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DO NEARCTIC NORTHERN WHEATEARS (*OENANTHE OENANTHE LEUCORHOA*) MIGRATE NONSTOP TO AFRICA?

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Abstract. We present data suggesting that Northern Wheatears (*Oenanthe oenanthe leucorhoa*) breeding in West Greenland and Canada may be able to accomplish migration to their wintering grounds in West Africa in one direct, transatlantic crossing of more than 4000 km (great circle distance). This conclusion is based on analyses of wing lengths, body weights, and timing of departure from West Greenland and arrival on an island 350 km off the coast of Morocco. Previously, it has been suggested that Nearctic wheatears migrate to Africa by a two-step journey, the first leg comprising a shorter transatlantic crossing to western Europe. A long, direct flight has previously been considered unfeasible as the predicted flight costs were considered to be too high. However, recent insights in aerodynamic theory make these long ocean crossings appear more feasible, especially when taking the use of tailwinds into account.

Key words: maximum flight range, migration, Oenanthe oenanthe leucorhoa*, transoceanic flights.*

¿Migran los Individuos Neárticos de la Especie *Oenanthe oenanthe leucorhoa* de Modo Ininterrumpido hasta África?

Resumen. Presentamos datos que sugieren que los individuos de *Oenanthe oenanthe leucorhoa* que crían en el oeste de Groenlandia y Canadá pueden ser capaces de migrar a sus sitios de invernada en el oeste de África en un solo vuelo transatlántico directo de más de 4000 km (distancia del círculo mayor). Esta conclusión está basada en el análisis del largo de las alas, el peso corporal y el tiempo entre la partida desde el oeste de Groenlandia y el arribo a una isla a 350 km de la costa de Marruecos. Previamente, se ha sugerido que los individuos neárticos de *O. o. leucorhoa* migran a África en un vuelo con dos etapas, en el que la primera etapa corresponde a un vuelo trasatlántica más corto hacia el oeste de Europa. Un único vuelo largo y directo ha sido previamente considerado como inviable, ya que se ha predicho que el costo del vuelo sería demasiado alto. Sin embargo, hallazgos recientes en teoría aerodinámica hacen que estos vuelos oceánicos largos parezcan más viables, especialmente considerando el uso del viento de cola.

The Northern Wheatear (*Oenanthe oenanthe*) flies considerable distances between its breeding areas in the northern hemisphere and its wintering grounds in tropical Africa. *En route* some populations cross habitats, including oceans, with few or no exploitable food resources. Such ecological barriers are presumably overflown as extended nonstop flights. Several subspecies of Northern Wheatears exist and to reach their African wintering grounds birds of the subspecies *leucorhoa* from the eastern Nearctic (including North America and Greenland; Brown and Gibson 1983) need to traverse the Atlantic Ocean. This extraordinary task has been a subject of investigation for decades (Snow 1953, Lee 1963, Salomonsen 1967, Alerstam 1996, 2001).

On the basis of observations of large numbers of wheatears on islands in the northwestern Atlantic Ocean it has been suggested that *leucorhoa* wheatears leaving South Greenland or Iceland make landfall in northwestern Europe (Williamson 1958, 1961). Band recoveries also indicate the Nearctic breeding population of ssp. *leucorhoa* flies to Africa via western Europe. The concentration of band recoveries in the Biscay region (southwestern France and northern Spain) could indicate that birds leaving southwest Greenland make their first landfall there, a nonstop journey of approximately 3000 km (great circle distances used throughout). A subsequent change of course to south-southwest would bring them to the West African wintering grounds (Salomonsen 1967, Alerstam 1996). Alternatively, if landfall were first made on the coast of northwestern Africa at central Morocco, more than 1000 km would be added to the transoceanic journey. Williamson (1958, 1961) proposed that *leucorhoa* wheatears leaving South Greenland head southeast and take advantage of the prevailing westerly winds to cross the northern North Atlantic Ocean. Subsequent landfall in western Europe would then vary according to wind drift along the route.

Some American songbirds, e.g., the Blackpoll Warbler (*Dendroica striata*), make regular autumnal transatlantic flights of up to 4000 km between northeast North America and South America (Drury and Keith 1962, Nisbet et al. 1963), although some controversy exists as to whether these crossings are normally initiated from the northeast or farther south

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in North America (Murray 1989, Nisbet et al. 1995). Still, such long overwater flights are probably unusual in passerines, although in the Charadriiformes nonstop, intercontinental flights are a widely adopted migration strategy. For example, Semipalmated Sandpipers (*Calidris pusilla*), with body mass and fuel-load characteristics similar to those of Nearctic Northern Wheatears, undertake a direct, 3000–4500 km oceanic flight from southeast Canada to South America (Hicklin 1983, Stoddard et al. 1983). It has even been suggested that Bar-tailed Godwits (*Limosa lapponica*) may make an 11 000 km nonstop flight from Alaska to New Zealand (Piersma and Gill 1998, Gill et al. 2005).

Here, we report wing lengths and weights for Northern Wheatears captured during autumn migration at Selvagem Grande off the coast of southern Morocco. Additionally, we report counts of Northern Wheatears and other landbirds at Selvagem Grande. To evaluate the feasibility of long overwater flights we calculate potential maximum flight ranges on the basis of aerodynamic theory and empirical flight cost estimates for wheatears leaving their eastern Nearctic breeding grounds. We then discuss which of a direct transatlantic crossing or a two-leg journey fits the observations best. This is done by looking at (1) the timing of migration for *leucorhoa* populations described in the literature, (2) weights of wheatears on Selvagem Grande, and (3) the correlation among numbers of different species of migratory landbirds on Selvagem Grande.

METHODS

There are several subspecies of the Northern Wheatear, which breed from northeast Canada, east across Eurasia, to Alaska. However, almost the entire world population winters in Africa in a wide belt south of the Sahara. Two subspecies are long-distance migrants: nominate *oenanthe* breeds in Europe and Scandinavia and across the Russian and Siberian tundra all the way to Alaska, and is found throughout the wintering range in Africa. Subspecies *leucorhoa* breeds in Iceland, Greenland, and eastern Canada and winters in West Africa, primarily from Senegal and Sierra Leone to Mali in the east (Fig. 1; Cramp 1988). On migration, ssp. *leucorhoa* passes through North Africa west of 3°E (Cramp 1988), and is found in Europe in both autumn and spring. Autumn migration is recorded mainly in Britain, Ireland, on the west coast of Norway, and in western France. The two subspecies differ in average wing length, with ssp. *leucorhoa* having longer wings (Svensson 1992).

From 3 to 20 September 1990, passerine migrants were counted (Table 1) and several, including 12 Northern Wheatears, were trapped throughout the period and measured during a study of resident Berthelot's Pipits (*Anthus berthelotti*) on Selvagem Grande (Folmer and Ortvad 1992). Located 350 km off the coast of Morocco in the northeast Atlantic Ocean, Selvagem Grande (30°N, 16°W) is the largest (2.2 km^2, 0–154 m elevation) of the three islands of Selvagem. The nearest land is Tenerife 190 km to the south and Madeira 290 km to the north. The barren

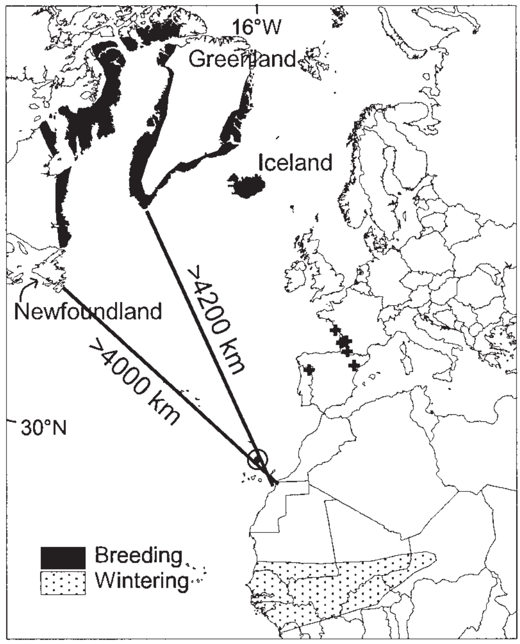

FIGURE 1. Breeding and wintering distributions of Northern Wheatears (*Oenanthe oenanthe leucorhoa*). Plusses represent autumn band recoveries of nestlings banded in West (n = 5) and South (n = 2) Greenland. The position of Selvagem Grande is shown by a circle with a dot in the middle. The suggested migration flights from Newfoundland or South Greenland across the Atlantic are indicated (great circle distance). The figure shows an equidistant azimuthal map projection centered on Selvagem Grande.

islands have little vegetation and cover for migrants. All observations of migrants were noted, but no standardized recording procedure was followed. Due to the relatively small size of the island and sparse vegetation, this procedure presumably allowed for relatively accurate estimates of the number of birds present. Weather conditions were generally stable with a north-northeast breeze and good visibility, except on 11 and 12 September when the wind turned south and was accompanied by light rain showers.

STATISTICAL ANALYSES

Correlations between daily totals of different species on Selvagem Grande were investigated using Spearman's rank correlation coefficient (r_s). We also calculated daily arrivals as positive differences between the daily totals on two consecutive days, and examined these correlations using Spearman's rank correlation coefficients (r_s) excluding days with no arrivals. Differences between population means were tested using two-tailed independent t-tests. Statistical analyses were performed using SAS version 8.2 (SAS Institute 1990). Data are reported as means ± SD.

TABLE 1. Daily numbers of migrant passerine species at Selvagem Grande, 3–18 September 1990 (data from Folmer and Ortvad 1992).

	Date																
Species	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Northern Wheatear *Oenanthe oenanthe*	2	2	6	3	3	3	3	3	5	4	9	6	7	6	10	9	81
Willow warbler *Phylloscopus trochilus*	0	1	0	8	11	5	2	5	5	5	2	0	0	0	0	0	44
Other species[a]	1	7	9	10	10	9	8	12	10	1	11	3	5	3	5	4	108

[a] Other species include Whinchat (*Saxicola rubetra*), Redstart (*Phoenicurus phoenicurus*), Reed Warbler (*Acrocephalus scirpaceus*), Icterine Warbler (*Hippolais icterina*), Olivaceous Warbler (*H. pallida*), Garden Warbler (*Sylvia borin*), Whitethroat (*S. communis*), Orphean Warbler (*S. hortensis*), Chiffchaff (*Phylloscopus collybita*), Spotted Flycatcher (*Muscicapa striata*), Pied Flycatcher (*Ficedula hypoleuca*), Tree Pipit (*Anthus trivialis*), and Grey Wagtail (*Motacilla cinerea*).

FLIGHT RANGE ESTIMATES

We used program FLIGHT 1.11 (Pennycuick 2001, described in Pennycuick 1998, Pennycuick and Battley 2003) to calculate maximum flight ranges of Northern Wheatears based on aerodynamic theory (Pennycuick 1989). We ran the program with default flight parameters but bounding flight style with power fraction = 0.75, and using values of fat-free weight = 26 g, migratory weight = 50 g (from Ottosson et al. 1990), wingspan = 0.30 m (from measurements of *leucorhoa* on Helgoland; J. Delingat, Institute for Avian Research "Vogelwarte Helgoland," pers. comm.), and wing area = 0.015 m^2 for Northern Wheatears.

Additionally, we calculated maximum flight ranges on the basis of empirical flight cost estimates. We used an allometric relationship for the power requirement $P = 0.21\ M^{0.813}$ (Norberg 1996), and calculated the maximum flight range D_{max} according to Klaassen (2003):

$$D_{max} = E_f * V/P,$$

with E_f (maximum fuel store) $= 30\ (2.09\ M^{0.944} - M)$, V (flight speed) $= 12.67\ M^{0.02}$, and M (body mass in g) = 50 g.

RESULTS

With daily counts of 2–10 individuals, the Northern Wheatear was the most regularly recorded and numerous passerine migrant encountered on Selvagem Grande (Table 1). If counting new arrivals only, a minimum of 18 Northern Wheatears, 15 Willow Warblers (*Phylloscopus trochilus*), and 28 individuals of other migrant species were noted on the island. Daily totals of Northern Wheatears and the sum of other landbird migrants showed a negative, but not statistically significant, correlation, as did the correlation between daily arrivals of Northern Wheatears and arrivals of other landbird migrants summed. The correlation between daily totals of Wheatears and Willow Warblers (the second most numerous migrant species) was $r_s = -0.49$ ($P = 0.06$, $n = 16$), and the correlation between daily arrivals of the two species was $r_s = -0.87$ ($P = 0.003$, $n = 9$).

Wings measured 103.3 ± 2.8 mm (range = 99–109 mm, $n = 12$). These are much longer than those of migratory *oenanthe* from Scandinavia (wing length = 97.4 ± 2.4 mm, $n = 267$, $t_{277} = -8.2$, $P < 0.001$, Falsterbo, Sweden or wing length = 97.1 ± 2.7 mm, $n = 194$, $t_{204} = -7.6$, $P < 0.001$, Öland, Sweden; data from August–September; L. Karlsson, Falsterbo Bird Observatory, pers. comm.; J. Stedt, Öland Bird Observatory, pers. comm.). However, the wings of birds on Selvagem appear to be shorter than those of a sample of birds from the West Greenland breeding population of ssp. *leucorhoa* (wing length = 105.0 ± 2.7 mm, $n = 57$, $t_{67} = -2.0$, $0.05 < P < 0.10$; R. Sandberg, Lund University, pers. comm.). The *leucorhoa* population breeding in Iceland has shorter wing lengths (96–107 mm, average 100.8 mm; Cramp 1988) than the populations breeding in Greenland and the birds caught on Selvagem Grande.

The masses of the five birds weighed were 22 g (wing length 99 mm), 23 g (101 mm), 25 g (104 mm), 22 g (106 mm), and 22 g (109 mm), with an average of 22.8 ± 1.3 g. No correlation between wing length and mass was found. These masses are significantly lower than those of premigratory individuals in Greenland (body mass = 26.2 ± 2.8 g, fat classes 0–1, wing length = 105.0 ± 2.7 mm, $n = 31$; Ottosson et al. 1990, $t_{34} < 2.6$, $P < 0.05$), whereas size, measured as wing length, does not differ ($t_{34} = 1.3$, $P > 0.05$). Migrating birds from Greenland were much heavier (body mass = 52.4 ± 3.1 g, fat classes 7–8, wing length = 105.6 ± 2.4 mm, $n = 9$; Ottosson et al. 1990).

According to aerodynamic theory, wheatears should be able to cross the Atlantic in still air with maximum fat loads. However, using empirical flight cost estimates, it seems unfeasible for birds to cross the Atlantic directly unless they make use of tailwinds. We calculated maximum flight range without a tailwind to be around 2800 km, and even taking into account the loss of body mass

TABLE 2. Timing of Nearctic Northern Wheatear (ssp. *leucorhoa*) autumn migration.

Location (latitude/longitude)	Beginning of migratory period	Peak migratory period	End of migratory period	Reference
Canada				
Breeding area (50°–80°N, 90°–55°W)	mid Aug		late Sep (rare to Nov)	Bruun 1980
(50°–80°N, 90°–55°W)			late Sep–Oct	Koes 1995
Greenland				
Breeding area (60°–75°N, 70°–15°W)	mid Aug	early–mid Sep	late Sep–Oct	Salomonsen 1967
Southernmost (60°N, 45°W)		late Aug[a]		Boertmann 1979
NE Atlantic				
Ship records (45°–60°N, 50°–5°W)		late Aug–late Sep		Snow 1953
Fair Isle (60°N, 2°W)	Sep	high numbers following cyclonic conditions[b]		Williamson 1958, 1959, 1961
Heligoland (54°N, 8°E)	Aug	late Sep	Oct	Dierschke and Delingat 2003
Europe				
Western Europe (35°–60°N, 10°W–10°E)	mid Aug	Sep–Oct		Cramp 1988
Biscay region (40°–47°N, 10°–0°W)	5 Sep (1[c])	1–18 Oct (6[c])		Band recoveries, ZMUC[d]
Africa				
Northwest Africa (25°–35°N, 15°W–5°E)		Sept–Oct		Cramp 1988
Wintering grounds (9°–16°N, 18°W–5°E)	Oct	usually later than ssp. *oenanthe*		Cramp 1988

[a] Some days extremely common (up to 75 on a few 100 m^2) in valleys—all gone next day (Julianehåb 1979; where the species is a rare breeding bird, only).
[b] 1000+ during 20–21 September 1959.
[c] Sample size.
[d] ZMUC = Zoological Museum, University of Copenhagen.

during flight (using a 20% smaller mass) a direct Atlantic crossing was still not theoretically possible. However, with an added average tailwind of 5 m s^{-1} the birds were predicted to be able to cross the ocean without stopping.

DISCUSSION

According to the measurements and counts, notable numbers (most common migrant) of *leucorhoa* wheatears from the Nearctic were found in early and mid September on Selvagem Grande. The timing of these observations is similar to the timing of the main departure from Greenland and Canada (Table 2). The birds were significantly lighter than average non- or premigratory wheatears in Greenland, and close to the lowest weights recorded for *leucorhoa* wheatears (Williamson 1958), indicating they had completed a long-distance journey. Along with the lack of or negative correlations with arrivals of other landbird species, this suggests that wheatears on Selvagem arrived after a direct flight from their Nearctic breeding grounds without a stopover in Europe.

The timing of migration of ssp. *leucorhoa* (Table 2) indicates that there should be almost a month between departure from breeding grounds and arrival in the Biscay region of Europe. With one exception, wheatears banded in Greenland were recovered later in Europe (1–18 October) than the birds found on the Selvagems (Fig. 1) and almost a month later than the main departure from Greenland. European records of ssp. *leucorhoa* in general are from later in autumn migration (Table 2), but it is not certain if these relate to Nearctic (excluding East Greenland) populations. On Helgoland the main passage is presumably in late September (Dierschke and Delingat 2003).

Assuming wheatears follow the shortest route from Canada (Newfoundland) to Africa and thus pass the Selvagems (4100 km), our maximum flight range calculations based on aerodynamic theory indicate that wheatears could fly directly from Canada without wind assistance, whereas calculations based on empirical flight cost estimates show the birds would need some tailwind assistance. In 1990 the birds arrived on Selvagem Grande when strong westerly winds prevailed in the northern part of the

North Atlantic Ocean and moderate or weak northerly winds prevailed in the southeastern part of the North Atlantic Ocean (NOAA-CIRES Climate Diagnostics Center 2002). This wind pattern generally would provide a tailwind for the Atlantic crossing, and is not unusual at this time of the year (NOAA-CIRES Climate Diagnostics Center 2002).

The numbers of wheatears present on Selvagem Grande may indicate that such direct flights are not uncommon in *leucorhoa* wheatears. However, a number of factors could argue against such a conclusion: (1) islands often disproportionately attract migrants that have drifted or are otherwise off course, (2) numbers of wheatears may have seemed disproportionately high due to differential stopover times among species, (3) only part of the migration period is covered in our study and *leucorhoa* wheatear migration at Selvagem could peak later, and (4) records at sea and on islands along the direct route are relatively scarce.

According to Williamson (1958), the occurrence of ssp. *leucorhoa* on the Canary Islands peaks in September, coinciding with our coverage on Selvagem Grande. Koes (1995) speculated that birds breeding in Canada may depart on the transatlantic crossing from Newfoundland and use the Azores, Madeira, and the Canary Islands as stepping stones to cross the Atlantic. However, only ten specimen records of Northern Wheatears exist from these islands, all from the autumn and all belonging to ssp. *leucorhoa* (7 Azores, 1 Madeira, 2 Cape Verde). No specimens or banding records of ssp. *oenanthe* have been reported from islands in the central or eastern Atlantic Ocean in autumn (Bannerman 1963, Bannerman and Bannerman 1965, 1966, 1968). Recent observations from the Azores (Clarke 1999) suggest the species may be a regular but rare migrant to these islands in the autumn. The only migration route passing over the Azores is a direct route from Canada; presumably larger numbers of wheatears breed in Greenland. Records from ships in the Atlantic Ocean suggest that Northern Wheatears from Greenland fly to the British Isles in autumn (Snow 1953, Luttik and Wattel 1979), but populations from West Greenland and Canada may not be detected from the more northerly positioned ships. In Atlantic Canada relatively few Northern Wheatears are reported, most of which (usually fewer than 10 all autumn) are found in Newfoundland (B. Maybank, The Nova Scotia Checklist Committee, pers. comm.), but Koes (1995) reports frequent sightings of autumn migrants south of the breeding range.

For birds breeding in Canada there is relatively little difference between crossing from Newfoundland to Europe (Spain: 3500 km) or to Africa (Morocco: 4100 km) and, unless they fly via Greenland, a long nonstop flight must therefore be undertaken either way. A migration route from their breeding grounds in southern Labrador to their wintering grounds in West Africa via southern Greenland or the Biscay region represents a considerably longer detour to birds from Canada than from Greenland. Alerstam (2001) developed formulas to evaluate the possible energetic advantage of a detour, based on the assumption that flight is more cost effective when flying shorter distances with a smaller fuel load than longer distances with a larger fuel load. He concluded that detours via western Europe are favorable for Northern Wheatears departing from Greenland. However, following Alerstam (2001), a detour via Spain for birds departing from Canada would not be favorable (a direct barrier crossing of 4100 km compared to an extra detour of 1800 km with a barrier crossing of 3400 km) if the birds are able to cross nonstop.

In summary, our data and simulations indicate that the wheatears observed on Selvagem Grande may have migrated directly from northeast North America or Greenland. In accordance with Williamson (1958, 1961), such a migration would be expected to occur if wheatears heading southeast when departing from the Nearctic follow the prevailing winds across the North Atlantic Ocean. The distance flown by these birds would be among the longest known in passerines.

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