



Tracking wintering areas and post-breeding migration of a declining farmland bird – An indispensable basis for successful conservation

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ABSTRACT

Many farmland birds, such as the Eurasian Curlew (*Numenius arquata*; here in after Curlew), are in steep decline. So far, decreased reproduction and, hence, an insufficient number of offspring to compensate for adult mortality has been considered the main driver of the recent population collapse. However, despite extensive conservation measures in most breeding areas, there are no signs of a general reversal of the population trend. Accordingly, conservation has to focus on decreasing adult mortality outside the breeding areas as well. For Curlews breeding in NW Germany, ring recoveries suggest that the main wintering areas are the coastlines of western France and southern England. However, such data are often biased in space and time. Here, we used GPS tracking to investigate the wintering areas and post-breeding migration of Curlews of the main German breeding population based on large sample size. Altogether, we tagged 86 adult breeding birds at 23 subareas across a transect of about 250 km (in length) in NW Germany. Curlews started post-breeding migration right after finishing breeding or attempting to breed, which was mainly in mid-June. We identified the coastlines of Great Britain/Ireland, western France and the Netherlands, in particular the Rhine-Meuse-Delta and the Wadden Sea, as the main wintering areas of Curlews breeding in NW Germany. We found a latitudinal structuration of migration, with birds nesting further north using more northerly wintering areas. However, in some cases, wintering areas of birds of the same subpopulation were located more than a thousand kilometres apart from each other. All three main stopover areas identified by our study (German/Dutch Wadden Sea, Dutch Rhine-Meuse-Delta, French Normandy) overlap in large parts with the main wintering areas. Since Curlews spend most of the year outside their breeding areas, and wintering and stopover areas also suffer from rapid environmental change, conservation has to additionally focus on these areas. Nearly one third (29%) of the tracked birds wintered in France or used French stopover areas. Accordingly, they might potentially be affected by a resumption of hunting, which is currently in discussion in France. Our study provides an

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important basis for the protection of wintering and stopover areas of the main German breeding population but also for other wader species migrating along the East Atlantic Flyway.

1. Introduction

Across the northern hemisphere, farmland birds are in steep decline (BirdLife International, 2017; Stanton et al., 2018; Correll et al., 2019; Keller et al., 2020; Reif and Hanzelka, 2020; Kämpfer et al., 2022). As the main drivers of the recent population collapse within this group of bird species, two contrasting processes have been identified: (i) intensification of land use on productive soils and (ii) abandonment of marginal land (Henle et al., 2008; Kleijn et al., 2009). Both have led to a loss of nutrient-poor, open habitats and a homogenization at the landscape level (Butler and Gillings, 2004; Devereux et al., 2004). In migratory species, in addition to alterations in the breeding areas, environmental changes in stopovers and wintering areas may also have a decisive impact on the populations (Morrice et al., 2022). Therefore, knowledge on the location of and the environmental conditions within stopovers and wintering areas is indispensable to assess the main causes of population decreases (Chan et al., 2019; Morrice et al., 2022). This applies in particular to species whose populations are declining over large parts of its range, such as the Eurasian Curlew (*Numenius arquata*; hereinafter referred to as Curlew) (Roodbergen et al., 2012). A substantial proportion of the Curlew population in Europe breeds in agricultural grasslands and arable fields (Bauer et al., 2012; Silva-Monteiro et al., 2021). The European population has decreased by 25–29% in three generations (BirdLife International, 2021). As a result, the species is considered near threatened in Europe (BirdLife International, 2021). The German breeding population is estimated at 3600–4800 pairs (Gerlach et al., 2019) and has declined by more than 40% since the early 1970s (Hötker et al., 2007; Gedeon et al., 2014). Accordingly, the species is even considered threatened with extinction in Germany (Ryslavý et al., 2020).

So far, decreased reproduction and, hence, an insufficient number of offspring to compensate for adult mortality has been considered the main driver of the recent Curlew population collapse (Roodbergen et al., 2012). The low reproduction rates are particularly attributed to (i) high nest and chick losses by mammalian predators and (ii) intensive agricultural management practices (Grant et al., 1999; Zielonka et al., 2019). Consequently, in many European countries, extensive and costly conservation measures have been implemented to increase reproductive success in Curlew populations. Such measures include nest marking to avoid destruction by farming activities, electric fencing of nests and surrounding habitats to prevent mammalian predation, rewetting of grasslands and further measures to promote habitat quality in the breeding habitats (Kipp and Kipp, 2003; Düttmann et al., 2006; Junker et al., 2006; Boschert, 2018). In a few protected areas, these measures have been successful in fostering reproductive output and, thus, compensating for adult mortality (Gedeon et al., 2014; Gerlach et al., 2019). However, in most breeding areas, there are no signs of a general reversal of the population trend. Therefore, potential threats outside the breeding areas should be taken into account for conservation planning.

Despite the ongoing decline, the Curlew is still listed in the EU Birds Directive as a game bird in Denmark, France, Ireland and the United Kingdom (Brown, 2015). However, hunting bans were established in all these countries between 1982 and 2019 and remain in place. Nevertheless, since 2020 five cases of illegal killing of GPS-tagged Curlews were documented in France (Jiguet et al., 2021c, unpubl. data). Moreover, France is currently considering a reintroduction of Curlew hunting at the wintering areas based on a national adaptive harvest management plan (AEWA Eurasian Curlew International Working Group, 2019). Any future hunting of migrating and wintering Curlews, however, should not jeopardize the achievements of the extensive conservation measures in the breeding areas. Consequently, there is an urgent need to know (i) which proportion of the different Curlew breeding populations winters in or migrates through France and (ii) where exactly the wintering and stopover areas are located in France.

In wader species with a large breeding area, timing, stopovers and wintering areas of migrating birds can considerably differ between breeding populations or even within one breeding population (Hooijmeijer et al., 2013; Loonstra et al., 2019; Verhoeven et al., 2021). This is also true for the Curlew (Pederson et al., 2022). Breeding birds from Ireland appear to be largely resident, while most Curlews breeding in Britain seem to be short-distance migrants that winter in SW Britain, Ireland and France (Bainbridge and Minton, 1978). By contrast, Curlews nesting in subarctic regions are long-distance migrants with important wintering areas in the Wadden Sea and along the Atlantic coasts of western Europe (Bocher et al., 2017; Schwemmer et al., 2021; Pederson et al., 2022).

The German Curlew breeding population consists of two subpopulations: a small one in southern Germany and a large one in northern Germany (Gedeon et al., 2014). For Curlews breeding in NW Germany, ring recoveries suggest that the main wintering areas are the coastlines of southern England and western France (Bairlein et al., 2014). However, ring recoveries are subject to heterogeneities in ringing effort and of recovery probability in space and time (Korner-Nievergelt et al., 2010). Consequently, it is unclear whether these ring recoveries fully represent the current migration routes of the NW-German breeding population, i.e. the main wintering and stopover areas. Additionally, it has been shown that ongoing climate change (IPCC, 2021) has already had strong effects on post-breeding migration of many migratory birds (Potvin et al., 2016; Illán et al., 2022). Accordingly, recent shifts in wintering and stopover areas also seem possible for Curlews.

In this study, we investigated the wintering areas and post-breeding migration of Curlews of the main German breeding population based on a large sample size of GPS-tagged individuals. To obtain a representative overview, we tagged a total of 86 adult breeding birds over two consecutive springs at 23 subareas across a transect of about 250 km (in north-south) in NW Germany. So far, conservation efforts for the rapidly declining Curlew have mainly focused on measures within the breeding areas. However, wintering areas and migration routes of migratory birds are also affected by rapid environmental change, e.g. climate change or plans for anticipating an open hunting season for Curlews in France (see above). Our study provides an important basis not only for the

protection of wintering and stopover areas of the main German breeding population but also for other wader species migrating along the East Atlantic Flyway.

2. Material and methods

2.1. Study area

The study was carried out in the German Federal States of Lower Saxony, Bremen, and North Rhine-Westphalia (NW Germany). To obtain a representative overview of the migratory behaviour of Curlews breeding in NW Germany, we tagged 85 adult breeding birds in spring 2020 and 2021 at 23 subareas (mean $\pm$ SE: 3.8 ± 0.7 birds per subarea) across a transect of about 250 km (in length) ranging from the Wadden Sea islands in the north to the Westphalian Basin in the south (Fig. 1). Breeding habitats of Curlews on Wadden Sea islands were dominated by mosaics of high marshes and natural dune grasslands (Kämpfer and Fartmann, 2022). By contrast, breeding habitats at the mainland were characterized by different types of agricultural grasslands, which were primarily used for haymaking

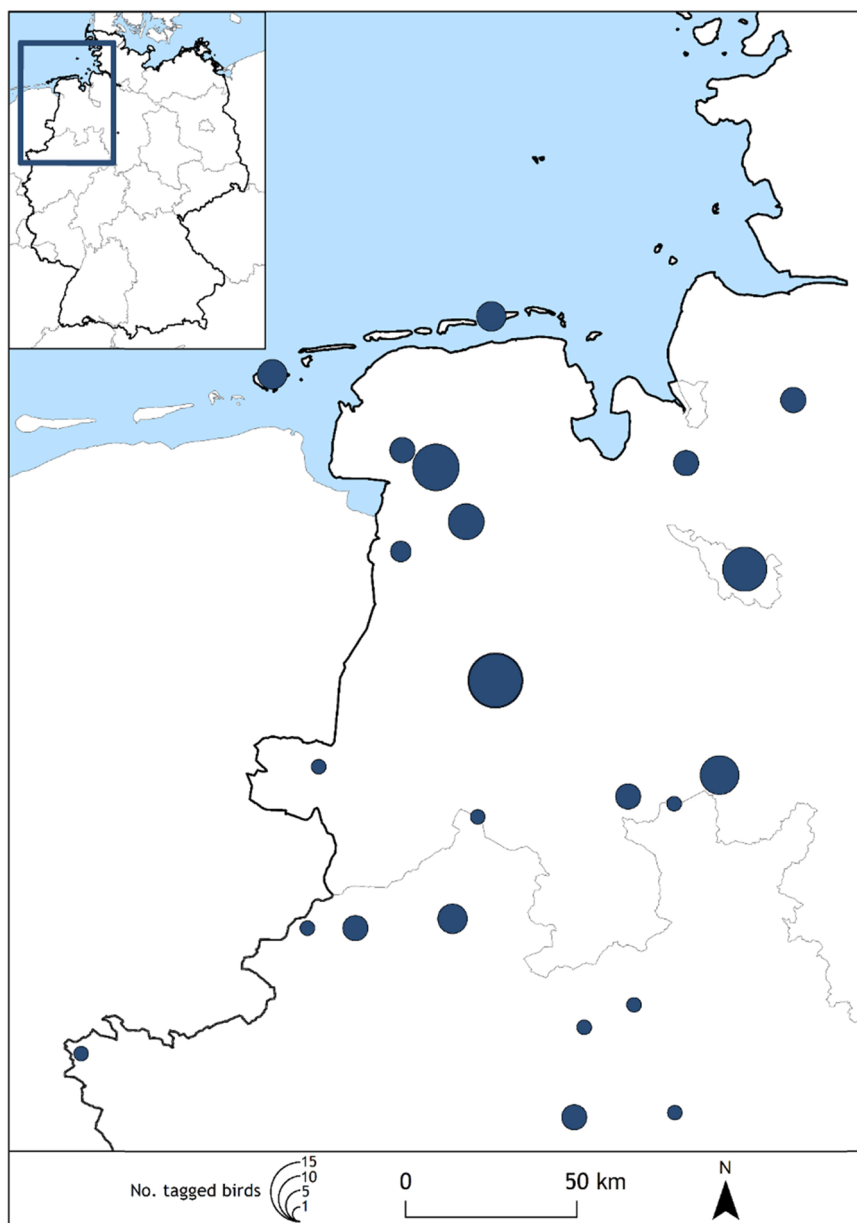


Fig. 1. Overview of the 23 subareas in NW Germany where Eurasian Curlews were tagged. $N = 86$. The size of the circle corresponds to the number of individuals tagged (see legend).

and silage production (Blickensdörfer et al., 2022). In these mainland breeding habitats, usually conservation measures for nesting waders were conducted. These measures ranged from simple protection of nest sites through marking and fencing of nests to rewetting of grasslands in combination with adapted grassland management (EEA, 2019).

2.2. Tagging

In both 2020 and 2021, Curlews were caught with a clap net on the nest between late April and the beginning of June (Fig. 1). Trapping was performed when the birds had been incubating for at least two weeks to minimize the risk of clutch abandonment. We (i) measured body weight and bill length, (ii) marked the birds with metal rings (“Vogelwarte Helgoland”) and in 2021 additionally with colour rings and (iii) equipped them with solar-powered GPS backpack tags with GSM data transmission (type Ornitrack 10 by Ornitela, 10 g). The tags were attached using a breast harness (cf. Thaxter et al., 2014; Schwemmer et al., 2021). Tag weight was 1.7% of the bird’s body mass at maximum, which is below the recommended load limit (Kenward, 2001; Bodey et al., 2018). After tagging, Curlews were immediately released into their nesting habitats.

We additionally incorporated tracks of one bird that was caught with mist nets at its wintering area in 2019 in the National Nature Reserve of Moëze-Oléron near La Rochelle (France). This bird nested in 2020 on the Wadden Sea island of Spiekeroog, which is part of our study area. It was equipped with the same tag as used in our study (cf. Jiguet et al., 2021a). However, the tag was fitted with a silicone leg-loop harness and the bird received colour rings.

All tags were programmed to record geographic positions every 10 min. Data were stored in the Movebank database (www.movebank.org). We used bill length to determine the sex of each individual according to Summers et al. (2013). From 68 of all 86 tagged birds, we gathered additional information on nesting success based on observations in the field. Nests were considered successful when breeding pairs raised at least one fledgling (Steenhof and Newton, 2007).

2.3. Post-breeding migration and wintering areas

We defined the start of post-breeding migration (= migration departure) as the timestamp of the last location that was less than 1 km away from the recorded nest before the bird had moved at least 50 km away from the nest. We assigned all locations of post-breeding migration to four different regions: (i) the Netherlands (NL), (ii) Great Britain and Ireland (GB/IE), (iii) France including the Channel Islands (FR) and (iv) the Iberian Peninsula (Spain and Portugal, ES/PT) (overlay with the map ‘countries’ in R-package ‘rworldmap’, South, 2011). Locations of individuals on the water were attributed to the nearest of the four regions.

To determine wintering areas, we first extracted all areas after migration departure where a bird stayed within a radius of 10 km for at least 3 days. Because the birds arrived in their wintering area not later than end of July, we defined the last position before 31 August as a sufficiently late threshold date. For the arrival timestamp, we used the first location in the wintering area with GPS speed below 1 m/s. Based on the location and date of migration departure and arrival in the wintering area, we calculated the migration distance (Vincenty’s distance) and duration. Additionally, we extracted stopover areas. A stopover area was defined as an area along the migration route where Curlews stayed for at least 6 h in an area with a radius of less than 10 km. The first/last location in this area with a speed below 1 m/s, indicating that the bird was on the ground, was considered as the entry and exit timestamp, respectively, of the stopover.

2.4. Statistical analysis

We performed all statistical analyses using R 3.6.1 (R Core Team, 2021). The effects of (i) breeding success and sex on migration departure and of (ii) sex on the number of stopovers and migration duration were analysed by using generalised linear mixed-effects models (GLMM; R package ‘lme4’, Bates et al., 2015). The effects of (i) migration distance on the number of stopovers, (ii) migration distance and the number of stopovers on migration duration and (iii) geographical latitude of the nesting site on latitude of the wintering area were assessed by using linear mixed-effects models (LMM) or GLMMs depending on the distribution of the data. For GLMMs with a discrete response variable, we applied Poisson linkage. Continuous response variables were modelled using gamma error structure. Differences in migration distance, migration duration and the number of stopovers between the four groups of wintering areas were assessed by GLMMs using Tukey’s test as a post-hoc test (R package ‘multcomp’, Hothorn et al., 2008).

In all models, tagging location (‘subarea’, Fig. 1) was used as a random effect to account for potential spatial autocorrelation. Variance explained by fixed effects (marginal R^2) and variance explained by both fixed and random effects (conditional R^2) were calculated according to Nakagawa et al. (2017) using the function ‘r.squaredGLMM’.

3. Results

3.1. Tagging statistics

From 86 tagged individuals, 39 were females and 47 males. Of the 68 tagged birds for which breeding success was determined, 23 successfully raised at least one chick (breeding success: 38%).

3.2. Wintering areas

The tracked Curlews used four different wintering areas along the coastline of the North Sea and Atlantic Ocean: (i) Great Britain/Ireland (44%, 38 out of 86 birds; not only southern England but also Ireland, northern England and Wales), (ii) France/Channel Islands (29%, 25 birds; mainly Brittany), (iii) the Netherlands (16%, 14 birds; particularly the Rhine-Meuse-Delta and the Wadden Sea) and (iv) the Iberian Peninsula (9%, 8 birds) (Fig. 2). One female, which bred on the Wadden Sea island of Spiekeroog, did not migrate and stayed there after both breeding seasons (2020/21 and 2021/22).

Geographical latitude of the nesting site was related to the latitude of the wintering area; i.e. birds nesting further north used more northerly wintering areas (Fig. 3). However, birds that had nested only a few kilometres apart from each other showed marked differences in their wintering areas. While some birds migrated to the nearby Netherlands, others wintered in Ireland or the Iberian Peninsula (Fig. 2).

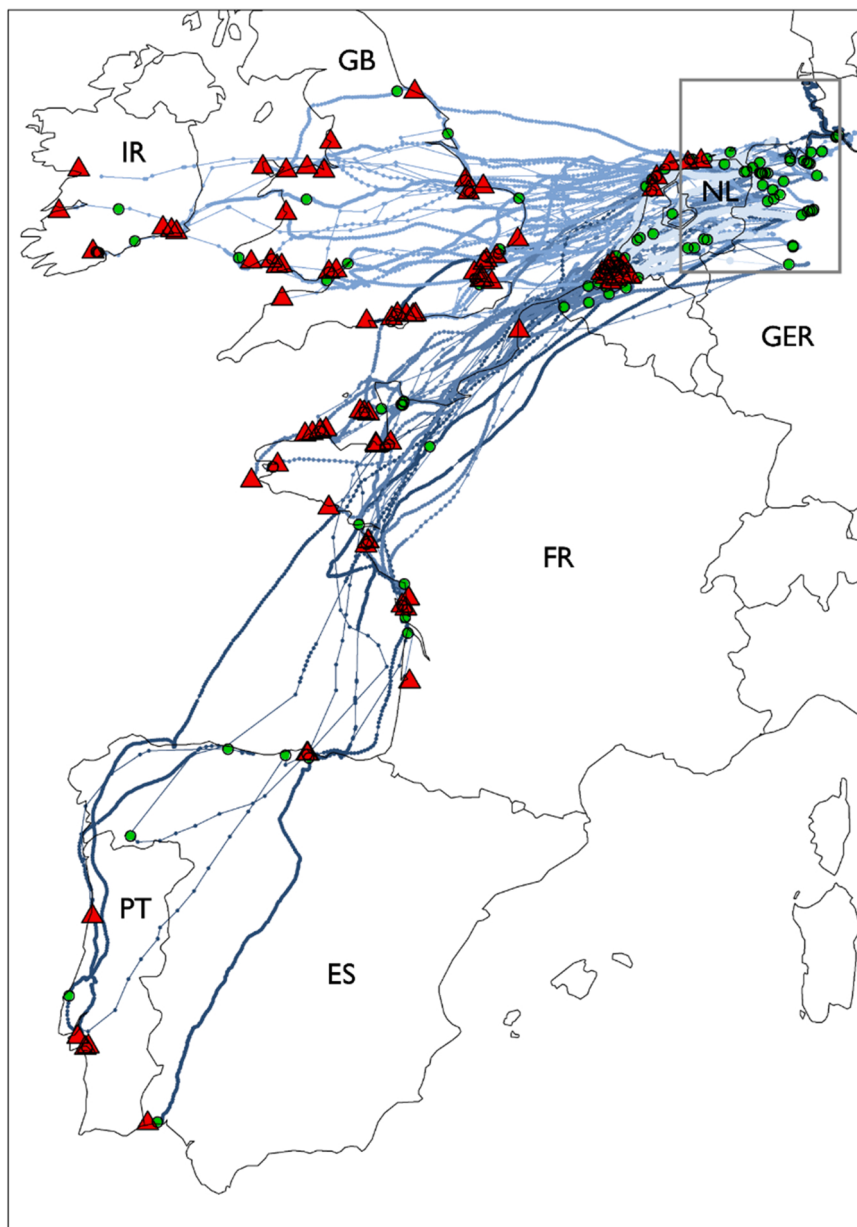


Fig. 2. Tracks of post-breeding migration of tagged Eurasian Curlews breeding in NW Germany. $N = 85$. Wintering area: red triangle, stopover: green dot, study area (cf. Fig. 1): grey square. ES: Spain, FR: France, GER: Germany, GB: Great Britain, IE: Ireland, NL: Netherlands, PT: Portugal.

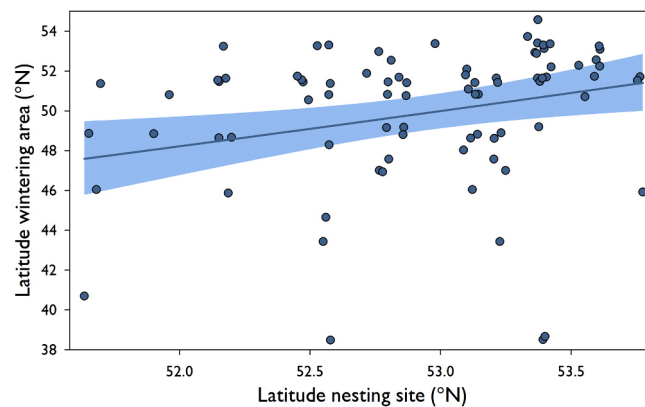


Fig. 3. Relationship between latitude of nesting site and wintering area of tagged Eurasian Curlews breeding in NW Germany. $N = 85$. GLMM (Gamma error structure): latitude breeding area – estimate $\pm$ SE: 0.36 ± 0.13 , z/t : 0.43, $** P \leq 0.01$, variance explained by fixed effects (R^2_m) = 0.07, variance explained by both fixed and random effects (R^2_c) = 0.07 (Nakagawa et al., 2017).

3.3. Post-breeding migration

Migration departure at the breeding area varied from June 1 to July 11 in 2020 and from May 17 to July 22 in 2021. However, in both years, the departure peak was mid-June (Fig. 4). The GLMMs revealed that sex and breeding success affected the timing of departure (Table 1a). Females departed on average seven days earlier than males, and birds that did not breed successfully left the breeding area on average eight days earlier than birds of successful pairs.

For shorter tracks, birds used the most direct route between the breeding and wintering areas (Fig. 2). Birds migrating to the Netherlands either crossed overland or went along the coastline to the Rhine-Meuse-Delta. Those wintering in Great Britain/Ireland crossed the North Sea and then flew over the country if heading for Wales or Ireland. Birds wintering in France/Channel Islands moved along the coastline after leaving the Netherlands. Those that wintered at the French Biscay Bay coast already turned south in Normandy or eastern Brittany and flew overland, thus using the ‘beeline’ route. Birds that continued their migration to the Iberian Peninsula mainly crossed the Bay of Biscay and then migrated along the Iberian Atlantic coast.

The average ($\pm$ SE) migration distance was 789 ± 45 km (Fig. 5a). However, migration distance varied strongly and ranged from 99 to 2119 km. Almost 50% of the birds reached their wintering area in less than three days, and the average ($\pm$ SE) migration duration was 6.3 ± 0.8 days (Fig. 5b). Overall, however, duration also varied widely with a range of 0.3–30.4 days. Two birds, for instance, although wintering in the nearby Netherlands, stayed at a stopover not far away from the breeding ground for 28 and 19 days, respectively. As a result, the duration of post-breeding migration was not affected by the distance between breeding and wintering area or by the birds’ sex (Fig. 5b, Table 1b and d). However, it increased with the number of stopovers (Table 1c). Birds arrived at the wintering areas mainly in mid-June (mean: June 23, SD: 10.9) with arrivals varying between May 31 and July 24.

Approximately three fourths of the tagged birds (72%, 62 out of 86 birds) used up to five stopover areas during their migration. The length of stay at the respective stopover site was between 0.4 and 27.9 days (mean $\pm$ SE: 2.7 ± 0.4 days). The mean ($\pm$ SE) number of

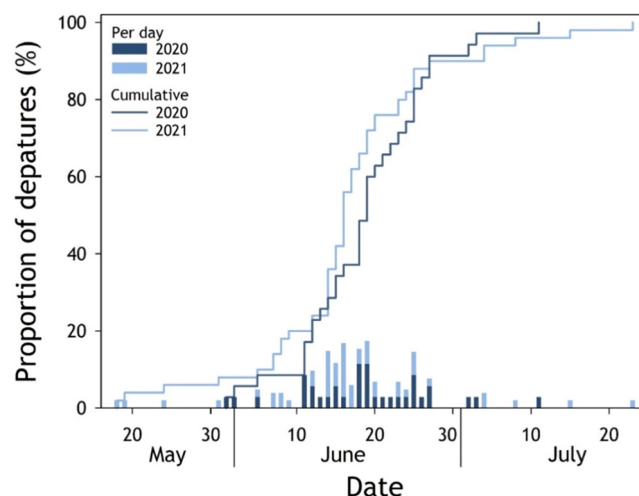


Fig. 4. Departure of post-breeding migration of tagged Eurasian Curlews breeding in NW Germany. $N_{2020} = 35$, $N_{2021} = 50$.

Table 1

Results of LMMs and GLMMs: Relationship between migration departure (a), migration duration (b, c, d) and number of stopovers (e, f), respectively, and predictor variables. R^2_m = variance explained by fixed effects, R^2_c = variance explained by both fixed and random effects (Nakagawa et al., 2017). n.s. = not significant, * $P \leq 0.01$, *** $P \leq 0.001$.

Model (response ~ explanatory)	Parameter	Estimate $\pm$ SE	z/t	P
a) Migration departure (day) ~ sex*breeding success (GLMM^a)				
$R^2_m = 0.30$, $R^2_c = 0.43$	Intercept	3.32 $\pm$ 0.04	73.94	
	Breeding success (successful)	0.17 $\pm$ 0.05	3.50	***
	Sex (male)	0.16 $\pm$ 0.05	3.40	**
b) Migration duration (days) ~ migration distance (GLMM^b)				
$R^2_m = 0.01$, $R^2_c = 0.06$	Intercept	1.41 $\pm$ 0.25	5.61	
	Distance (km/100)	0.04 $\pm$ 0.02	1.70	n.s.
c) Migration duration (days) ~ no. of stopovers (GLMM^b)				
$R^2_m = 0.36$, $R^2_c = 0.41$	Intercept	0.52 $\pm$ 0.15	3.39	
	No. of stopovers	0.63 $\pm$ 0.07	9.61	***
d) Migration duration (days) ~ sex (GLMM^b)				
$R^2_m = 0.01$, $R^2_c = 0.03$	Intercept	1.95 $\pm$ 0.19	10.15	
	Sex (male)	-0.29 $\pm$ 0.23	-1.29	n.s.
e) No. of stopovers ~ migration distance (LMM)				
$R^2_m = 0.17$, $R^2_c = 0.21$	Intercept	0.46 $\pm$ 0.30	1.54	
	Distance (km/100)	0.13 $\pm$ 0.03	4.11	***
f) No. of stopovers ~ sex (GLMM^b)				
$R^2_m = 0.02$, $R^2_c = 0.05$	Intercept	0.54 $\pm$ 0.13	4.03	
	Sex (male)	-0.27 $\pm$ 0.18	-1.48	n.s.

^a Poisson error structure

^b Gamma error structure

stopovers was 1.5 ± 0.2 (Fig. 5c). The three stopover areas, which were used most frequently were (i) the Wadden Sea (GER, NL) for birds migrating to Great Britain/Ireland, (ii) the Rhine-Meuse-Delta (NL) for birds wintering in the Netherlands, France/Channel Islands and Iberian Peninsula and (iii) the coast of Normandy (FR) for birds heading to western France and the Iberian Peninsula. Not surprisingly, the number of stopovers differed with the distance of the wintering area to the breeding area (Table 1e): It was lowest for birds wintering in The Netherlands and highest for those spending the winter at the coasts of the Iberian Peninsula (Fig. 5c). By contrast, sex-specific differences in the number of stopovers failed to appear (Table 1 f).

4. Discussion

4.1. Wintering areas

Along the coasts of the North Sea and Atlantic Ocean, we identified three main wintering areas of Curlews breeding in NW Germany: (i) England, Wales and Ireland, (ii) France/Channel Islands and (iii) the Netherlands, here especially the Rhine-Meuse-Delta and the Wadden Sea. Additionally, some birds wintered along the Atlantic coast of the Iberian Peninsula and one single individual did not migrate at all and stayed next to its breeding site at the German Wadden Sea. Overall, our findings expand the knowledge about wintering areas of Curlews of the NW-German breeding populations based on ringing recoveries, which identified the coastlines of southern England and western France as the most important wintering areas (Bairlein et al., 2014).

We consider four possible explanations for the different results of our study with GPS-tagged birds compared to the findings of previous ringing analyses. First, the identification of new wintering areas can partly be due to a higher sample size, i.e. 86 birds in our study versus 52 observations in Bairlein et al. (2014). Second, ring recoveries are subject to heterogeneities in ringing effort and of recovery probability in space and time (Korner-Nievergelt et al., 2010). Accordingly, the results are often biased. Third, in recent decades, several short-distance migrants (e.g. the Northern Lapwing [*Vanellus vanellus*]) have shifted their wintering areas northwards due to global warming (Lehikoinen et al., 2013; Potvin et al., 2016; Illán et al., 2021). Hence, the increased number of birds wintering more northerly in the Wadden Sea may also indicate northward shifts of the wintering area due to climate change. Fourth, adult survival is likely to differ between Curlew wintering areas. Since 2020, at least five tagged Curlews were illegally killed in northern France (Normandy, Haut de France) (Jiguet et al., 2021c, unpubl. data). As a result, different adult survival in the wintering areas might lead to a shift towards wintering areas with higher survival rates. However, further research on this topic is urgently needed.

In general, geographical latitude of the nesting site was related to the latitude of the wintering area; i.e. birds nesting further north used more northerly wintering areas. In line with this, a tracking study with Curlews of the breeding population of southern Germany identified wintering areas at the Atlantic coasts of southern France, the Iberian Peninsula and Morocco (LBV, 2022; Pederson et al., 2022). As a result, the wintering areas of NW- and S-German breeding populations only partly overlap.

Despite the general relationship between the geographical latitude of the nesting site and wintering area, some birds of the same local breeding population differed markedly in their wintering area. Similar observations have been obtained for Black-tailed Godwits (*Limosa limosa*) in the Netherlands (Verhoeven et al., 2021). Since individuals of the same subpopulation are expected to share some genetic background, especially in species with high nest-site fidelity such as the Curlew (Valkama et al., 1998), our findings raise the question of the underlying processes of these individual differences. Tracking over multiple years or even lifetime tracking in

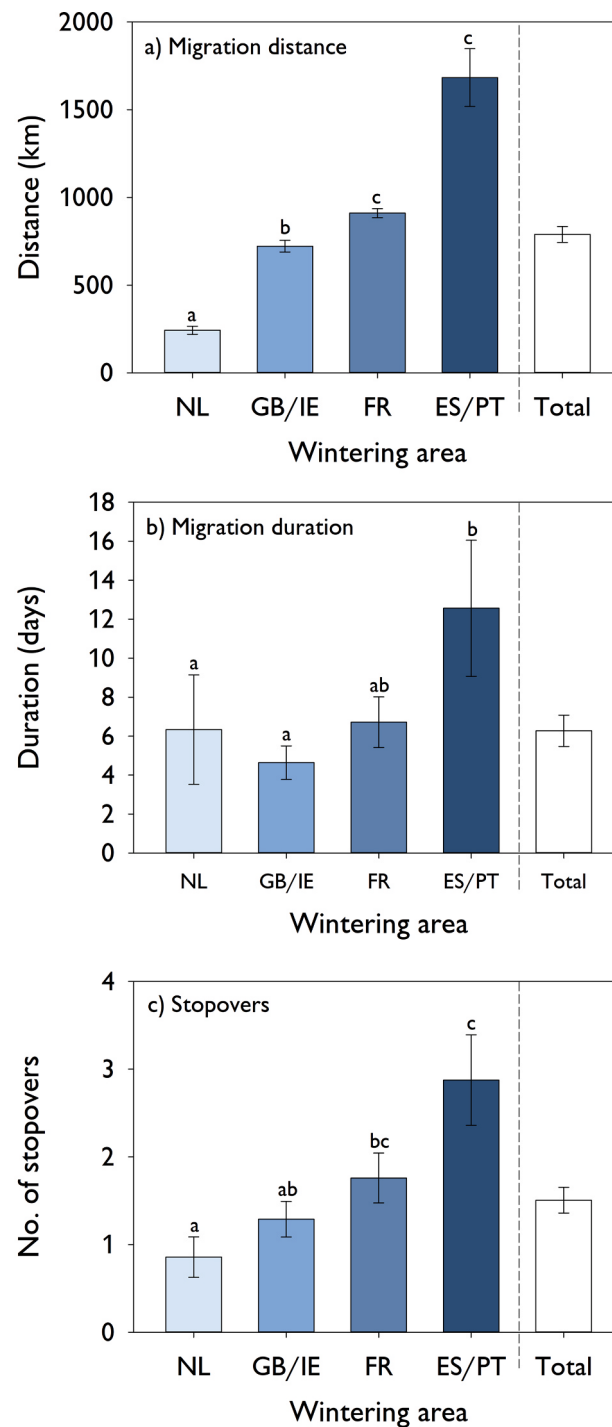


Fig. 5. Migration distance (a), migration duration (b) and number of stopovers (c) of tagged Eurasian Curlews breeding in NW Germany depending on the wintering area. NL: the Netherlands, GB/IE: Great Britain and Ireland, FR: France and Channel Islands, ES/PT: Spain and Portugal (Iberian Peninsula). Differences between groups were tested using GLMMs and Dunn's test as a post-hoc test. Different letters indicate significant differences between groups (* $P \leq 0.05$).

combination with ontogenetic experimental approaches can help to untangle the mechanisms behind this variation in wintering areas (Verhoeven et al., 2021).

4.2. Post-breeding migration

Curlews breeding in NW Germany started post-breeding migration in mid-June, right after finishing breeding or attempting to breed. The timing of migration departure in our study corresponded well with the arrival dates of colour-marked individuals in a wintering area in Great Britain (Sanders and Rees, 2018) and GPS-tracked Curlews breeding across other parts of Europe (Schwemmer et al., 2021; Pederson et al., 2022). As in other species of Curlews (Carneiro et al., 2019), female Curlews have been observed to leave their chicks earlier than males (Currie et al., 2008). In accordance with this, we detected the same sex-specific difference in the Curlews of the NW-German breeding population.

The migration routes of many tagged Curlews followed the coastlines. Possible explanations for this behaviour are (i) the high availability of foraging habitats along the coasts (Masero et al., 2000) and (ii) geographical cues that facilitate orientation during migration (Alerstam, 1996; Meyer et al., 2000). However, we also observed overland flights, which significantly reduced the migration distance and enabled an early arrival at the wintering areas.

In our study, the average migration duration was about 6 days, and almost 50% of the tagged birds even reached their wintering area in less than three days. Early arrival at the wintering areas has the advantage that the birds can occupy and defend the most suitable foraging habitats against newcomers (Pederson et al., 2022). However, some birds migrated over several weeks, while others flew the same distance in just a few days. Strong individual differences in migration behaviour have already been obtained in other wader species (Hooijmeijer et al., 2013; Loonstra et al., 2019; Verhoeven et al., 2021; Pederson et al., 2022). Besides individual fitness (Anderson et al., 2019; Jiguet et al., 2021b) and initial fuel reserves before departure, habitat quality—including prey availability at stopovers—is also an important factor that determine the number of stopovers to reach the wintering areas (Anderson et al., 2021). Stopovers are also known to be important (i) for recovery after strenuous migration, (ii) to avoid adverse environmental conditions for flight and (iii) for further reasons such as minimising predation, spatio-temporal adjustments or social interaction (Linscott and Senner, 2021; Schmaljohann et al., 2022). However, for a better understanding of the use of certain stopovers by Curlews in general and the marked individual differences in particular, further studies are needed.

The mean ($\pm$ SE) migration distance between nesting sites and wintering areas in our study (789 ± 419 km) was three times shorter than for Curlews that breed in Russia and winter in the German Wadden Sea (2339 ± 612 km) (Schwemmer et al., 2021) and even four times shorter compared to birds nesting in other parts of Europe (Estonia, Poland, S Germany) (3362 ± 1351 km) (Pederson et al., 2022). This confirms the high variability of migratory behaviour of different Curlew breeding populations, ranging from residents in Ireland (Wernham et al., 2002) to long-distance migrants in Russia (Pederson et al., 2022).

5. Implications for conservation

Despite extensive conservation measures in German breeding areas, most Curlew populations are still in decline (Gedeon et al., 2014; Gerlach et al., 2019). Since Curlews spend most of the year outside their breeding area (Bauer et al., 2005; Bairlein et al., 2014) and wintering and stopover areas also suffer from rapid environmental change (see Introduction), conservation efforts should additionally focus on these areas (Schuster et al., 2019). Based on our study, the coastlines of Great Britain/Ireland, western France and the Netherlands are the main wintering areas of Curlews breeding in NW Germany. We identified the Wadden Sea, the Rhine-Meuse-Delta and the coasts of the French Normandy as the most important stopover areas for this breeding population. Since Curlew breeding populations are declining in many European countries, the consideration of a resumption of Curlew hunting in France during the migration period and in winter (see AEW Eurasian Curlew International Working Group, 2019) deserves further attention. The increasing number of wintering Curlew in Great Britain during the 1980s and early 1990s, for instance, can at least partly be explained by the cessation of hunting in the early 1980s: it reduced adult mortality and led to a decrease of disturbance of wintering Curlews (Taylor and Dodd, 2013; Woodward et al., 2022), which has been shown to displace birds on the wintering grounds (Madsen and Fox, 1995).

In general, an increase in adult mortality must be compensated by higher reproductive success to maintain a stable population size. Based on the proportion of tagged birds that rested or wintered in France, it is estimated that Curlew hunting in France will affect about 30% of the birds of the NW-German breeding population, whereby the effect may be different between subpopulations. Moreover, there are reports of curlew poaching in France despite the current hunting moratorium (Jiguet et al., 2021c). In northern France (Normandy, Haut de France) in particular, where hunting on the coast is traditional and open in August, one month earlier than on the mainland, there are indications of high hunting pressure. Moreover, the species might be sensitive to wind farm collision (Jiguet et al., 2021a; Schwemmer et al., 2022), which could further jeopardize conservation efforts on breeding grounds. Although Schwemmer et al. (2023) observed horizontal and vertical avoidance behaviour of migrating Curlews facing offshore windfarms, a considerable proportion of the curlew population might cross offshore windfarms at rotor heights resulting in a potential risk of collision. In Lower Saxony, productivity in different subpopulations currently ranges between 0.18 and 0.84 fledged chicks per breeding pair (C. Peer-enboom, NLWKN unpubl. data). However, in most subpopulations, productivity is below 0.45 chicks per pair. According to a long-term study on the productivity of a Curlew population in North Rhine-Westphalia, it is suggested that a minimum of 0.41 fledged chicks per breeding pair is required for a stable population. On a global scale Viana et al. (2023) found a productivity of 0.68 to be needed to achieve a stable population. In summary, we conclude that most Curlew subpopulations breeding in NW Germany are currently incapable of compensating for higher adult mortality (e.g. by hunting).

Further research is necessary to secure long-term survival of Curlew populations. Regarding influences of Curlew hunting, comparative survival analyses should be carried out for adult and juvenile birds as it is likely that unexperienced juvenile Curlews might suffer a higher mortality risk when they arrive in the wintering areas in August, when the hunting season is already open in France. Therefore, tracking of juvenile birds is important, which we have started in 2022. Detailed studies on the habitat quality at stopover and wintering but also at breeding areas for Curlews are urgently needed as well. The same is true for the underlying processes behind the individual differences in migration behaviour of birds of the same subpopulation. Global warming is rapidly accelerating and changing environmental conditions (IPCC, 2021). Accordingly, it is likely that climate change will affect Curlew migration routes in general and the importance of the current stopover and wintering areas in particular. Therefore, research on this topic is also required. Overall, such research will be an important basis to predict the ability of Curlews to track current and future environmental change (Senner et al., 2020; Verhoeven et al., 2021).

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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