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Small Space but High Diversity: Spatial and Temporal Habitat Use by Endangered Eurasian Curlew at Wintering Sites Throughout Europe

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Abstract

Coastal, and to a lesser extend inland wetlands, are critical habitats for wintering shorebirds. Given the significant population declines of most shorebird species worldwide, the current degradation of coastal habitats through climate change and human activities raises severe conservation concerns. In order to ensure sufficient and adequate habitats and maintain the populations, a thorough understanding of space use by wintering shorebirds is urgently required. However, overwintering strategies have rarely been investigated throughout the entire range of a shorebird species. This study thus aimed to investigate the spatio-temporal use of wintering habitats by Eurasian curlew *Numenius arquata* on a European scale, using a large international dataset. A total of 204 adult curlews were tagged with GPS devices at different wintering and breeding sites across Europe between 2014 and 2021, and the data were used to analyse home range size, habitat use, and phenology. The birds were faithful to their wintering sites throughout the winter. Their home ranges were small compared with other shorebirds but highly variable between individuals (533 ± 449 ha). Winter home range areas did not differ in relation to sex or body mass, but were weakly related to the wintering latitude, particularly linked to the many birds wintering in the Wadden Sea. Curlews used a high diversity of coastal and inland habitats, with higher occurrences on mudflats and saltmarshes. Despite the inter-individual variability in space use, the high wintering-site fidelity shown by this near-threatened species raises concerns about its capacity to respond to environmental modifications in coastal regions.

Keywords Avian Ecology · GPS Tracking · Coastal Wetland · Wintering Strategy · Home Range · Saltmarsh

Introduction

Many bird species use coastal habitats during some or all of their life cycle, including long-distance migrants that often rely on these areas for breeding, wintering, or stopover during migration (Hayman et al. 1986; Delany et al. 2009). However, various economic, social, and environmental pressures faced by coastal ecosystems may lead to a massive degradation or even a total loss of coastal habitats (Crain et al. 2009; Schutyser 2010; Nichols et al. 2019), thus reducing the sizes of the available habitats for bird and other animal communities (Feagin et al. 2005). As a result, more than two thirds of European coastal habitats and half of the species that use them currently have an unfavourable conservation status (Schutyser 2010). Understanding the patterns of coastal habitat use by birds is therefore crucial to inform bird conservation and management decisions (Mace et al. 1983; Weller 1999).

Knowledge about individual home ranges (HRs) is a major tool in assessing the patterns of space use by animals (Moorcroft 2012; van Moorter et al. 2016). A HR is defined as the area throughout which an individual carries out its regular activities such as foraging, mating, and rearing its young (Burt 1943; Powell 2000). The size and shape of an animal's HR are primarily driven by the distribution and availability of food resources (Brown 1975; Schoener 1983). However, HRs may also be directly affected by many other factors, such as age, sex, body mass, habitat structure, and weather conditions (Mace et al. 1983; Rolando 2002; Ottaviani et al. 2006; O'Donnell and Delbarco-Trillo 2020).

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In recent decades, biologging, i.e., the use of autonomous bird-borne devices such as GPS devices, has offered cost-effective opportunities to track animal HRs with high spatial and temporal resolutions (Hart and Hyrenbach 2010).

Migratory shorebirds visit a wide range of coastal habitats and inland wetlands during winter, i.e., outside their breeding and migration periods (Hayman et al. 1986; van de Kam et al. 2004; Delany et al. 2009; Conklin et al. 2014). They usually use intertidal habitats for feeding at low tide and supratidal habitats for roosting at high tide (Rogers 2003; Choi et al. 2014; Jourdan et al. 2021). The current degradation of coastal ecosystems thus has potentially important implications for shorebirds (Galbraith et al. 2002; Martin et al. 2007; Runge et al. 2014; Zurell et al. 2018; Koleček et al. 2021), with more than half of all shorebird species showing declining populations (Delany et al. 2009; Pearce-Higgins et al. 2017). The loss of their favoured habitats (Galbraith et al. 2002; Koleček et al. 2021; Santos et al. 2023) including intertidal mudflats (Evans and Pienkowski 1983; Studds et al. 2017), as well as reduced prey availability (Duijns et al. 2017), seem to be the main drivers within wintering grounds. In addition, high predation pressures (Van Den Hout et al. 2008; Dekker and Drever 2016), sea-level rises (Galbraith et al. 2002; Iwamura et al. 2013), and increasing human activities (Burger et al. 2004; Palacios et al. 2022) may also affect their winter survival (Goss-Custard 1980). Human activities in inland wintering habitats, such as drainage and agricultural intensification, also degrade habitats used for feeding and resting (Hayman et al. 1986; reviews in Sutherland et al. 2012). Low-quality wintering habitats may have carry-over effects, such as reduced breeding success (Gill et al. 2001; Gunnarsson et al. 2005), thereby affecting the fitness and dynamics of the populations (Pienkowski and Evans 1984; Marra and Holmes 2001).

The Eurasian curlew, including the subspecies *Numenius arquata arquata* (hereafter curlew), has notably undergone rapid population declines across Europe, with only an estimated 212,000–292,000 breeding pairs (Birdlife International 2022), and is therefore listed as Near-Threatened on a global scale. These declines are primarily driven by low reproductive success, and the trend can thus only be reversed by increasing productivity and/or adult survival (Brown 2015). An overview of the spatio-temporal use of wintering habitats by curlews is therefore required to identify the potential threats faced by the species in their wintering grounds, and to guide appropriate conservation measures. Few studies to date have focused on specific wintering sites used by curlews (Townshend 1981a; Mander et al. 2022); however, large-scale investigations covering the entire wintering range of the subspecies, extending from Western Europe to the Balkans and from the British Isles to Northwest Africa (Delany et al. 2009), are needed to provide a comprehensive understanding of habitat use by wintering curlews and to support the implementation of efficient strategic conservation decisions (Koleček et al. 2021).

In this study, we equipped 204 curlews throughout Western Europe with GPS tags, with the aim of providing the first data on the spatio-temporal use of wintering sites by curlews across their range. We first described individual spatial use by focusing on geographic distribution, local space use, and habitat use. Given that most shorebird species (including curlews) are predators specialized for feeding on intertidal mudflats during the winter (Lack 1986; van de Kam et al. 2004; Colwell 2010), we predicted that individuals would primarily utilize coastal habitats, particularly mudflats, during this period. We also investigated the effects of sex (Rolando 2002), body mass (Schoener 1983; Ottaviani et al. 2006), and latitude of the wintering site (Harestad and Bunnel 1979) on the sizes of individual wintering HRs, and analysed the wintering phenology of the species (i.e., beginning, end, and duration of the wintering period) according to the latitude of the wintering sites. We hypothesized that curlews carried out chain migration (i.e. birds wintering at northern sites breed at higher latitudes; Pederson et al. 2022; Kämpfer et al. 2023), and therefore predicted that birds wintering in more northern areas would depart later to avoid unfavourable conditions at their breeding grounds (Schwemmer et al. 2021), but would have similar wintering durations.

Materials and Methods

Study Area and Tagging of Curlews

We tagged 204 adult curlews in seven countries and 16 sites across eight programs in Europe between 2014 and 2021 (four German, one Polish, one Estonian, and two French, one of which included tagged birds in France, Estonia, Finland, the Netherlands, and the United Kingdom) (Fig. 1, Table 1). Birds were caught either at their breeding grounds ($n = 145$) using nets (scoop, clap, or mist nets) or cage traps placed at the nest, or at their wintering grounds ($n = 59$) in the German Wadden Sea and in French Pertuis Charentais using mist nets placed at high-tide roosts (Table 1, Fig. 1).

Birds were ringed and weighed at the time of capture. Bill, wing, and tarsus lengths were measured to the nearest mm (Redfern and Clark 2001) and age was estimated based on their plumage patterns (Prater et al. 1977). Individuals captured as juveniles that were subsequently tracked for several years were considered as adults after their first migration to their breeding area. Sex was determined by genetic analysis of blood samples ($n = 28$; Tauros Diagnostics, Berlin, Germany), morphologically based on bill length (shorter in males than in females, $n = 164$; 144.5 ± 10.6 mm in females and 116.7 ± 7.5 mm in males; Summers et al. 2013), or

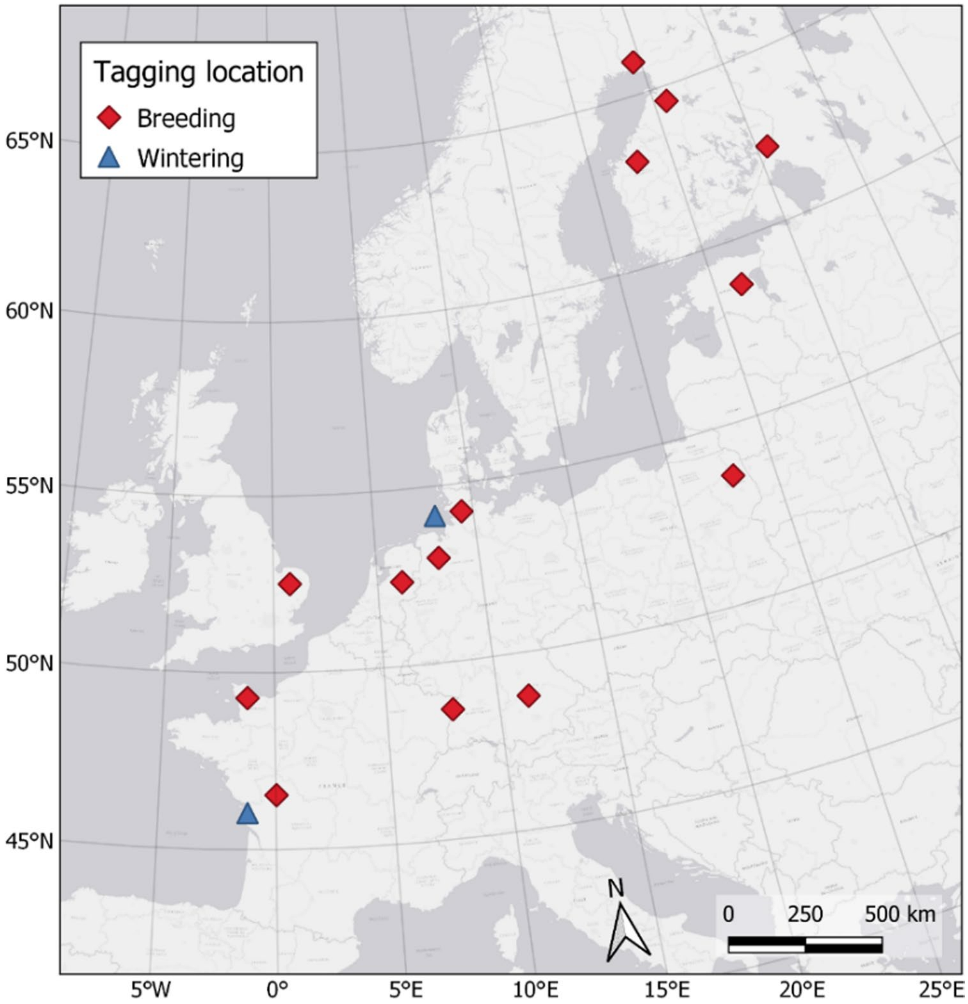


Fig. 1 Locations of tagging sites for curlews tagged during the winter or breeding season

by visual inspection of relative size at breeding catching sites (*n* = 8). There was no difference in sex determination between the molecular and morphometric methods (*n* = 27) (Pederson et al. 2022). The tracked birds included 111 males and 90 females, and three individuals could not be sexed.

Thirteen different types of solar GPS tags from four manufacturers were used (Table 1), including five models from Ornitela, Lithuania (OT-10 (10 g); OT-15 (15 g); OT-20 (20 g); OT-E10 (12 g); OT-E20B (20 g)), three by Ecotone, Poland (Sterna (7.5 g); Saker L (17 g); Skua (17 g)), one from Milsar, Poland (M-9 (16 g)), and four from e-obs, Germany (e-obs (14,5 g, 27 g, 28 g, 40 g)). None of the tags weighed > 5% of the bird's body mass (1.6 ± 0.6%, n = 178, not all birds were weighed) (Cochran 1980). The devices were positioned using the "wing-loop" (*n* = 139) (Guillaumet et al. 2011) or "leg-loop" method (n = 65) (Mallory and Gilbert 2008). The bird's movements were tracked at time intervals of 1 min to 1 h, according to the model and battery charge.

Data were recorded for multiple years for some individuals, but a single wintering period per bird was selected in this study (i.e. the longest period recorded) (Mitchell et al. 2019). Among the retained wintering periods, 75 were complete and 129 were incomplete due to loss or malfunctioning of the GPS tags or bird mortality.

Wintering Home Range

Adults with a minimum of 2000 GPS fixes recorded during a minimum of 90 wintering days (Jourdan et al. 2021) were selected for HR analyses (*n* = 172).

The location of the first wintering roost was determined visually using satellite images as the first area where birds stayed after their post-breeding migration. The start of the wintering period was defined as the time of arrival at the first wintering roost. The wintering period ended when the birds first moved > 20 km away from the wintering area to start their pre-breeding migration. If the birds did not initiate pre-breeding migration, GPS fixes located > 20 km from the first wintering roost for up to 7 days were considered as belonging to another wintering site.

Space use was investigated by estimating the utilization distribution (UD), i.e., the probability density of an animal

Table 1 Overview of tagging information. n = number of individuals with a complete wintering period

	Tagged adults	Males	Females	Unknown	n	Device model	Device mass (g)	Time interval range (min)	Median time interval (min)	Study event	Activity when tagging	Attachment method	Catching method	Sexing method
Germany North	31	15	15	1	15	Skua, OT-10, OT-15, OT-20	10–20	1–60	5	2014–2022	Breeding (1) Wintering (30)	Wing-loop	Scoop net Mist net on roost	Genetics
Germany South	8	3	3	2	6	OT-E10 Saker L	12–17	10–60	15	2017–2021	Breeding	Wing-loop	Cage trap on nest	Biometrics
Germany Southwest	9	5	4	0	6	e-obs OT-E20B	14,5–40	5–20	19	2014–2022	Breeding	Wing-loop	Cage trap on nest	Visual
Germany Northwest	86	47	39	0	23	OT-10, OT-E10	10	1–5	5	2020–2022	Breeding	Wing-loop	Clap net on nest	Biometrics
France	41	24	17	0	11	Sterna, OT-10, OT-E10	7,5–12	2–30	5	2015–2022	Breeding (12) Wintering (29)	Leg-loop	Cage trap on nest or Mist net Mist net on roost	Biometrics
Poland	12	4	8	0	7	Milsar M9	16	4–10	9	2013; 2017–2020	Breeding	Leg-loop	Cage trap on nest	Biometrics
Estonia	6	5	1	0	3	e-obs OT-E10	12–28	5	5	2015–2016; 2020	Breeding	Wing-loop	Cage trap on nest	Biometrics
Finland	7	6	1	0	4	OT-E10	12	5	5	2020–2022	Breeding	Leg-loop	Cage trap on nest	Biometrics
The Netherlands	3	2	1	0	0	OT-E10	12	5	5	2021–2022	Breeding	Leg-loop	Cage trap on nest	Biometrics
United Kingdom	1	0	1	0	0	OT-E10	12	5	5	2021–2022	Breeding	Leg-loop	Cage trap on nest	Biometrics
Total	204	111	90	3	75									

being present in a given area (Jennrich and Turner 1969). The UD was calculated by the kernel estimation method (kde; van Winkle 1975) using the 'kernelUD' function ('adehabitatHR' package, Calenge 2023) in R (version 4.0.5, R Core Team 2021). The HR (95% kde) and core area (CA: 50% kde) were calculated for each wintering site for each individual (Worton 1989). The HR was defined as the area throughout which an individual carried out its regular activities (Burt 1943; Powell 2000), here feeding and roosting (Harris et al. 1990), and a CA corresponded to the preferred area used by an animal inside its HR, from which a high proportion of the locational records was obtained.

The accuracy of the kernel representation was determined by a single smoothing factor (*h*), allowing us to compare the HRs of all tracked individuals. To determine *h*, we visually compared the kernels of several individuals with more- or less-dispersed HRs (Schuler et al. 2014). An *h* of 80 m was determined to be the best compromise between under- and over-smoothing and was therefore used in this study. The cell size was adjusted to 20 m because of a minimum accuracy of all the GPS tags of 10 m. Albers equal-area projection was used to produce HRs due to the range of wintering site latitudes (World Geodetic System 1984, minimum latitude = 32°53′58.45" N; maximum latitude = 57°37′21.18" N) and longitudes (mean longitude = 0°30′00.89" W). This equivalent projection allowed us to preserve the surface areas locally (Snyder 1993) and compare the HR sizes for all individuals, regardless of the latitude of their wintering sites. In view of the high fidelity of curlews to their wintering sites across years (Bainbridge and Minton 1978; Delany et al. 2009; Brown 2015; Schwemmer et al. 2016; Sanders and Rees 2018), we compared the HRs of all individuals regardless of the year. For birds using both coastal and inland habitats during the same wintering period, HRs were produced separately at both locations. All maps were generated using QGIS software (3.10 A Coruña, QGIS Development Team 2019).

Habitat Identification

Four wintering site statuses were attributed to the 204 individuals: birds were considered as “coastal” if they wintered along the coastline; “inland” if they only used terrestrial habitats ≥ 2 km from the coast; “coastal and inland” if they visited coastal and inland areas simultaneously, with a CA covering both; and “coastal then inland” if they used coastal habitats before switching inland during their wintering period.

The main habitats used by wintering curlews were determined visually by cross-referencing the HR of each bird with satellite images from the same wintering year extracted from Google Earth. Eight habitats were characterized according to the European nature information system (EUNIS) classification (European Topic Centre on Biological Diversity 2012): mudflats (A2.3), saltmarshes (A2.5), marshes (C1.5), sandflats (A2.2), meadows (E2.2), crops (I1), saltworks (J5.12), and rocky shores (A1.4) (Fig. 2). An “other” category was created to include specifically human infrastructures. The presence or absence of these habitats within the HR was recorded but not quantified for each individual.

Statistical Analyses

We distinguished between birds equipped in winter and those equipped in summer, to avoid overestimating the weights of the two study sites where birds were tagged during winter (Fig. 1).

All statistical analyses were performed using R software (version 4.0.5, R Core Team 2021). The mean (± standard deviation) wintering duration, arrival date, departure date, and HR size were compared among individuals wintering in the Wadden Sea, the Pertuis Charentais, and at other wintering sites, using Kruskal–Wallis rank sum tests using the ‘kruskal.test’ function (‘stats’ package, R Core Team 2021). Curlews wintering in the Wadden Sea and the Pertuis Charentais were separated from other birds because of the high respective numbers of individuals ($n = 39$ and $n = 33$, respectively). Groups with significantly different medians were determined by nonparametric Dunn’s post hoc tests using the DunnTest function (‘DescTools’ package, Signorell 2023). Relationships between the wintering site latitude and the duration and end date of the birds’ wintering period were determined by Kendall’s correlation tests using the ‘cor.test’ function (‘stats’ package).

The effects of sex (Rolando 2002), body mass (Schoener 1968; Ottaviani et al. 2006), wintering-site latitude (Harestad and Bunnel 1979), and wintering duration on individual HR size were jointly tested by generalized additive models (GAMs) using the ‘gam’ function (‘mgcv’ package, Wood 2017). Because body mass is highly collinear with sex, with females being bigger than males (Prater et al. 1977; Cramp et al. 1983), the observed body mass values were replaced by the deviations of the values from the sex-specific mean values (842.7 ± 113.4 g in females, 705.9 ± 83.0 g in males). The non-binomial distribution was recognized as the most appropriate distribution after comparing the Akaike information criterion values of different distribution families and was therefore used to fit the model.

Results

Distribution of Tracked Curlews

Tracked curlews wintered at 66 sites spread over a large geographical area from Morocco (32°58′44" N) to Scotland (57°36′07" N) (Fig. 3, Online Resource 1). Most curlews were “coastal” (85.3%), while some were “coastal and inland” (10.3%), “coastal then inland” (2.4%), or “inland” (2.0%) (Figs. 3 and 4).

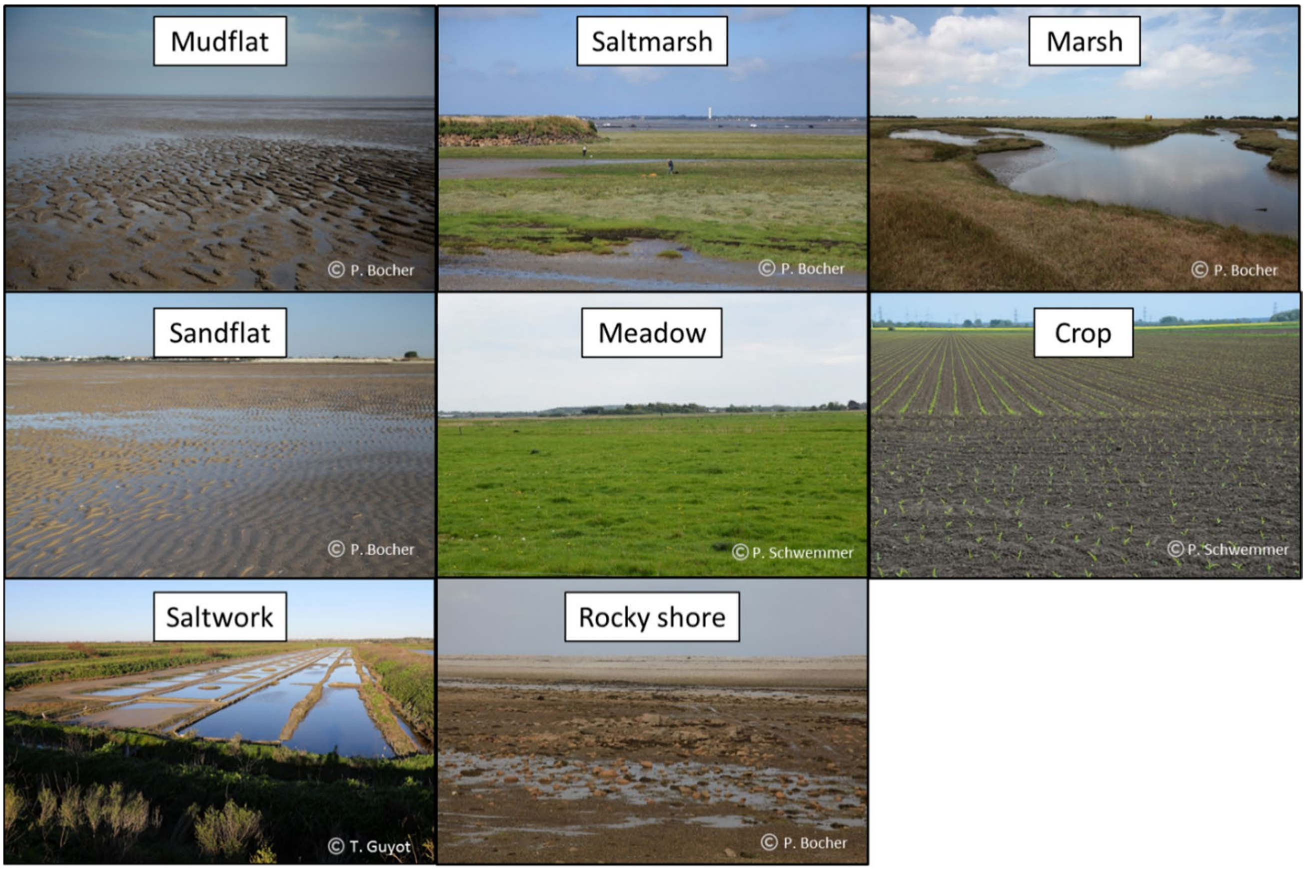


Fig. 2 Habitats used by wintering curlews in this study

Only 13 of the 204 birds (6.4%) moved to another site during the wintering period (mean distance: 265 ± 258 km; range: 40–1,003 km), either permanently ($n = 3$) or by exploiting one ($n = 4$) or two ($n = 1$) other sites before returning to their original site at the end of the wintering period. Five of these birds that moved were not tracked over the entire wintering period and it was therefore unknown if they returned to their original site before starting their pre-breeding migration. Nine of the moving birds used coastal and inland habitats, while the other four only used coastal habitats.

Wintering Phenology

The wintering period lasted an average of 8.5 months (mean: 263 ± 20 days, n = 75), starting between May and August (May 30 – Aug 2; $n = 176$) and ending between February and April (Feb 3 – Apr 30; $n = 93$) (Table 2, Fig. 5a). The wintering durations were longer in the Wadden Sea and the Pertuis Charentais (Dunn's test, Wadden Sea: mean rank difference = 32.9, $P < 0.001$; Pertuis Charentais: mean rank difference = 25.56, $P < 0.01$) due to later pre-breeding migration departures (Wadden Sea: mean rank difference = 49.36, $P < 0.001$; Pertuis Charentais: mean rank difference = 34.02, $P < 0.001$). Birds tagged during winter (i.e. at the Wadden Sea and Pertuis Charentais) mostly left their wintering sites to reach northern breeding sites in Russia and Finland (Wadden Sea 70.7% and Pertuis Charentais 65.5%) (Fig. 5b). Moreover, individuals in the Wadden Sea started their wintering period significantly later than individuals wintering in other sites (mean rank difference = 31.594, $P < 0.01$) (Table 2), except for the Pertuis Charentais ($P = 0.457$).

The wintering duration was significantly longer for birds that wintered further north (Kendall's correlation test, tau = 298, $P < 0.001$) (Online Resource 2a). This tendency can be explained by a late departure to the breeding grounds for some northern-wintering birds (tau = 331, $P < 0.001$) (Online Resource 2b), especially for birds wintering in the Wadden Sea.

HR Size

Curlews exploited average HRs of 533 ± 449 ha, with high variability between individuals (range: 46–2,397 ha, $n = 172$) and mean CA surfaces of 62 ± 52 ha (range:

Fig. 3 Location of wintering sites for all tracked curlews and their coastal or inland status ($n = 204$)

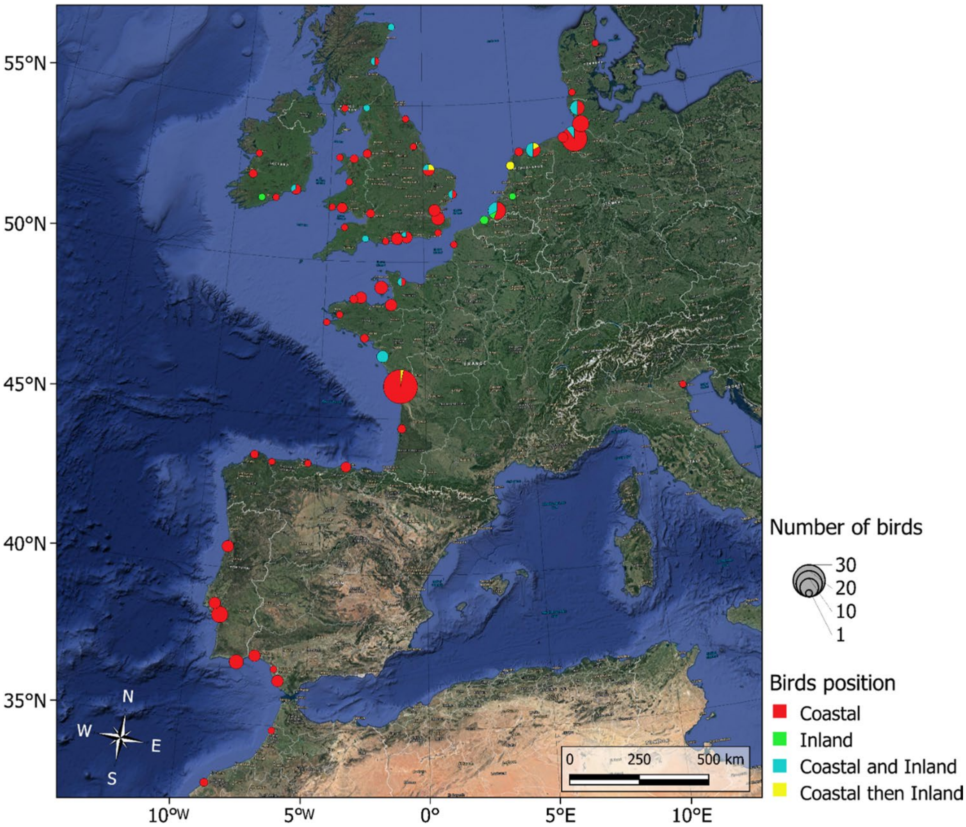


Fig. 4 Numbers of curlews tagged during the breeding and wintering periods according to coastal or inland status

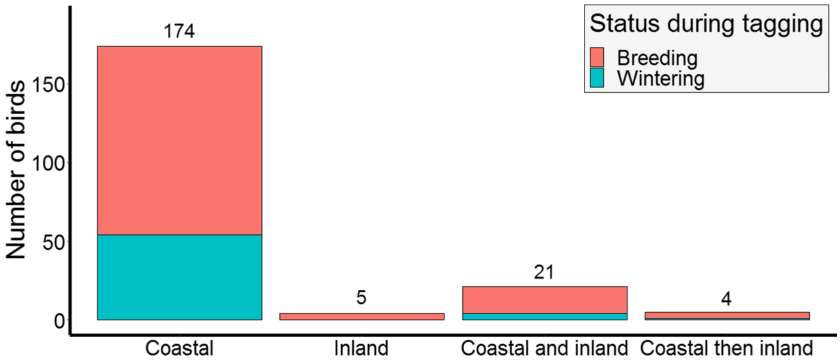
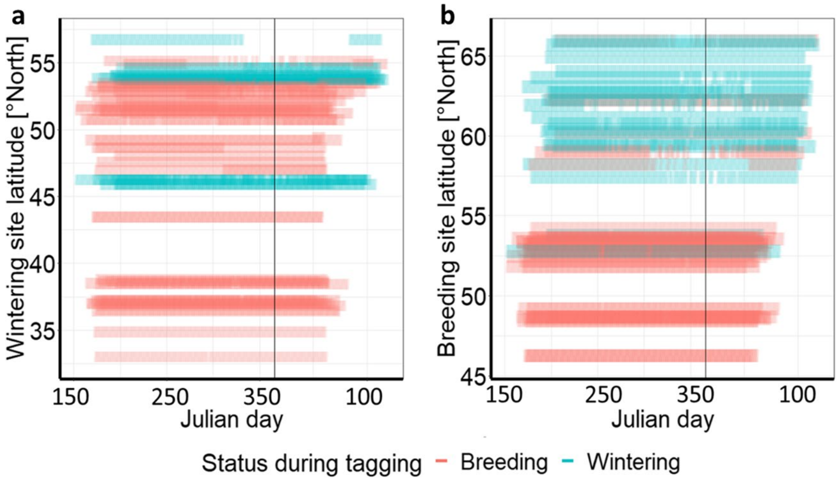


Table 2 Duration and arrival and departure dates (mean ± standard deviation (n) (range)) of wintering periods for curlews tagged at either their wintering (Wadden Sea or Pertuis Charentais) or breeding grounds (Others). Values with shared letters are not significantly different from each other ($P > 0.05$)

Wintering ground	Wintering duration (days)	Arrival date	Departure date
Wadden Sea	283 ± 14 ($n = 18$)^{a} (239–312)	Jul 2 ± 13 ($n = 35$)^{c} (Jun 9 – Jul 30)	Apr 17 ± 12 ($n = 22$)^{e} (Mar 3 – Apr 30)
Pertuis Charentais	277 ± 21 ($n = 8$)^{a} (233–298)	Jun 27 ± 12 ($n = 15$)^{cd} (May 31 – Jul 14)	Apr 6 ± 13 ($n = 22$)^{e} (Mar 2 – Apr 22)
Other sites	254 ± 15 ($n = 49$)^{b} (224–282)	Jun 23 ± 12 ($n = 126$)^{d} (May 30 – Aug 2)	Mar 3 ± 15 ($n = 49$)^{f} (Feb 3 – Apr 30)

Fig. 5 Phenology of wintering periods for individuals tagged during the breeding and wintering periods (represented by each horizontal line) according to (**a**) wintering-site latitude and (**b**) breeding-site latitude (only for individuals with entire wintering period recorded, *n* = 75)



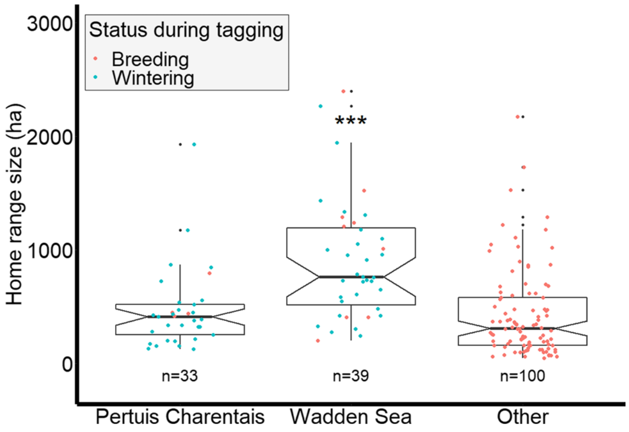


Fig. 6 HR sizes for curlews tagged during the breeding and wintering periods wintering in the Pertuis Charentais, Wadden Sea, and other wintering sites. Medians, 95% CIs, and number of individuals per category (*n*) are shown

5–296 ha, *n* = 172). Birds wintering in the Wadden Sea had significantly larger HRs (mean: 902 ± 523 ha; range: 201–2,397 ha, *n* = 39) than those wintering in the Pertuis Charentais (mean: 466 ± 355 ha; range: 125–1,927 ha, *n* = 33, Dunn's test, mean rank difference = 42.95, $P < 0.001$) and those in other wintering sites (mean: 432 ± 391 ha; range:46–2,170 ha, *n* = 100, mean rank difference = − 54.78, $P < 0.001$) (Fig. 6).

Wintering-site latitude was positively related to HR size (GAM: Z = 4.02, $P < 0.001$) (Table 3). However, wintering duration ($P = 0.059$), sex ($P = 0.760$), and body mass ($P = 0.341$) did not explain the observed high variability in HR size (Table 3).

Habitat Use

Curlews used an average of 2.8 ± 1.0 (range: 1–6) habitat types (defined according to the EUNIS list, see Methods) considering HR surface (95% kde) and 2.3 ± 0.8 (range: 1–5) habitats considering CA surface (50% kde) (see Fig. 7 for examples). More than half of the individuals exploited mudflats (*n* = 137) and saltmarshes (*n* = 125), even considering only birds tagged during breeding (*n* = 78 and *n* = 84, respectively; Fig. 8). More than a quarter of the birds also exploited marshes (*n* = 58), sandflats (*n* = 54), and meadows (*n* = 48), while crops (*n* = 27), saltworks (*n* = 16), and rocky shores (*n* = 13) were less frequently used. Only a few individuals exploited human infrastructures such as artificial green spaces around airport runways (*n* = 2), sports grounds (*n* = 2), harbours (*n* = 1), and mines (*n* = 1).

Table 3 GAM results showing partial effects of selective explanatory variables on HR size in wintering curlews. Relative proportion of overall variance explained = 11.7%. Std. error = standard error

Parametric coefficient	Estimate	Std. error	Z value	*P* value
Intercept	5.79	0.25	22.79	***
Sex (male)	0.04	0.12	0.31	0.76
Body mass	0.00	0.00	0.95	0.34
Latitude	0.05	0.01	4.02	***
Duration	0.00	0.00	1.89	0.06

Significance of individual model predictors: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Mixed Habitat Use

The 21 "coastal and inland" birds wintered at 14 different sites. Most of the 18 birds with enough GPS fixes to define their HRs used meadows in addition to mudflats (*n* = 11) or sandflats (*n* = 6). They used larger spaces to carry out their activities in coastal compared with inland areas (mean coastal HR size: 445 ± 359 ha; range: 21–1,034 ha; mean inland HR size: 247 ± 207 ha; range: 71–1,042 ha; Wilcoxon's signed rank exact test, V = 159, $P < 0.05$).

The five "coastal then inland" birds initially wintered at four different wintering sites (Fig. 9). Most birds partially switched

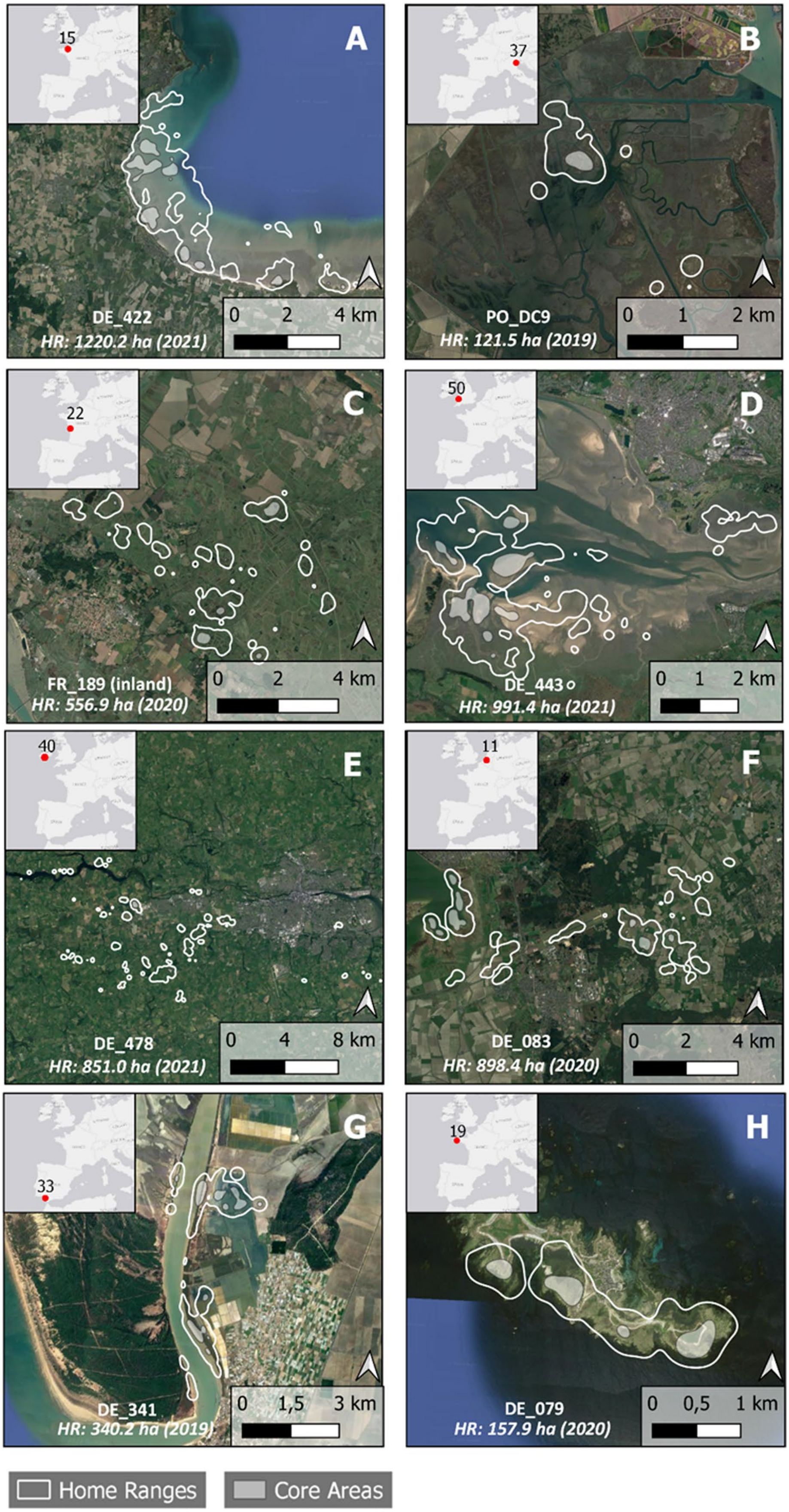


Fig. 7 Example HRs for each dominant habitat. **a** Mudflat, **b** saltmarsh, **c** marsh, **d** sandflat, **e** meadow, **f** crops, **g** saltworks, and **h** rocky shore

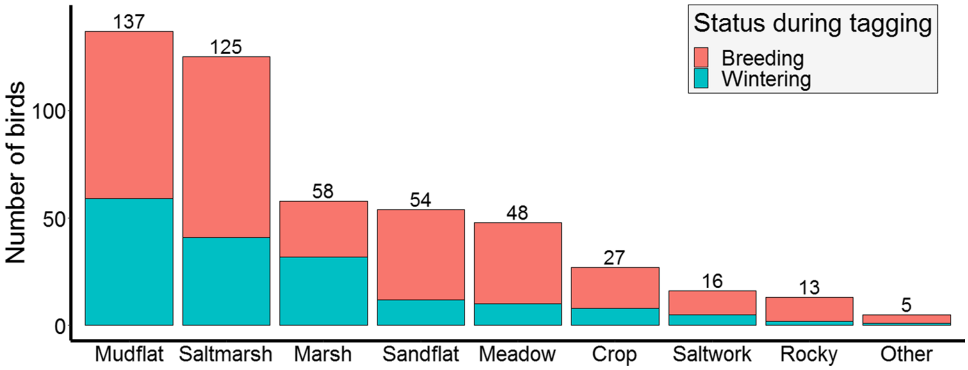


Fig. 8 Number of individuals tagged during the breeding and wintering periods that used different habitat types during winter. Birds used 1–6 habitats during the individual study periods

inland between September (*n* = 1) and October (*n* = 3), although one bird switched inland at the end of July (DE_071) (Fig. 9). All individuals used both coastal and inland habitats for some time before staying in inland habitats.

Discussion

The present study provides an overview of the spatial distribution and phenology of wintering curlews throughout the species' range distribution. As expected, the birds' wintering duration was driven by the latitude of their breeding ground, with northern breeders leaving their wintering sites later to avoid snow cover at their breeding grounds (Amélineau et al. 2021; Schwemmer et al. 2021). The HR sizes were variable and could be partly attributed to the latitude of their respective wintering site; however, this trend was mainly explained by Wadden Sea birds, which had very large HRs. Curlews used a wide range of coastal and inland habitats, especially mudflats containing their preferred prey (Goss-Custard et al. 1977; Schwemmer et al. 2012; Bocher et al. 2014) and saltmarshes used for both feeding and resting.

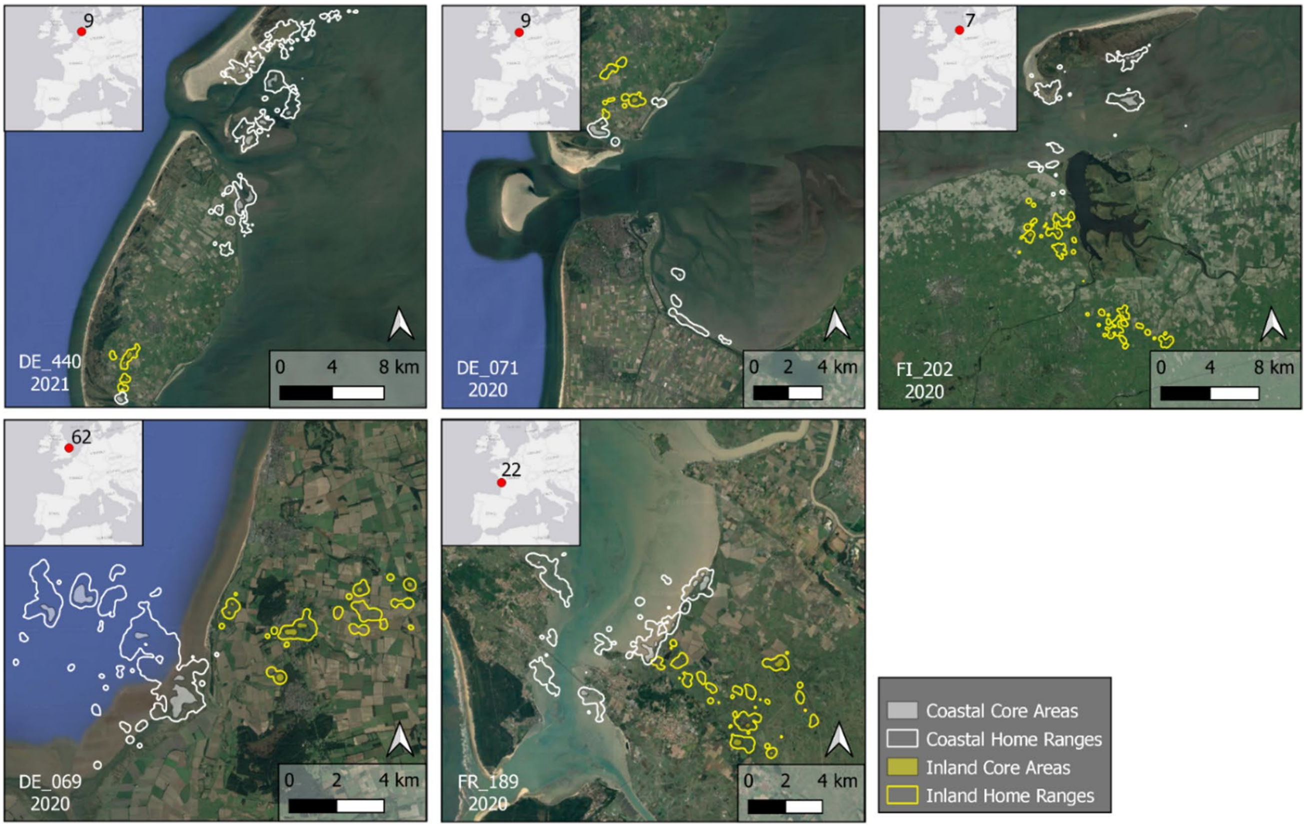


Fig. 9 Coastal and inland HRs for the five curlews that shifted from coastal to inland habitats during the wintering period

Large-scale Distribution and Wintering Phenology

The current results showed that, despite chain migration, curlews from the same breeding populations wintered at sites distributed over a wide latitudinal gradient; indeed, birds exploited a large geographical area covering most of the subspecies' range (Delany et al. 2009; Kämpfer et al. 2023). We therefore assumed that the study included a representative sample of the wintering population of the subspecies, allowing us to define the main habitats of the different wintering populations.

This study confirmed an earlier investigation of the distribution of wintering curlews along the Atlantic coasts of West Europe and Northwest Africa (Brown 2015). The latitudinal distribution seems to be related to the chain-migration pattern shown by curlews (Pederson et al. 2022; Kämpfer et al. 2023), with birds breeding at more northern latitudes wintering further north and west, and birds breeding at lower latitudes wintering further south (Lundberg and Alerstam 1986; Smith et al. 2003). Birds tagged during breeding in France and South Germany were predominantly found to winter on the coast of the Iberian Peninsula, although the proportion of the whole wintering population in this region is considered to be very low (1%; Birdlife International 2004; Brown 2015).

Our results also demonstrated that most curlews inhabited a single site during their wintering period. Curlews were thus largely faithful to the same site throughout the wintering period, as shown previously on the basis of single wintering sites (Brown 2015; Mander et al. 2022), although the current study provides the first evidence for this on a multi-population scale. However, a few birds changed sites or visited several sites during the winter, indicating a degree of individual flexibility in habitat use. A decrease in site quality, e.g., due to a depletion of food resources, can thus cause individuals to redistribute according to the buffer effect (Gill et al. 2001). Gill et al. (2007) and Jourdan et al. (2022) described a similar pattern in black-tailed godwits *Limosa limosa*, which used two distinct functional sites during the wintering period. However, unlike godwits, curlews show high intra-annual site fidelity at their wintering sites (Bainbridge and Minton 1978; Sanders and Rees 2018) and more than half of the site changes were large-scale changes (i.e., > 100 km). Studies covering consecutive years are needed to enable us to determine if this nomadic behaviour is triggered endogenously or is the result of exogenous factors, such as bad weather or anthropogenic disturbances (Piersma and Lindström 2004; Rehfisch et al. 2004; Maclean et al. 2008). However, winters were mild to normal during the bird-tracking period (Jones et al. 1997), and colder winters in previous decades could have led to more birds changing wintering sites during the wintering period.

The wintering period ended later in birds with more-northerly breeding sites. On average, birds from the Wadden Sea and the Pertuis Charentais began their pre-breeding migration between early and mid-April, while birds from other wintering sites that bred mainly at southern latitudes began their pre-breeding migration on average in early March. This confirms the effect of breeding-site latitude on the pre-breeding migration of the species (Amélineau et al. 2021; Schwemmer et al. 2021). Snowmelt, and therefore access to trophic resources, occurs later in more-northerly regions (Reneerkens et al. 2016; Saalfeld et al. 2019), and the later departure of birds breeding at higher latitudes is likely to allow these birds to benefit from resources as soon as they arrive at their breeding sites and thus increase their chance of reproductive success. Accordingly, the tested relationship between wintering latitude and the date of pre-breeding migration departure appears to be linked to the fact that birds that breed further north also winter further north (Pederson et al. 2022).

HRs of Wintering Curlews

Curlews had mean HRs of 533 ± 449 ha. Similar-sized HRs have been reported for other shorebird species, including American oystercatchers *Haematopus palliates* (279 to 7,029 ha; Loring et al. 2017) and bar-tailed godwits *Limosa lapponica* (248 to 581 ha; Jourdan et al. 2021). However, some waders such as dunlin *Calidris alpina* (1,080–56,470 ha; Sanzenbacher and Haig 2002; Choi et al. 2014) and red knot *Calidris canutus* (1,000–80,000 ha; Piersma et al. 1993; Leyrer et al. 2006), have much larger HRs. The differing sizes of HRs for different wader species can mostly be explained by differences in prey availability and/or species-specific differences in the use of foraging habitats (Piersma et al. 1993; Choi et al. 2014). Dunlin and red knot are gregarious and thus move towards prey-rich habitats according to a group decision, and their HRs are therefore very large (van Gils et al. 2015). Conversely, more-territorial species use prey locally across different habitats to avoid strong intraspecific competition for the trophic resource, and their HRs are thus more restricted (Jourdan et al. 2021). The small HRs of curlews compared with other gregarious shorebirds and the high plasticity of individuals in using different habitats suggest that curlews are only slightly gregarious on a small-scale during the wintering period; indeed some studies even showed that curlews exhibited territorial behaviour in winter (Ens 1979, 1983; Ens and Zwarts 1980; Townshend 1981b; Colwell 2000).

The large number of wintering sites used by the tracked curlews did not allow us to distinguish between roosting and feeding habitats or to quantify the proportion of each habitat within the HR. We therefore examined other factors that might influence the size of the curlews' wintering HR. Our results confirmed that HR size was not affected by the wintering duration, thus allowing us to compare the spaces used by all birds, regardless of the tracking duration. In addition, the present study confirmed that curlews were faithful to their respective wintering sites within a winter period, and large-scale movements of individuals were rare; notably, only a few birds shifted from coastal to inland habitats. We aimed to minimize the occurrence of unregistered movements by only selecting birds with at least 2,000 GPS fixes covering 90 days of wintering for HR analyses, corresponding to a much higher number of GPS tracking fixes and days than most telemetric bird-tracking studies (e.g. Anderson et al. 2019; Campion et al. 2020; Jourdan et al. 2021; Mander et al. 2022).

The high inter-individual variability in HR size was partly explained by latitude, with northern birds having larger HRs, and Wadden Sea birds having notably larger HRs. This pattern has also been observed in mammals in relation to decreasing primary productivity with latitude (Heip et al. 1992; Henkel and Nelson 2018). However, Bocher et al. (2007) found no clear north–south gradient in the composition or size of most common mollusc species (i.e., potential prey for curlews) in intertidal areas in Northwest Europe. Even if the density of each species varies with the latitude, with some species being more abundant in the south and others in the north, this should not affect birds that manifest food-expediency behaviour (Schwemmer et al. 2012). It is therefore likely that this pattern can be explained by the large number of tracked individuals using the Wadden Sea, suggesting that other parameters are involved. Indeed, the Wadden Sea hosts 10–12 million waders every year (Meltofte et al. 1994), including more than 250,000 wintering or resting curlews (Kleefstra et al. 2022). Curlews may therefore need to exploit a larger area to avoid high levels of competition for the trophic resources. Comparative studies of prey abundance within different wintering sites in relation to HR size would enable us to draw further conclusions on this issue.

In line with the results of Mander et al. (2022) for the Humber Estuary (UK), the present study revealed no sex-specific difference in HR size, which was unexpected given the differences in bill length and body size between male and female curlews (Cramp et al. 1983). Indeed, Alves et al. (2013) showed that sexual dimorphism in black-tailed godwits was related to different prey accessibility, resulting in a spatial segregation of individuals on intertidal flats. The same pattern of habitat use was observed in colour-ringed curlews, with longer-billed females preferentially foraging on intertidal flats and shorter-billed males on grasslands (Townshend 1981a). However, the larger HRs of Wadden Sea birds suggest that curlews use of space might be partly site-dependent, potentially masking any sex effect. Similarly, body mass did not account for the variability in HR size. Body mass reflects the quantity and quality of food needed to meet the individual's energetic requirements (Ottaviani et al. 2006), and HR size should thus vary in relation to both body mass and resource density (Haskell et al. 2002). However, further studies combining all the factors known to affect the HR size of birds at a given site are needed to confirm our results, especially concerning the distribution and availability of food resources (Brown 1975; Schoener 1983).

Coastal vs. Inland Habitat Use

Curlews strongly favoured coastal habitats, especially intertidal mudflats, during the wintering period, confirming that curlews, like many wintering shorebirds, are specialized predators for prey items found on intertidal mudflats (van de Kam et al. 2004; Colwell 2010). Indeed, polychaetes, crustaceans, and bivalves found in mudflats represent major components of the curlews' diet (Goss-Custard et al. 1977; Schwemmer et al. 2012; Bocher et al. 2014). Although the high number of individuals tagged directly on mudflats during winter might have overestimated the use of this habitat, this trend remained when the analysis was restricted to birds caught during the breeding period.

Our results highlight the fact that individual curlews can use several habitats at their respective wintering sites simultaneously. For many birds, the use of foraging habitats depends on individual preferences, with the preferred habitats often selected first and other habitats only being used when the first ones are no longer available (Navedo et al. 2013), in situations where trophic resources are no longer optimal (Vickery et al. 1995) or to prevent excessive competition in feeding areas (Vahl et al. 2005). The current study was unable to determine if the habitats were used for foraging or resting; however, it is likely that curlews used the available habitats to rest during high tide, thus favouring muddy and sandy substrates for feeding at low tide. This is notably the case for marshes in the Pertuis Charentais, which are mainly used as roosts by many shorebirds at high tide (Jourdan et al. 2021), and for saltmarshes in the Wadden Sea, which are also known to be used as roosts at high tide, with individuals favouring the extensive mudflat for feeding at low tide (Koffijberg et al. 2003). Nevertheless, saltmarshes can fulfil both functions, as shown by Calbrade et al. (2008) in the Colne Estuary (UK). This suggests that curlews can accommodate different foraging habitats and are therefore not obligate mudflat specialists like other shorebirds, such as red knot (Piersma 1994; Calbrade et al. 2008). We therefore expect that curlews may be more flexible than other waders in escaping the coastal squeeze due to climate change, given that sufficient terrestrial options are also available.

Some individuals used inland habitats, especially meadows, in addition to coastal ones during winter. This behaviour is relatively common and has also been shown in other shorebird species (Caldow et al. 1999; Masero and Pérez-Hurtado 2001; Smart and Gill 2003; Gunnarsson et al. 2005). Human disturbance in exposed intertidal areas, such as shellfish fishing, can reduce the time allocated by birds for food prospecting, as well as depleting the available trophic resources (Navedo and Masero 2007; Stillman et al. 2007). Shorebirds are thus likely to extend their feeding grounds to inland areas in order to meet their daily energy demands (Navedo et al. 2013). Moreover, Townshend (1981a) showed that curlews could switch to inland foraging habitats when the availability of polychaetes in intertidal habitats declined due to decreasing temperatures. The use of meadows by foraging waders would not necessarily be disadvantageous, even if the density of prey items was lower than in the coastal habitats (Gunnarsson et al. 2005). The tidal rhythm allows the birds to ingest several small portions of food throughout the day (Gutiérrez et al. 2012), and in addition, curlews mainly use meadows located near the coast, which freeze less during winter than inland meadows (DeCourcy Ward 1906). Earthworms, which represent an important food source for inland-breeding curlews (Berg 1993), are therefore often available to the birds (Evans and Guild 1947; Gerard 1967). Meadows may thus act as supplemental foraging habitats for many individuals during winter (Urfi et al. 1996; Smart and Gill 2003), even if few birds settle there during all or part of their wintering period.

Conclusion

The present study demonstrates that curlews are faithful to their respective wintering sites throughout the wintering period. In addition, the sizes of the birds' HRs are small compared with gregarious shorebirds, but are also highly variable between individuals. Although HR size was apparently unaffected by sex and body mass, we cannot exclude the possibility that latitude might play a minor role. Curlews can also exploit a wide range of coastal and inland habitats, but most birds utilize mudflats and saltmarshes. This high inter-individual variability in the use of space could help the species to respond to global climate change; however, their high site fidelity during winter suggests that many individuals might be unable to adapt their habitat use or change sites if necessary. Further investigations on the specific selection of foraging habitats over several consecutive years are needed to provide quantitative data to support these results.

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Data Availability The datasets generated during and/or analyzed during the current study are not publicly available due to a very large amount of data making the files difficult to share and the different rules regarding data sharing of each program, but they are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or nonfinancial interests to disclose.

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