, K., T. E. Ortvad, and J. Rabøl (2006). Do Nearctic Northern Wheatears (*Oenanthe oenanthe leucorhoa*) migrate nonstop to Africa? *The Condor* 108:446–451.
- Wikelski, M., E. Tarlow, A. Raim, R. H. Diehl, H. Visser, and R. P. Larkin (2003). Avian metabolism: Costs of migration in free-flying songbirds. *Nature* 423:704.
- Williams, T. C., and J. M. Williams (1990). Open ocean bird migration. *IEEE Proceedings F* 137:133–137.
- Williamson, K. (1958). Bergmann's rule and obligatory overseas migration. *British Birds* 51:209–232.
- Yamaguchi, N., Y. Arisawa, Y. Shimada, and H. Higuchi (2012). Real-time weather analysis reveals the adaptability of direct sea-crossing by raptors. *Journal of Ethology* 30:1–10.