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Original research article

Home ranges and hatching success of threatened Eurasian curlew in north-eastern Europe relates to habitat type: Natural vs. agricultural landscapes

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A R T I C L E I N F O

Keywords:
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Grassland
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Natural afforestation
Bog
GPS-tracking

A B S T R A C T

Farmland birds are among the most threatened species in Europe, largely as a result of the intensification of agriculture leading to widespread biodiversity losses. Ground-breeding shorebirds in grassland and arable habitats are particularly exposed to human threats and predation in highly modified landscapes; however, parts of their populations still breed in natural habitats and could provide a reservoir for threatened populations. This study aimed to improve our knowledge of the spatio-temporal use of breeding habitats by Eurasian curlew *Numenius arquata arquata* in a core area of the population in remote north-eastern Europe. A total of 83 adult birds across Europe were tagged with GPS devices between 2014 and 2022 to analyse their home-range sizes, habitat use and hatching success. Birds were distributed at breeding sites from 52°N to 66°N between Finland and the Ural Mountains. Forty-one percent of individuals nested in bogs, 33% in grassland, and 20% in abandoned farmland. Birds nested predominantly in bogs at northern latitudes and in grassland at southern latitudes, while abandoned farmland was mainly used at intermediate latitudes. The mean home range was largest for birds breeding predominantly in grassland while birds in bogs had the highest hatching success rate. Russia and Finland host the core population of the subspecies *N. a. arquata* during breeding period, which is essential for preserving the species on a European scale. Their survival may depend on well-preserved bogs and the maintenance of grassland areas, given that large areas of abandoned farmland are destined to become either forest or to be reclaimed for cereal crops or fodder grass in the short and medium terms. Given the large breeding populations in both countries, Russia and Finland have major responsibilities to maintain these essential populations on a biogeographical scale.

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1. Introduction

Many species are distributed broadly across wide environmental gradients with variable habitat qualities within their distribution range. The abundance and demography of local populations can thus be affected by range-wide variations in habitat quality (Brown, 1984; Pironon et al., 2017). There may be differences between core populations inhabiting stable well-connected habitats, and peripheral populations, which are often patchily distributed and exposed to greater isolation with more limited and variable resources (Brown, 1984; Hardie and Hutchings, 2010). Core large populations maintain greater amounts of gene flow resulting in higher levels of genetic diversity, which increases the evolutionary potential of the population and its resilience to stochastic events (Frankham, 1996). In the context of the conservation of endangered species, core areas with large populations or well-connected smaller populations are essential for ensuring the survival of the species (Wolf et al., 1996; Fiedler, 2012).

The Eurasian curlew *Numenius arquata* is a large shorebird that is widely distributed throughout the Eurasian continent during breeding period (del Hoyo, 1996). Among the three described subspecies, *N. a. arquata* (subsequently referred to as curlew) occurs in the western part of the continent, breeding between Western Europe and the Ural Mountains up to the Arctic circle (Keller et al., 2020). Curlews in open natural (e.g., peat bogs, floodplain meadows), semi-natural (e.g., unimproved grassland), and highly transformed (e.g., arable fields) habitats show noticeable differences in population sizes and trends among countries (Brown, 2015; Pearce-Higgins et al., 2017). After breeding, curlews migrate towards the coast and winter mainly in north-western Europe, from June/July (autumn migration) to March/April (spring migration), their breeding period extending between four to 10 weeks according to breeding success and latitude of the breeding site (Pederson et al., 2022).

The Eurasian Curlew is classified as a globally Near Threatened species and considered to have declined at the European continental scale for more than 30 years (BirdLife International 2023). The species has disappeared as breeding bird in several European countries (Brown, 2015). Curlews are unequally distributed in Europe during the breeding season, with a population estimate of 212,000–292,000 breeding pairs (BirdLife International 2023). Most European countries host a maximum of a few thousand breeding pairs. The latest UK population estimate was 58,500 pairs (Woodward et al., 2020), while European Russia and Finland host 45,000–100,000 and 50,000–90,000 estimated pairs, respectively (Valkama et al., 2011; Keller et al., 2020). These three countries thus hold the core population and are essential for maintenance of this subspecies throughout its entire distribution area.

In Russia, 70%–80% of pairs breed within taiga-dominated biomes (Sviridova, 2020). In Finland, curlews generally breed in agricultural habitats, but used predominantly bogs in the north of the country (Valkama et al., 2011). In agricultural landscapes, this ground-nesting bird is exposed to threats such as habitat degradation (Berg, 1993, Grant et al., 1999) including afforestation (Douglas et al., 2021), destruction of eggs by agricultural practices (Beintema and Muskens 1987), and high predation level (Valkama et al., 1999; Zielonka et al., 2019). Some local populations may decline because of farmland abandonment and subsequent increases in the vegetation height, rendering large areas unsuitable for nesting (Broyer and Roche, 1991; Douglas et al., 2014; Mischenko et al., 2019). Despite farmland abandonment may be accompanied by a spatial redistribution of curlews, leading to denser nesting in more suitable grassland areas (Sviridova et al., 2008), land abandonment has become a major threat for species in the north of European Russia, causing loss of breeding habitat as a result of overgrowth by bushes and trees (hereafter 'natural afforestation'; Kuitunen et al., 2003; Mischenko et al., 2019). Drainage, habitat fragmentation and total destruction by peat extraction or agriculture are the main threats to curlews inhabiting bogs (Nikolaev, 1998); however, some bogs, particularly in the north of European Russia, are known to be the least altered or completely preserved remaining natural habitats (Tanneberger et al., 2021).

The information on the choice of breeding habitat by curlews in many parts of its core area in NE Europe is currently lacking due to the vast and remote areas, which are difficult to access and monitor. The degree to which curlews in European Russia use peat bogs, as another important habitat type in addition to unflooded grassland (Preobrazhenskaya, 2019; Mischenko, 2020), is particularly poorly known. The recent development of GPS telemetry allows to study the behaviour and movements of birds at a distance with increasingly high spatial and temporal resolutions.

The current study uses of data generated by GPS telemetry enabling us to locate the positions of the nests precisely and to determine breeding success but more surely the hatching success, even in very remote and inaccessible areas. The objectives of the study were: 1) to create maps of the breeding distribution; 2) analyse and quantify the habitat choice in relation to four generalized agricultural and natural habitat types (grassland, abandoned farmland, bog, and arable land); 3) to quantify home ranges across the different habitats; and 4) to quantify hatching success in the different habitats based on GPS tracks.

Table 1
Overview of tagging information.

	Tagged Adults (n)	Males (n)	Females (n)	Unsexed (n)	Complete Breeding event (n)	Position interval range (min)	Study period	Attachment method	Sexing method	Catching method
Germany	31	16	14	1	26	1–360	2014–22	Breast	Genetic	Mist-net
France	39	20	19	-	37	1–60	2016–22	Leg-loop	Morphology	Mist-net
Estonia	4	2	1	1	2	5	2022	Breast	Genetic	Cage
Finland	4	3	1	-	3	5	2020–22	Leg-loop	Morphology	Cage
Russia	5	4	1	-	2	5–360	2021–22	Breast	Morphology	Cage
Total	83	45	36	2	70					

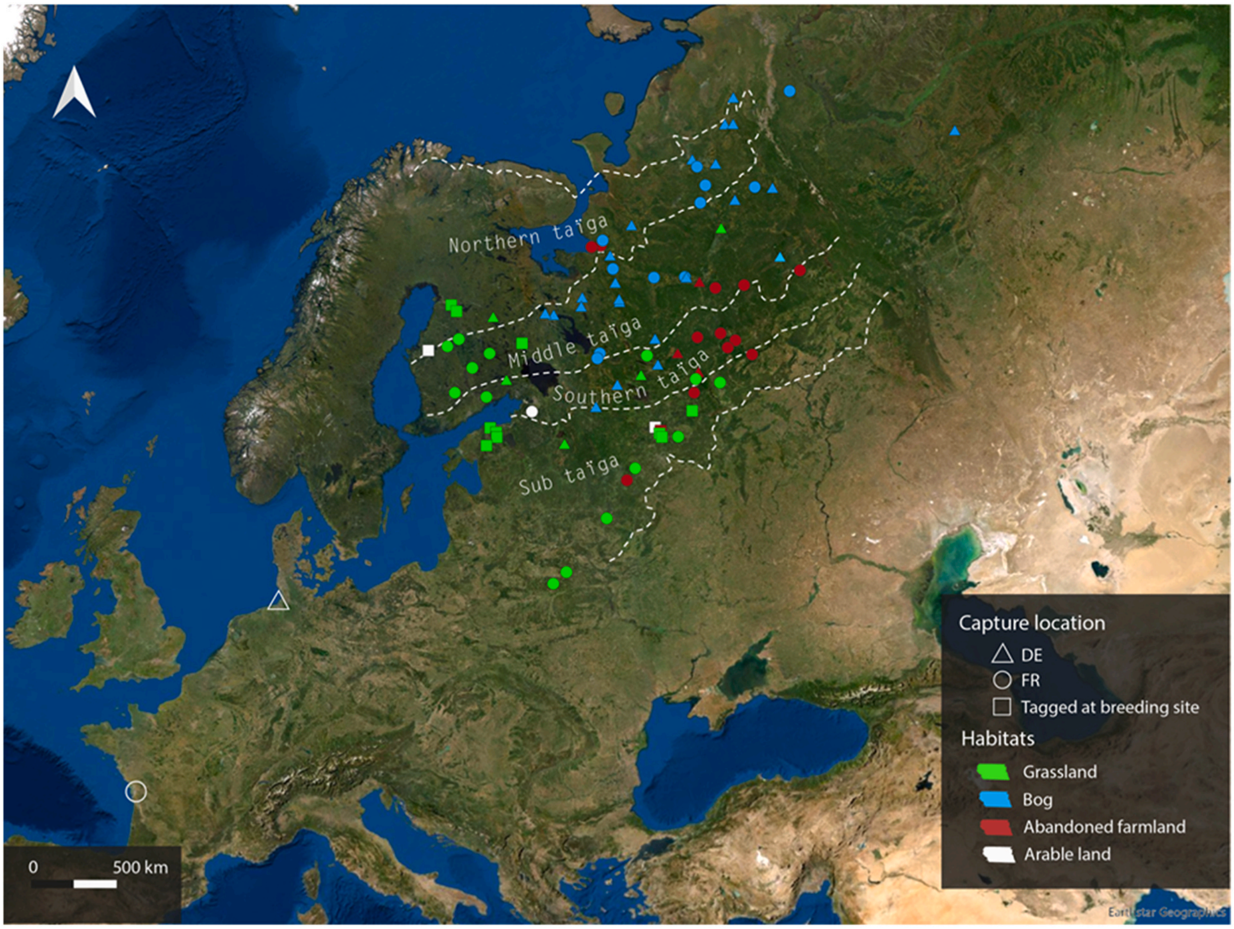

Fig. 1. Locations of breeding sites of Eurasian curlews with origin of catching. The biome limits are reported according to the "The Biomes of Russia" map (Ogureeva et al., 2018), with extrapolation of the biome limits for the area between Finland and Belarus according to Karlsen et al., (2002) and András et al., (2017).

2. Methods

2.1. Catching and tagging curlews

The curlews were caught using either cage on the nest (breeding curlews during the incubation stage) or with mist nets (wintering curlews). A total of 83 adult curlews were equipped with GPS-tags between 2014 and 2022 (Table 1, Fig. 1). Of these, 70 individuals were caught and tagged at two wintering sites on the central French Atlantic coast (Pertuis Charentais (n = 39)) and the eastern German Wadden Sea (western Schleswig-Holstein and Lower Saxony (n = 31)) (Table 1). Thirteen individuals were caught and tagged at breeding sites in Finland (n = 4), Estonia (n = 4), and Russia (n = 5), respectively (Table 1).

All birds were measured (i.e., flattened wing, tarsus, bill lengths), weighed, and ringed. Different types of solar tags from two GPS-tag manufacturers were used, none of which was >3.5% of the bird's body mass (Phillips et al., 2003). Four tag models were manufactured by Ornitela, Lithuania (OT-10 (10 g, n = 1), OT-15 (15 g, n = 24), OT-20 (20 g, n = 2), OT-E10 (12 g, n = 28)) and two by Ecotone, Poland (Sterna (7.5 g, n = 15), Skua (17 g, n = 13)). The tags were either attached using a breast harness (Guillaumet et al., 2011) or leg-loop harness (Mallory and Gilbert, 2008). Tag intervals ranged from 1–60 min (except for 4 individuals with intervals of 360 min; Table 1). The accuracies of the GPS-tags were between 5 and 10 m, according to the manufacturers. Birds were sexed either morphologically (n = 48; Summers et al., 2013) or genetically (n = 33; Tauros Diagnostics, Berlin), with no difference in sex determination between the molecular and morphometric methods (n = 27; Pederson et al., 2022). The age of the individuals caught in winter was determined according to plumage characteristics (Prater et al., 1977; Demongin, 2016). The adult birds included 45 males and 36 females, and the sex of two birds was unknown (Table 1).

2.2. Breeding events

The process of selection of breeding events and the different breeding characteristics with the different filtering steps are explained in detail in Supplementary Fig. A1. We recorded 124 breeding events, including 1–5 breeding years per bird. Among all breeding events for the 83 individuals, 104 were complete (arrival and departure dates are known) and 20 were incomplete because of malfunction or loss of the tag or death of the bird. In this analysis, we only retained the first breeding event for each individual to avoid replication, or the second event if the first was incomplete. Analyses of home range and phenology were only performed for complete breeding events and for birds for which enough GPS data were collected (i.e., minimum of 500 locations; n = 67). Individuals with incomplete breeding cycles were only used to define their breeding positions and main breeding habitat (Fig. 1), but not to investigate habitat use.

2.3. Locations of nests and nesting habitat

All analyses were performed using R (version 4.0.5) (R Core Team 2021) and GPS fixes were visualized using QGIS (version 3.22 Białowieża; QGIS Development Team, 2021). Male and female curlews share egg incubation and are therefore regularly immobile during the 28-day incubation period (Currie et al., 2001). We extracted the nest positions from the GPS tracks by isolating the breeding period of the 83 selected individuals and counting the number of positions within each cell of a grid (0.0001° × 0.0001°, corresponding to about 11.1 m x 11.1 m) covering the range of longitudes and latitudes visited by each individual during the breeding period. The centre of the cell containing the highest number of fixes was then defined as the most likely location of the nest site. Once identified by the script, the nest position was checked visually to confirm if it corresponded to the highest concentration of GPS fixes. For seven individuals, the method failed to identify the nest site because they did not attempt to breed or failed early in the breeding season. In 11 cases, no nest position was identified but the individual was still considered to be a breeder if its core area (see Section 2.5) was <50 ha and no more than three patches in the core area (reflecting the establishment of a territory), and if its phenology was consistent. For these birds, the nesting habitat was defined as the habitat where the birds spent most time during the breeding period (Fig. 1 and Supplementary Fig. A1). We defined the start and end of the study period for each bird as the first (arrival date) and last (departure date) location, respectively, within a 20 km radius from the centre of the cell containing the highest number of fixes.

2.4. Breeding phenology

Once the position of the nest was established, the distance between the nest and each recorded GPS position was calculated throughout the breeding season and plotted (Fig. 2). If prolonged and regular periods with distances close to zero were identified, the bird was considered to be incubating or staying near the nest. Curlew chicks leave the nest under parental supervision 1–2 days after

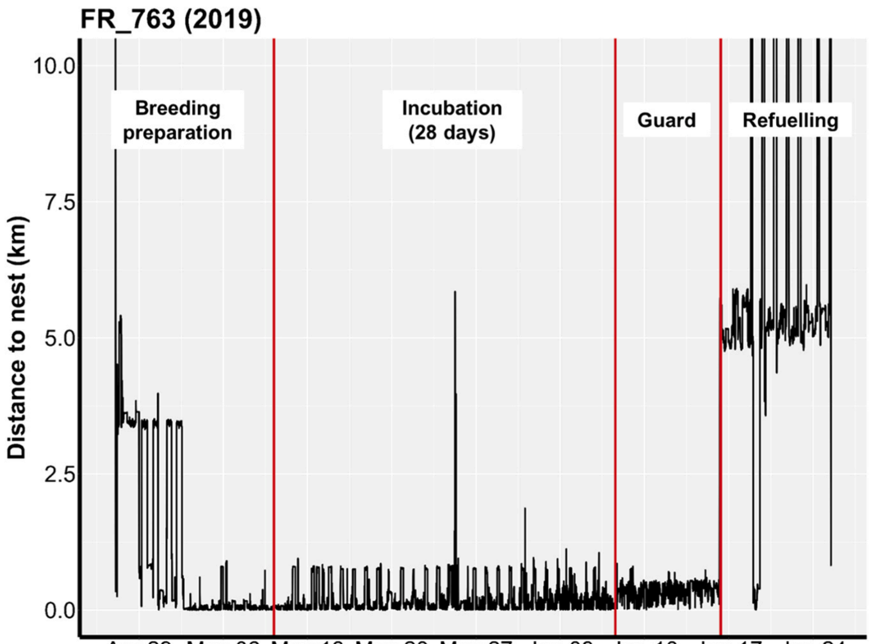

Fig. 2. Distance between each recorded GPS fix and the nest during the breeding season, used to distinguish the different key stages of a typical curlew breeding cycle.

hatching (Currie et al., 2001), and incubation was thus considered to have ended when the distance from the nest increased regularly, with no return to the nest position. Once the hatching date was estimated, it was possible to determine the laying date by subtracting the 28-day incubation period. The period before laying was considered as the pre-incubation period, and the period after hatching as the rearing period, when the adults guide and accompany their chicks to feeding areas and shelter (Fig. 2).

If the incubation period was shorter than 28 days, we considered that the breeding event had failed. It was difficult to interpret the results and to distinguish the different reproductive phases if the birds fed close to the nest. In these cases, we reduced the core area ordinate scale (<1 km) to better define the incubation period. Finally, we classified breeding events according to three categories: hatching success (birds incubated for ≥28 consecutive days), failed, or uncertain.

Once breeding is completed (successfully or not), curlews move to feeding areas close to their breeding site to prepare for migration to the wintering grounds (Fig. 2). We did not consider this refuelling period in the study of the breeding phenology, even if it was inside the 20 km radius, considering that it occurred after chick rearing or failed breeding. We therefore considered that breeding had ended when the individual did not return to the nest site for at least 24 consecutive hours.

2.5. Breeding home ranges

The estimation of the utilization distribution (UD), i.e., the probability of finding each bird at any location (Calenge, 2021), was used to analyse space use by curlews. Kernel density estimates (KDE; Worton, 1989) were used to describe the UD (Laver and Kelly, 2008) with the "kernelUD" function from the R package "adehabitatHR" (Calenge, 2021). The spatial distribution of bird locations and the corresponding time spent in an area were considered by a KDE method to estimate the home ranges (at 90% isopleth) and core areas (at 50% isopleth) for each individual (Worton, 1989). The kernel home ranges were estimated using a compromise between undersmoothing of the least square cross-validation and oversmoothing of the reference bandwidth (*ad hoc*), with a smoothing factor *h* of 50 (50 m) of the minimum reference value obtained by the "ad hoc" bandwidth (Kie et al., 2010; Schuler et al., 2014). The smoothing factor was determined using forests and human structures as realistic geographic limits where kernel representations should not overflow (Fig. A2). After estimating the UDs, the breeding distributions were computed, excluding the positions relating to the refuelling phase before migration departure, which were not considered in the calculation of the breeding home ranges and core areas. There was considerable disparity in the number of GPS records for the 67 birds (ca. 500 and ca. 30,000) related to the model and settings of the GPS-tags used. The minimum number of GPS data points required to calculate the home range (500 locations) was

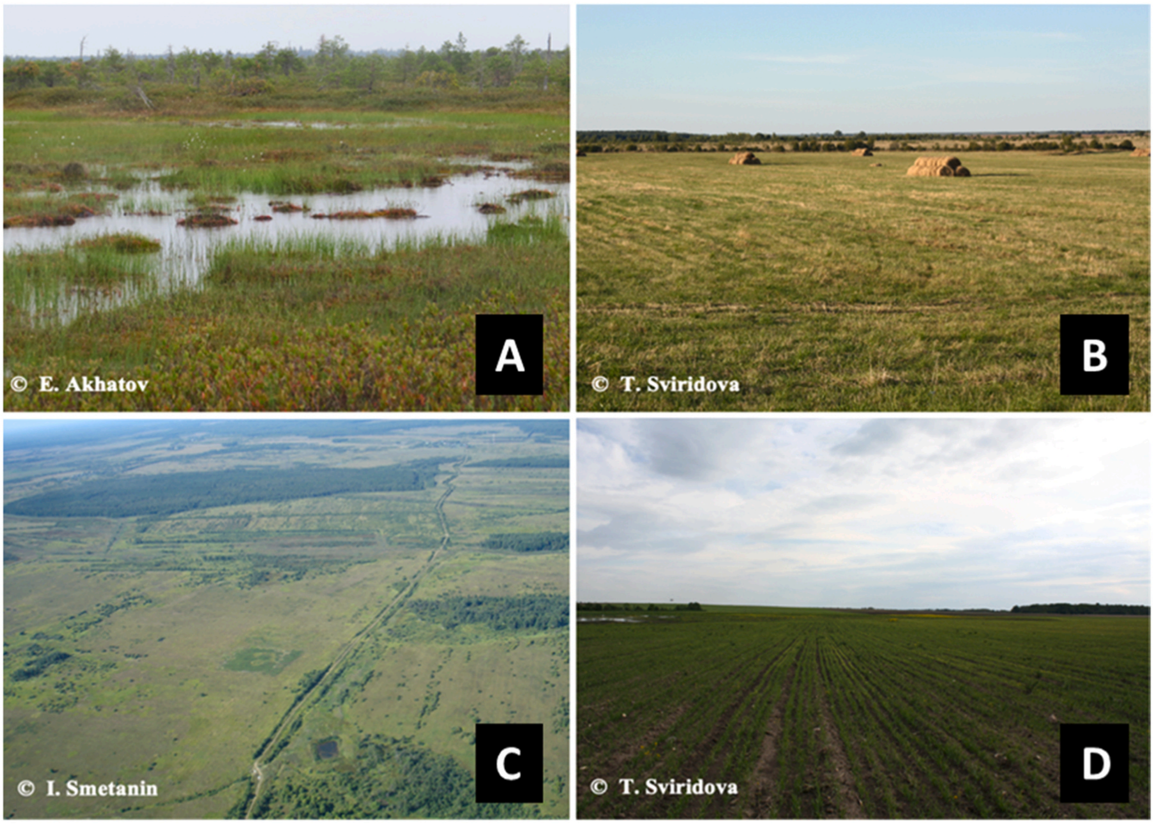

Fig. 3. Illustrations of the four main habitats. (A) bog, (B) grassland, (C) abandoned farmland, and (D) arable land.

determined by adding 50 by 50 points drawn randomly from each individual to reach a plateau near 100% home range (see Jourdan et al., 2021).

2.6. Habitat uses

The terminology relating to the classification of farmland habitats and peatlands differs among countries, and we have therefore defined the terms used. We analysed habitat use by curlews within their breeding range in north-eastern Europe. The habitats of the nest locations and within the home range and core area were defined according to the visual interpretation of satellite images based on our field experience of some sites including the four main habitats (Fig. A3).

Because agricultural practices can change from year to year, satellite images corresponding to the specific breeding year were used with the Google Earth Pro® time slider. Images for the preceding and succeeding years were also used if necessary. In addition, Sentinel 2 satellite images were downloaded and imported into QGIS as a raster for habitat identification and calculation of the area within the home range and core area. According to the area of each habitat inside the home range and core area, the proportion of habitat used was estimated for the entire breeding period (pre-laying, incubation, guarding) per bird. For some analyses, each home range/core area was also categorized according to the dominant habitat (highest habitat area inside home range/core area). The distances from the nest to forest edges and human buildings were calculated as possible sources of predation and disturbance.

The habitats were divided into four main classes: bog, grassland, abandoned farmland, and arable land (Fig. 3). An "other" habitat category comprised forests, rivers, roads, and buildings. Bogs are oligotrophic raised and transitional (mesotrophic) mires with relatively sparse cover with Scots pine (*Pinus sylvestris*), spruce (*Picea* sp.), and birch (*Betula* sp.), and wide-open mossy areas (predominantly *Sphagnum* spp.), as well as aapa-mire complexes (Joosten et al., 2017; Tanneberger et al., 2021). More watery complexes (with open flarks, floating vegetation, and lakes; Fig. 3A) of ridge-hollow and ridge-pool raised bogs and aapa-mires generally prevailed in the northern taiga (north of European Russia and Finland) as well as in some most western regions of European Russia (e.g., in Novgorod, Tver, and Pskov Oblasts), with few well-watered bogs in the central and eastern parts of the middle taiga, which included large, open, flat areas of moss-cotton grass-sedge. The total area of single bog was decreased in the southern taiga and sub-taiga and was characterised by fewer or absent open-water bodies and denser tree cover (Preobrazhenskaya, 2019). Grassland (actively exploited meadows; Fig. 3B) included any unimproved grass habitats currently used for hay and pasture, i.e., fields of perennial sown grasses (poor herb species composition, frequent re-seed cycle) and more semi-natural permanent meadows (often rich in herb species).

Vast areas of farmland in the north of European Russia were abandoned in recent decades, leading to a rich mosaic habitat structure ranging from weed associations, to open abandoned farmland with single shrubs, to significantly natural afforested areas (Fig. 3C). Arable land (Fig. 3D) referred to land with any type of annual crops under intensive agricultural cultivation (including improved grasses in first year of sown and bare fallow).

2.7. Statistical analyses

All statistical analyses were performed using R software (version 4.0.5, R Core Team, 2021). To analyse the space used by breeders, the mean (± SD) home range and core area sizes were jointly analysed by sex, latitude, total breeding duration, hatching success and dominant habitat type using generalized additive models (GAMs, 'gam' function of 'mgcv' package, Wood, 2017). After comparing the Akaike information criterion values of different families, the non-binomial and the Tweedie distributions were respectively used to fit the models. We tested if the use of the main habitat depended on the breeding latitude by an analysis of variance with the 'aov' function followed by Tukey's *post-hoc* tests using the 'pairwise.t.test' function ('stats' package, R Core Team, 2021). A binomial GAM was then used to test the effects of nest habitat, breeding latitude, distance to forests and to houses on hatching success (binomial outcome = 0: hatching success; 1: hatching fail).

3. Results

3.1. Breeding sites

All 83 tagged birds were distributed across breeding sites at latitudes from 52.4°N to 66.3°N, between the Baltic Sea and the Ural Mountains, Russia (Fig. 1) with only one individual bird recorded beyond the Arctic Circle. Two individuals crossed the Ural Mountains but were designated as non-breeders because no central place movements could be detected for these individuals. Curlews tagged at breeding sites wintered in Germany (n = 1), The Netherlands (n = 3), Belgium (n = 3), the UK (n = 3), and three birds from Central European Russia wintered on the Mediterranean coast.

3.2. Nesting habitat

The nest location and habitat were assessed for 49 individuals but only the dominant breeding habitat in the home range area was recorded for the other 11 birds with breeding attempts. Twenty-five of these 60 individuals nested in bogs (41.7%), 19 in grassland (31.7%), 12 in abandoned farmland (20.4%), and four in arable land (6.6%) (Fig. 1). Birds nested predominantly in bogs at northern latitudes in the north-eastern part of the study area and in grassland at southern latitudes in the south-western part of the study area. Abandoned farmland was used predominantly at intermediate latitudes, mainly in the southern taiga, and grassland was predominantly used in Finland (Fig. 1). Nests in grassland were located slightly closer to forest (394 ± 452 m (mean ± SD), 19–1493 m, n = 16) than those in bogs (445 ± 288 m, 27–1193 m, n = 19) or abandoned farmland (519 ± 985 m, 17–3251 m, n = 10). Nests in grassland were closer to farm buildings (665 ± 701 m, 100–2314 m, n = 16) than nests in abandoned farmland (1816 ± 1464 m, 148–3803 m, n = 10) or bogs (17,711 ± 10,130 m, 832–88,772 m, n = 20).

3.3. Breeding period and duration

The mean date of arrival at the breeding site for all tagged birds was 27 April (24 March to 7 June, n = 77) and the mean departure date (including estimated refuelling period) was 23 June (27 May to 9 August, n = 76), with a mean duration of presence at the breeding sites of 56.7 ± 13.2 days (17.3–98.5 days, n = 70, including refuelling stage and non-breeding birds). One bird that arrived at the breeding site on 7 June was considered as a non-breeder.

3.4. Breeding home range

The mean home range area (without refuelling stage) for 67 curlews with complete breeding events was 99.1 ± 103.8 ha (11.1–561.2 ha) and the mean core area was 15.7 ± 17.0 ha (3.3–92.2 ha). There was no difference in home range or core area size between males and females and between individuals who succeeded and those who failed to maintain eggs until hatching (GAM, $p > 0.05$), but both differed negatively with latitude (home range: Chi.sq = 8.56, $p < 0.05$; core area: F = 5.99, $p < 0.01$; Table 2). Breeding duration was also positively related to home range size (Chi.sq = 15.03, $p < 0.01$).

Examples of the smallest and largest home ranges for each main breeding habitat are illustrated in Fig. 4. Non-breeding individuals had a particularly scattered and widespread home range (291.6 ± 191.8 ha, n =7; Fig. 4D). There was no significant difference in home range and core area sizes among all the habitats (GAM: $p > 0.05$; Table 2). However, the mean home range and core areas were slightly larger for breeders with grassland as a dominant habitat (home range: 96.6 ± 69.0 ha (14.1–299.0), n = 20; core area: 15.7 ± 11.5 ha (4.0–48.5), n = 21) than for those in abandoned farmland (home range: 77.3 ± 62.3 ha (22.4–240.0), n = 13; core area: 11.6 ± 7.4 ha (4.0–29.4), n = 11) (Fig. 5). In contrast, the mean home range and especially the core area were smaller in bogs (home range: 54.7 ± 31.6 ha (11.1–153.0), n = 23; core area: 8.2 ± 4.0 ha (3.3–16.1), n = 25) than in other habitat categories. Only four birds had arable land as the dominant habitat in terms of home range (101.6 ± 80.5 ha (14.9–205.7)) and three for core area (10.8 ± 5.5 ha (4.6–15.0)). The number of distinct core area patches inside the home range was higher in grassland (3.6 ± 4.0, n = 20) than in abandoned farmland (2.4 ± 1.4, n = 13) or bog (1.6 ± 0.8, n = 23).

3.5. Habitat use

Considering only birds tagged at wintering sites, more curlews mainly used bogs (n = 28) compared with grassland (n = 17), abandoned farmland (n = 13), or arable land (n = 2) (Fig. 6), while birds tagged at breeding sites mainly used grassland (n = 3) or arable land (n = 4). Among birds that mainly used bogs, this habitat was used almost exclusively, excluding agricultural habitats (19/

Table 2
GAM results showing partial effects of selective explanatory variables on home range (A) and core area size (B) in breeding curlews. Std.error = standard error; edf = effective degree of freedom; Ref.df = reference number of degrees of freedom; Chi.sq = Chi-squared test.

(A)				
Parametric coefficient	Estimate	Std.error	Z value	*P* value
Intercept	4.52	0.25	18.06	***
Hatching success (success)	-0.18	0.21	-0.85	0.40
Sex (male)	-0.26	0.22	-1.19	0.23
Main habitat (Bog)	-0.04	0.29	-0.15	0.87
Main habitat (Grassland)	-0.10	0.26	-0.38	0.70
	edf	Ref.df	Chi.sq	*P* value
S(Duration)	3.83	4.69	15.03	**
S(Latitude)	1.57	1.93	8.56	*
(B)				
Parametric coefficient	Estimate	Std.error	Z value	*P* value
Intercept	2.65	0.24	10.95	***
Hatching success (success)	-0.36	0.19	-1.88	0.07
Sex (male)	0.01	0.18	0.05	0.96
Main habitat (Bog)	-0.10	0.24	-0.44	0.66
Main habitat (Grassland)	-0.11	0.25	-0.43	0.67
	edf	Ref.df	F	*P* value
S(Duration)	2.76	3.38	2.43	0.06
S(Latitude)	1.93	2.39	5.99	**

Significance of individual model predictors: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.
Relative proportion of overall variance explained = respectively 49.4% and 53.4%.

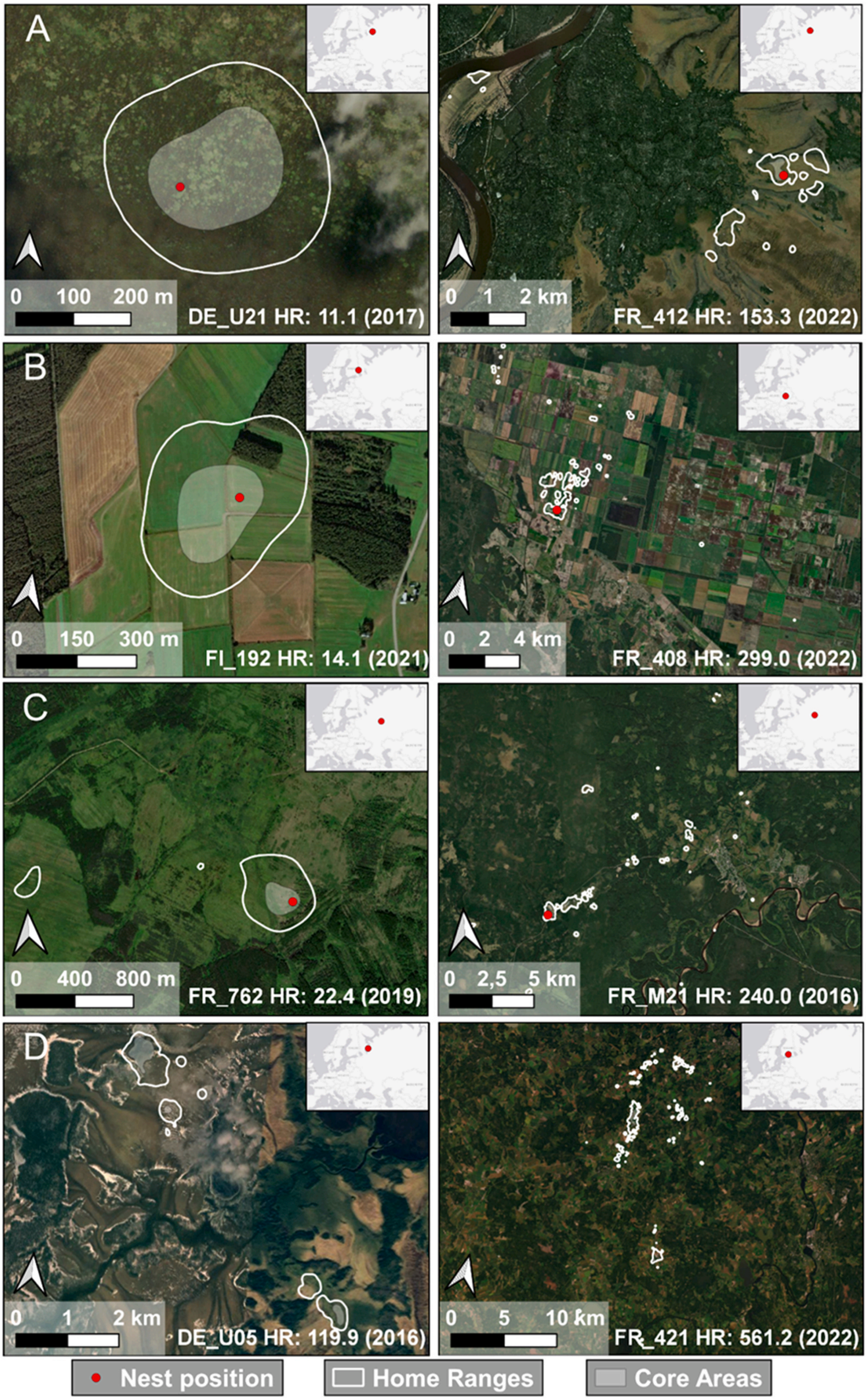

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Fig. 4. Illustration of smallest (left column) and largest (right column) home ranges for each dominant habitat type (bog (A), grassland (B), abandoned farmland (C)) and example of two non-breeding individuals (D). Individual code number, home range size in ha, and breeding year are shown.

28 individuals only used bog). We also found significant differences in the dominant habitats within the home range according to latitude (ANOVA, df = 2, $p < 0.001$), with home ranges with bog dominance being more frequent than home ranges with grassland or abandoned farmland dominance at high latitudes (Tukey's *post hoc* test, $p < 0.001$). Curlews breeding in southern Finland used grassland exclusively compared with breeders at similar latitudes in Russia (Figs. 1 and 6). Birds in Belarus and Estonia bred in arable habitats with highest proportions of arable land in home range.

3.6. Hatching success

Among breeders with nest position known (n = 49), we estimated the hatching status (i.e., successful hatching (n =25), hatching failure (n = 22) and uncertain (n = 2)) according to the pattern of distances from their nests (Fig. 2). Nests in grassland had the highest failure rates followed by abandoned farmland, whereas nests in bogs had the highest success rate of >70% (Fig. 7). Birds nesting in arable lands were not considered due to their small number (n=3). The success or failure rates differed significantly between bogs and grasslands as nesting habitats (GAM: Z = 2.27; $p < 0.05$; Table 1A). There was no difference in success or failure rates with the breeding latitude and the distance of the nest to buildings ($p > 0.05$). However, a relation was found between hatching success and distance of the nest to forest, with birds closer to forests having more hatching success (Z = 2.51; $p < 0.05$).

4. Discussion

This study provides the first large-scale investigation of the breeding biology of Eurasian curlews *N. a. arquata* in their core breeding area in north-eastern Europe (excluding the important subpopulation in the UK). The use of telemetry data thus could provide essential information on the distribution and breeding characteristics of the core curlew population in Russia, because it is particularly hard to monitor populations in this huge breeding area, and in reason of the inaccessibility of many breeding sites, and the lack of resources allocated to research and surveying fieldwork.

4.1. Breeding sites

Individuals tagged at two wintering sites, 1150 km apart, showed that curlew breeding sites were distributed over a very large area corresponding to the known distribution of the species in western Russia and Finland (Delany et al., 2009), underpinning the idea of a large core population of curlews located in north-eastern Europe. Previous studies, which included some of the birds tracked in our study, supported the distribution of birds wintering along the continental coast of Europe from Scotland to Morocco (Donnez et al., 2023) and exhibiting chain migration throughout Europe (Pederson et al., 2022). Furthermore, the two individuals that crossed the Ural Mountains demonstrated that the boundary between the ranges of the two subspecies *N. a. arquata* and *N. a. orientalis* is not as clearly defined by this geological barrier as previously thought (Engelmoer and Roselaar, 2012).

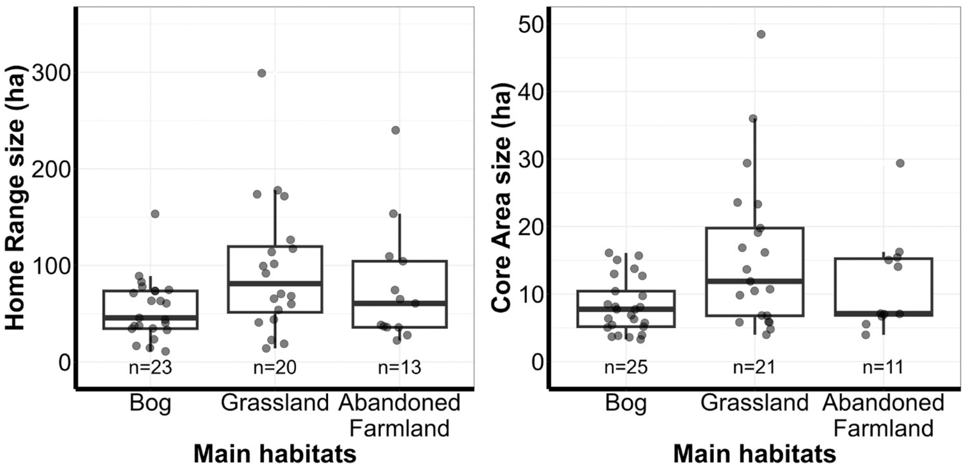

Fig. 5. Sizes of home range (A) and core area (B) according to dominant habitat in terms of surface proportion for curlews with identified nest locations. Plots show median and 95% confidence intervals, with lower and upper quartiles.

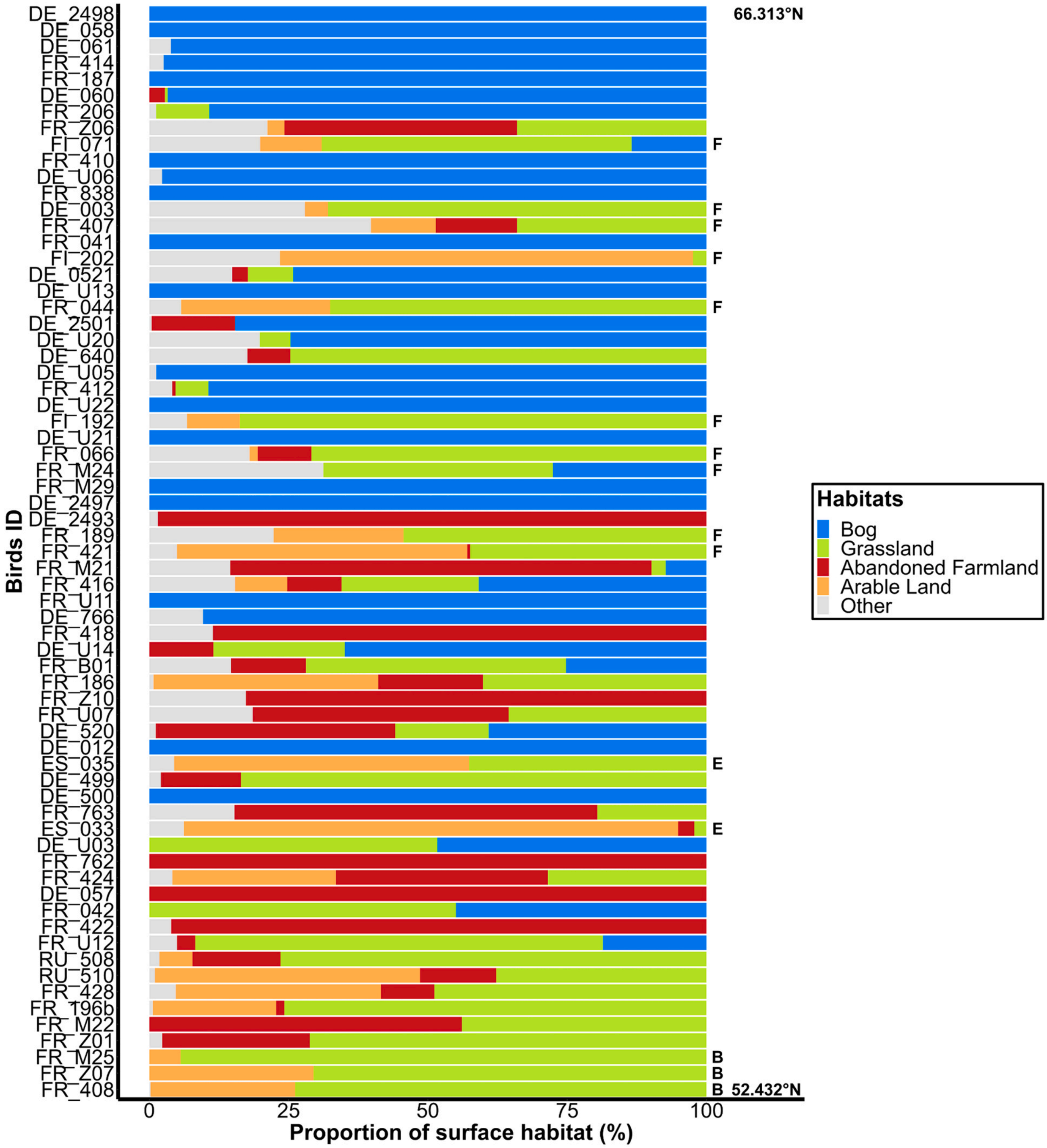

Fig. 6. Proportions of habitat use within the home range of each individual (tagged during breeding or wintering) along a latitudinal (northward) gradient (y-axis). F, individuals breeding in Finland; E, individuals breeding in Estonia; B, individuals breeding in Belarus. All other individuals bred in Russia.

4.2. Nest habitat choice

Curlews nested in open habitats within either purely agricultural landscapes or within different taiga biomes dominated by forests and bogs. Birds usually occupy meadows (exploited grassland or abandoned lands) and arable fields (e.g., winter wheat) with short vegetation when arriving, but tall grass or winter cereal towards the end of incubation and start of chick rearing, possibly providing camouflage from predators (Berg, 1992; 2020). However, individuals nesting in grassland are exposed to the risks of mowing and trampling by livestock, whereas birds in abandoned farmland and bogs are less subject to these threats, potentially increasing the

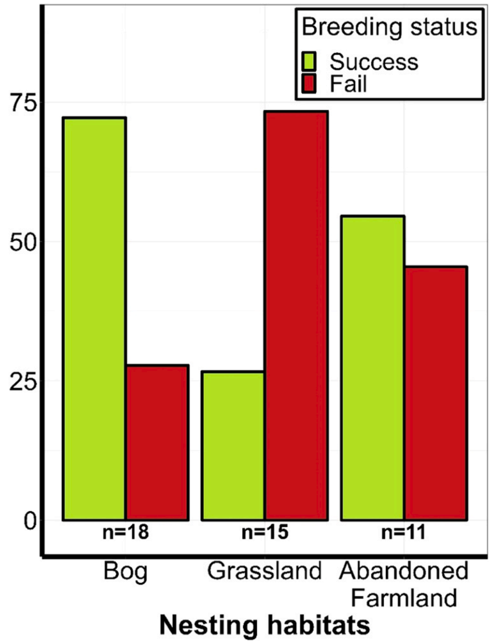

Fig. 7. Proportions of breeding outcomes (hatching success) according to nesting habitat.

chances of eggs and chick survival (Powers and Glimp, 1996; Pakanen et al., 2011). This is in line with the relatively lower hatching success of curlews nesting in grassland established in the current study. Only three birds in this study nested in arable land (four individuals used it as their main habitat), in contrast to frequent reports in Western Europe and Finland (Valkama and Currie, 1999; Brown, 2015), and two of the three birds achieved incubation to hatching. Our study demonstrated that the distances between nests and forest edges or farm buildings were lowest in grassland than in natural habitats, but surprisingly birds closer to forests had more hatching success. This suggests that birds nesting closer to forests in our study are not further affected by predation, given that terrestrial predators such as foxes are more likely to move from denser habitats such as forest as suggested in previous studies (Douglas et al., 2014, Krüger et al., 2018). Most curlew nests (86%) in grassland- and arable-dominated sites in the UK tended to fail at night, indicating mammalian predation (Ewing et al., 2023).

4.3. Breeding period

Arrival dates at the breeding site (start of breeding) were positively correlated with latitude, with individuals breeding at high latitudes arriving later than individuals at lower latitudes. According to Schwemmer et al. (2021a) and Amélineau et al. (2021), the arrival date shows surprisingly high individual repeatability, suggesting that curlews breeding scarcely in the sub-Arctic where bogs are common need to match their arrival at the breeding site with the snowmelt, so that breeding efforts correspond to periods of maximum food availability for the adults and their broods (Smith et al., 2010; Reneerkens et al., 2016; Saalfeld et al., 2019).

4.4. Home range size related to habitat

The observed differences in home range and core area sizes could be explained by different use of habitats according to the breeding region. However, the distribution and availability of resources are the main factors that determine an individual's home range (Brown, 1975). Feeding habitat choice around the nest is then likely to reflect the abundance, availability, and use of one or more specific resources by the individual (Valkama et al., 1998). Curlews are able to feed on a large range of invertebrates including arthropods, worms, and molluscs (Berg, 1993) and the quantity of invertebrates can vary between habitats (Pearce-Higgins and Yalden, 2003).

Individuals that mainly used bogs had the smallest home range and core areas, suggesting that these curlews did not need to prospect over large areas to find sufficient food. These results suggest that bogs can provide the necessary food for hatching success and more generally for the fledging success. The status and ecological requirements of bog-dependent species are still poorly understood (Fraixedas et al., 2017; Silva-Monteiro et al., 2021) due to the remoteness and difficult accessibility of these areas.

In contrast, the sizes of the home ranges and core areas of individuals that mainly used grassland and abandoned farmland were not significantly different and showed greater inter-individual variabilities. This might be because curlews can switch easily between different patches, and some factors, such as vegetation and the structure of the surrounding habitats, can influence their breeding density and distribution (Ewing et al., 2018; Söderström and Pärt, 2000; Douglas et al., 2021; Silva-Monteiro et al., 2021). Fragmentation of suitable habitats as a result of natural afforestation following land abandonment or because of newly established managed fields could explain the fluctuating home range and core areas required to find suitable feeding habitats.

4.5. Natural versus agricultural habitats in home range

This study confirmed the predominant use by curlews of natural breeding habitats in wetlands in north-eastern European Russia, and the use of agricultural habitats (exploited or abandoned) in south-western Russia where bogs are rarer. In Finland, curlews mainly breed in agricultural landscapes (Valkama et al., 1998, 2011; Kuitunen et al., 2003), but breed more frequently in bogs further north and in other areas with a low percentage of agricultural land, as the limit between natural and agricultural landscapes occurs at a higher latitude in Finland than in Russia (Tanneberger et al., 2021). However, Finland has recently developed conventional agriculture through the use of resistant and fast-growing cereal varieties and has become one of the most northerly agricultural regions among EU countries (Tiainen et al., 2020). Beyond their nesting habitat, the curlews surveyed in this study predominantly used three categories of open habitats to forage: bogs (transitional marshes with trees, wide-open mossy areas, predominantly *Sphagnum* spp.), grassland (active pasture, fodder grasses, or unimproved grassland), and abandoned farmland (tall abandoned grassland in process of natural afforestation). Although only five birds had arable land as the most-used habitat, 31% of the birds visited it during the breeding period. As in Western Europe, this habitat could be used to feed on earthworms or ground-dwelling arthropods on bare ground, especially during the pre-breeding period (Berg, 1993; Leprince et al., 2022).

4.6. Breeding perspectives

Curlews nesting in bogs tended to feed exclusively in this habitat, while birds nesting in abandoned farmland also visited nearby exploited meadows but rarely bogs, probably because they were not usually in the proximity (only seven birds used both habitats). The quality of breeding habitats is a decisive factor affecting the survival of individuals and their breeding success (Fuller, 2012). Berg (1992) accordingly found higher success rates in bogs in Sweden, with an average of 1.40 chicks/pair compared with an average of 0.25 chicks/pair in grassland. Valkama and Currie (1999) estimated a productivity of 0.32 chicks/pair in southern Finland, below the estimated productivity of 0.68 chicks/pair required to ensure a stable population (Viana et al., 2023). Bogs provide large, heterogeneous, and difficult-to-access habitats (Nikolaev, 1998), which could preserve chicks from ground predators and human disturbance compared with other habitats, while simultaneously providing sufficient food resources. Indeed, predation is considered to be one of the main factors contributing to curlew breeding failure in farmland (Berg, 1992; Grant, 1999; Zielonka et al., 2019; Ewing et al., 2023), associated with the destruction of broods by farm machinery in grasslands (Roodbergen et al., 2012). Although predation on curlew chicks in bogs by birds of prey has been documented (Ivanovsy 2012), terrestrial predators are less likely to move and gain access to nests or broods in large, well-watered bogs with sparse or no tree cover (Schwemmer et al., 2021b).

4.7. Conclusions

Our study clearly showed that natural habitats, such as bogs and abandoned farmland, were not disadvantageous for curlews compared with agricultural habitats, although they are now restricted to the highest latitudes in Europe (Fraixedas et al., 2017). These habitats are still inhabited by shorebirds, with good abundance and breeding success, regulated entirely by natural processes such as annual fluctuations in hydrological conditions, limitations in available food resources, and predation (Boström and Nilsson, 1983).

It is possible to question the future of northern landscapes that are particularly sensitive to climate change (Warszawski et al., 2013), and the potential effects of their future cultivation on the breeding habitat of curlews. Individuals breeding mainly on abandoned farmland were located at more temperate latitudes suitable for agriculture, including on land that was cultivated during the time of the former Soviet Union and was part of the 31–39 million hectares of agricultural land abandoned in Russia when the Soviet Union fell (Lesiv et al., 2018). Curlews are long-lived birds that are faithful to their breeding sites (Berg, 1994, Pakanen and Kylmänen, 2023) and were thus able to establish themselves in the years following the abandonment of the land, when the vegetation was still low. Unfortunately, the abandoned farmlands are now reverting to forests, thus threatening the breeding habitat of this ground-nesting species. Many individuals will need to alter their breeding strategies in light of ongoing habitat changes. Given the high inter-annual breeding-site faithfulness, it remains unclear if they will exhibit sufficiently high (genetic) flexibility to compensate for these alterations. In addition, climate change could allow the development of intensive agriculture at northern latitudes in Russia and its intensification in northern Fennoscandia (Unc et al., 2021).

Russia and Finland host the core population of the *N. a. arquata* subspecies (63% of the metapopulation; Keller et al., 2020), which is essential for the preservation of the species on a European scale. However, its survival may depend on the favourable ecological status of the bogs and the maintenance of grassland areas, given that abandoned farmland is destined to become either forest or to be reclaimed for cereal farming or fodder production in the short and medium terms. Through its agricultural policy under the EU CAP, Finland has an important role to play in maintaining essential populations of curlews at a biogeographical scale, as well as other birds inhabiting agricultural grassland habitats. Conservation practices in Russia are insufficiently developed for farmland birds and their habitats (Sviridova et al., 2020), except for some possibilities to preserve this species in administrative regions in south and central European Russia, where breeding populations of Eurasian curlew are included in the national Red Data Book (Sviridova, 2021). It is therefore imperative to preserve a network of grasslands within mosaic, polycultured agricultural landscapes and delayed mowing practices, to maintain suitable breeding conditions for curlews and other bird species inhabiting similar habitats. It is also essential to preserve bog habitats and prevent their degradation and drainage as part of a potential agricultural expansion to more northern latitudes driven by global warming.

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CRediT authorship contribution statement

Tatiana Sviridova: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing – original draft. **Philipp Schwemmer:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Audran Chenu:** Formal analysis, Methodology, Writing – original draft. **Pierre Rousseau:** Investigation, Resources, Validation. **Marie Donnez:** Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Frédéric Robin:** Investigation, Resources. **Pierrick Bocher:** Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Françoise Amélineau:** Data curation, Formal analysis, Methodology, Validation. **Riho Marja:** Conceptualization, Formal analysis, Methodology, Resources. **Jaanus Elts:** Funding acquisition, Investigation, Validation. **Markus Piha:** Data curation, Funding acquisition, Investigation, Methodology, Validation. **Frederic Jiguet:** Data curation, Funding acquisition, Investigation, Methodology, Resources. **Stefan Garthe:** Conceptualization, Funding acquisition, Supervision. **Jérôme Fort:** Formal analysis, Supervision, Writing – original draft.

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02851.

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