Migration and wintering strategies of a Eurasian Stone-curlew (Burhinus oedicnemus) continental population, and their conservation implications

Article *in* Avian Conservation and Ecology · January 2025

DOI: 10.5751/ACE-02772-200105

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AVIAN CONSERVATION & ECOLOGY

VOLUME 20, ISSUE 1, ARTICLE 5

Dedeban, E., P. Lagrange, A. Villers, S. Augiron, D. Chiron, L. Boussac, A. Martineau, W. Bouten, and V. Bretagnolle. 2025. Migration and wintering strategies of a Eurasian Stone-curlew (*Burhinus oedicnemus*) continental population, and their conservation implications. Avian Conservation and Ecology 20(1):5. https://doi.org/10.5751/ACE-02772-200105

Research Paper

Erratum: In the initial publication of this article there was an error in the author order. This error was corrected on 30 January 2025.

Migration and wintering strategies of a Eurasian Stone-curlew (*Burhinus oedicnemus*) continental population, and their conservation implications

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ABSTRACT. The Eurasian Stone-curlew (*Burhinus oedicnemus*) is a declining and threatened species, yet its migration and wintering strategies are little documented. Here, we used GPS trackers to collect accurate data on this species' migration routes, stopovers, flight altitude, and speed, and identified the wintering sites of 32 individuals from a western European population tracked between 2012 and 2020. In a comparison between individuals, we found that they used strikingly different migratory strategies, showing variability in wintering sites (Portugal, Spain, Morocco, or Algeria), stopovers (number, location, and duration), and migratory routes, despite the fact that they all belonged to the same breeding population. We also compared individual variability in migratory routes, migration timing, and wintering home range size, and found medium to high repeatability for most parameters. In contrast to many other migrant waders, spring migration in this species was not found to be shorter in duration than autumn migration. Our results provide insights into potential threats that may affect this species in the near future away from its breeding grounds, such as habitat quality or habitat loss in wintering areas because Iberian or Moroccan agriculture is changing very rapidly because of drought.

Stratégies de migration et d'hivernage chez l'Oedicnème criard (*Burhinus oedicnemus*) et implications en matière de conservation

RÉSUMÉ. L'Oedicnème criard (*Burhinus oedicnemus*) est une espèce en déclin et menacée en Europe de l'Ouest, dont l'écologie est relativement bien étudiée, mais dont les stratégies de migration et d'hivernage le sont beaucoup moins. Dans cette étude, nous avons utilisé des GPS pour collecter des données précises sur les trajets migratoires de cette espèce, les « stop-overs » (ou escales), comprenant altitude et vitesse de vol, et identifié les sites d'hivernage de 32 oiseaux d'une population du Centre Ouest de la France, entre 2012 et 2020. Bien qu'issus de la même population, les individus ont utilisé des stratégies de migration très différentes entre eux, à la fois concernant les trajets, le nombre et la durée des « stop-overs », mais aussi les sites d'hivernage (Portugal, Espagne, Maroc ou Algérie). Par contre, pour les individus pour lesquels plusieurs années de données ont pu être collectées, nous montrons qu'il existe une forte à très forte répétabilité de ces paramètres, qu'il s'agisse des trajets ou des zones d'hivernage, ou même de la taille du domaine vital, variable entre individus mais qui l'est faiblement pour un individu donné. Enfin, contrairement à de nombreux autres limicoles migrateurs, la migration pré-nuptiale n'est pas plus courte que la migration post-nuptiale chez cette espèce. Ces résultats et nouvelles données permettent, enfin, d'éclairer les menaces potentielles qui pourraient affecter cette espèce au-delà de ses sites de nidification, concernant notamment la qualité des sites d'hivernage et les menaces qui planent pour ces derniers au regard de l'évolution récente et marquée de l'agriculture en péninsule ibérique ou au Maroc, qui change très rapidement du fait de sécheresses répétées.

Key Words: *Burhinus oedicnemus; GPS tracking; home range; migration; stopovers; wintering*

INTRODUCTION

The migration patterns of many species of Western Palearctic birds are reasonably well known (Wernham 2002, Masden et al. 2009), with the number of resources available online increasing fast (e.g., Spina et al. 2022). Shorebirds, including waders (Charadriiform) often perform very long-distance migration, from the Palearctic/Nearctic to Afrotropical/Neotropical, and even on the opposite hemisphere (Gill et al. 2014, Piersma et al. 2022). In many migrating birds, pre-breeding migration has been found to be shorter in duration than post-breeding migration (Nilsson et al. 2013, Schlaich et al. 2017), because wind patterns differ between seasons and/or as a result of differential constraints in autumn, when birds need to save energy, and in spring, when the time available to breed is limited (Nilsson et al. 2013, Zhao et al. 2018, Duijns et al. 2019). A comparative analysis involving six different waders showed that spring migration is actually shorter in duration than autumn migration only in smaller species (Zhao et al. 2018), with curlews for instance showing equal length in spring and autumn migration (Pederson et al. 2022). Stopover

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migration sites have also been well studied in migratory species in general (Herbert et al. 2022), and waders in particular, as stopovers appear to be critical for refueling, both in coastal migratory shorebirds (Exo et al. 2019, Kuang et al. 2020) and in inland waders (Kasahara et al. 2020). Stopover sites are often located just prior to or after ecological barriers (sea, mountains), underlying their huge conservation importance (Herbert et al. 2022).

Satellite-based GPS systems and geolocation (GLS) are revolutionizing the study of bird migration (Bridge et al. 2011), including smaller species thanks to new devices (Åkesson et al. 2016, Newton 2023). However, detailed knowledge of migration pathways, especially at an individual level, is still only available for a handful of species (Brown et al. 2021, Kürten et al. 2022), particularly the largest. However, many long-distance migrants are declining, either because of threats on migratory routes (Newton 2006, Tøttrup et al. 2008, Hewson et al. 2016), climate change acting on non-breeding areas (Ockendon et al. 2012) or habitat change (Cresswell et al. 2007, Conklin et al. 2010). Many Palearctic wader migrants are currently in dramatic decline (Piersma et al. 2016, Beresford et al. 2019, Haest et al. 2021), and critical gaps remain for many species, even those with high conservation priorities. Therefore documenting migration routes, stopover sites, and wintering grounds could greatly contribute to our understanding of current or potential threats, and therefore the conservation perspectives over the entire lifecycle of these species.

Among threatened medium-sized farmland birds, the Eurasian Stone-curlew *Burhinus oedicnemus*, a steppic Palearctic terrestrial wader, is a species for which little data has previously been available in regard to migration and wintering areas. Stone-curlews are found in European farmlands and pseudo-steppes (Vaughan and Jennings 2005). After Spain, the second-largest European population is found in France, which hosts an estimated 19,000–28,000 breeding pairs (Issa and Muller 2015). The species has suffered a rapid and strong population decline since the second half of the last century (Cramp and Simmons 1983), with the suspected causes being agricultural intensification, loss of landscape mosaics, and changes in land use in the breeding areas (Green et al. 2000, Issa and Muller 2015, Gaget et al. 2019, BirdLife International 2024). At the world level, the species is considered of "Least-concern" (BirdLife International 2024), but at European level (BirdLife International 2021), it belongs to the Annex I of the Birds Directive, and is declining (Birdlife International 2021). In the UK, the species is classified as Amber listed, while in France it is in the Vulnerable category. The only population studied over the long-term in France has revealed decline in population size and several critical life history traits, in particular adult survival rate (Gaget et al. 2019). Until recently, there was limited knowledge of the movement ecology of the species, including its wintering range, migratory behavior, and habitat use. Ring recovery data have shown that the British population winters in France and Spain, while first-winter birds apparently winter in West Africa (Green et al. 1997). GLS and GPS trackers (and to a lesser extent, ring recoveries) indicate that a population breeding in northern Italy winters in Sardinia, Corsica, and Tunisia (Giunchi et al. 2015). Individuals belonging to four populations in Italy were fitted with GLS and GPS, and showed that sedentary behavior occurred more often in southern populations and that birds spent the winter in the Mediterranean basin (Cerritelli et al. 2020, Falchi et al. 2023). Based on this knowledge, stone-curlews seem flexible concerning migration and wintering, with populations, or individuals within populations, being either sedentary or migratory (Vaughan and Jennings 2005, Falchi et al. 2023). None of these studies however dealt with the conservation consequences of such migration behavior.

The aim of this study was to describe the migration timing and complete annual migratory pathways within a stone-curlew population in central-western France, precisely the population that has been monitored for 20 years and showed decreasing adult survival rates (Gaget et al. 2019), as well as to provide the first accurate and extensive data on wintering areas. As a large-bodied wader breeding at temperate latitude, we expected constraints acting on its migratory behavior to be less pronounced than it is for arctic breeders and/or smaller species, i.e., spring migration may not be shorter than autumn migration, and stopovers would be short and thus may not be critical for refueling. To test these hypotheses, we fitted 32 birds with high-resolution GPS devices and monitored these individuals for a period of time ranging between 56 and 1852 days. We analyzed the temporal and spatial patterns of migration, including arrival and departure dates, routes taken, and location of wintering areas, then focused on migration stopover sites, their numbers, position, and the duration of stay, as well as wintering sites and winter home range estimates. We also investigated whether variability in departure time affects the return time, whether the start of migration correlates with the time of arrival, whether instantaneous flight speed during migration is regulated by migration distance, as it is in migratory songbirds (e.g., Schmaljohann 2019), and provided repeatability estimates for some of these behaviors.

METHODS

Study area

The birds were monitored and captured in two nearby study sites, separated by 30 km (Fig. A1.1). The first is located in the Long-Term Social-Ecological Research (LTSER) zone known as "Zone Atelier Plaine & Val de Sèvre" (https://za-plaineetvaldesevre.com/), an intensively managed farmland within the Nouvelle-Aquitaine region in central-western France (Fig. A1.1; see Bretagnolle et al. 2018a, Berthet et al. 2019 for a general description). The LTSER covers 450 km² of farmland, where crops are dominated by winter annuals (cereals ~40% and rapeseed ~12–15% of the arable surface area), followed by spring crops (sunflower 15%, maize 10%), and grassland cover (10%). The study area encompasses a Special Protection Area (SPA FR5412007) designated to protect different bird species, including the stone-curlew (Bretagnolle et al. 2011). The second study site is located in the Special Protection Area (SPA FR5412013) known as "Plaine de Niort Nord-Ouest." This is also an intensive agriculture area, with landscapes very similar to the first study site (cereals ~45%, rapeseed ~12–15%, sunflower 15%, maize 10%). The site covers a surface area of 170 km² (Fig. A1.1), is crossed by a motorway, and in contrast to the first site, includes several wind farms, but less forested areas.

Study species

The stone-curlew is a rather plastic species regarding its breeding habitats, provided that there is drained soil, low vegetation height and density, and stones on the ground to optimize the anti-predation strategy of this cryptic species (Green et al. 2000). In France, farmland landscapes are its major breeding habitat, with more than 60% of the breeding pairs located in arable crops of central-western France (Issa and Muller 2015). Nesting starts in March and ends in September, with possibly up to two replacement clutches (Gaget et al. 2019). After the breeding period from September until November, stone-curlews congregate near their breeding place on gathering sites that are faithfully used from one year to the next. On the LTSER study site, a long-term breeding ecology and conservation research program is being conducted, including a color-ringing scheme since 2005 (both chicks and adults). The sex of captured birds is genetically determined with DNA from blood samples (Fridolfsson and Ellegren 1999). Adults are captured from March to September using the night-lighting technique, and the birds are equipped with unique metal identification bands (National Museum of Natural History, MNHN, Paris, France, Ringing programme no.1001) and a combination of 2–4 colored rings or one Darvic ring.

GPS devices and tracking data

Between 2012 and 2020, a total of 23 GPS trackers (UvA-BiTS, University of Amsterdam Bird Tracking System; see Bouten et al. 2013) weighing 15 g were fitted on adult stone-curlews. From 2020, we also deployed 10 OrniTrack 15-g GPS-GSM transmitters manufactured by Ornitela (https://www.ornitela.com/) yielding a total of 14 females, 16 males, and 2 of unknown sex fitted with GPS. All devices were attached with a Teflon ribbon harness backpack: the GPS and harness weighed 15.2–16.2 g, which is ~3.0–3.19% of body mass (mean ± SD = 505.6 ± 42.7 g). Although we used rather large loggers, given the body size of the studied species they remained in the safe zone of 3% of body mass, avoiding the undesirable effects that have been found in smaller waders, e.g. *Calidris* species (Pakanen et al. 2020). In contrast to the other system, data from the UvA-BiTS had to be downloaded to base stations, i.e., a bird was only detected when it was close enough and in view of one of the antennas spread across the study site (Bouten et al. 2013). This was a field constraint given that stone-curlews spend most of their time on the ground foraging or resting, limiting the amount of data that could be downloaded at once. We used several time settings on GPS beacons (see Table 1). Because GPS locations contain errors due to missing locations or location errors, we removed data with a coverage of less than 4 satellites and additionally visually checked for GPS errors and deleted these with "trip" in R (Summer 2011). The sampling rate was standardized to 1 location every 15 min, despite the original sampling rate being 5 min but some data were missing. We removed extreme altitude data and locations where the difference in altitude was discontinuously distant from the previous and following locations (20 m or more). The data recorded by GPS devices was uploaded to Movebank (https://urlz.fr/nI12).

Migration routes

For each individual and season (spring and autumn), migration departure and arrival was characterized by daily and hourly increase in distance and speed with a variation in latitude; hence we used a distance-threshold method to visually estimate migration date (see Cerritelli et al. 2020, for a comparison of four methods using the stone-curlew). We also visually assessed the flight paths to cross-check the information collected on the migratory dates. Autumn migration start was recorded as the last fix from the breeding area while the end of migration was the first point from the wintering area. A similarly but reversed method was used for spring migration. For each bird and migratory season, we recorded departure and arrival dates, the duration of migration, and a set of descriptive parameters, including the total migration distance and the average instantaneous flight speed. Total migration distance (i.e., the length of the route) was computed with the "geosphere" package (Hijmans et al. 2019) as the total sum of step lengths recorded between two consecutive locations (the Euclidean linear distance). To do this, we only used GPS positions between stopovers. The flying speed (speed above ground) was extracted from the instantaneous speed provided by the loggers. We removed unrealistic travel speed above a threshold value of 38 ms^{-1}. To evaluate the possible influence of light condition for departure decision, we calculated the difference between the date of departure and the date relating to the nearest full moon phase. Using sunset data from the "suncalc" package (Thieurmel and Elmarhraoui 2024), we also determined the differences between departure time and sunset. During migration, we identified clusters of successive positions where an individual bird did not move more than 20 km. Clusters spanning over at least 24 h were defined as stopover sites, used by individuals to refuel. Periods identified as stopovers were not included in the calculation of migratory variables in order to retain only information about direct routes.

Home ranges

We estimated winter home ranges using utilization distribution (UD), calculated at a 70% threshold and a 50% threshold (i.e., core areas) for every wintering season, with a kernel Brownian bridge function (Calenge 2006). This function considers that between two successive GPS locations, the animal has moved through a continuous path that is not necessarily linear. Other methods, like Kernel Density Estimators are available, but Brownian bridge models rely on fewer statistical assumptions and are better fitted to the nature of our data (see Horne et al. 2007). We could not obtain such data for all birds for every winter, so in total we were able to analyze 36 wintering home ranges for 21 birds (Table 1). The 70% threshold was used rather than the more usual 90% UD (Eichhorn et al. 2017) to prevent extremely high home range values as a consequence of birds using several distinct and distant areas over the course of the winter. The sig1 smoothing parameter was set to the speed of the birds and the sig2 related to the imprecision of the relocations, which was estimated at 30 m for stationary locations lasting at least 600 s (Bouten et al. 2013). We also compared home range size between breeding and wintering periods. Further, we assessed the percentage of overlap for individuals between different years with the "adehabitatHR" package using the "kerneloverlap" function (Calenge 2006).

Repeatability estimates for spring and autumn migration and wintering sites

To quantify the degree of individual consistency in migration behavior (timing and routes taken) and wintering behavior (home range size), we estimated repeatability (*r*), which represents the fraction of the total variance (within individual bird + between

Table 1. Details of GPS deployment between 2012 and 2020, per individual.

Device	Ring N°	Age	Sex	Capture date	GPS end date[†]	GPS intervals (day/night, min)	Duration (day)	Status	N. spring migration	N. autumn migration
U820	*620882	-	M	25/06/2012	11/09/2012	60/60	78	?	-	-
U1016	*50871	-	M	26/05/2013	12/10/2013	60/60	139	?	-	-
U5174	*101533	Ad	M	24/04/2015	24/07/2016	15/30	457	Breeder	0	0
U5175	*101536	Ad	M	30/04/2015	01/08/2017	15/30	824	Migrant	2	2
U5173	*101537	Ad	F	30/04/2015	04/05/2015	15/30	4	-	-	-
U5162	*101580	Ad	F	02/05/2015	27/05/2020[†]	15/30	1852	Migrant	4 + 1	4 + 1 without data
U5149	*101587	Ad	F	14/06/2015	14/06/2015	15/30	1	-	-	-
U5177	*588838	+2A?	M	20/04/2017	14/10/2020[†]	15/30	1273	Migrant	3	2 + 1
U5348	*592002	2A?	F	05/05/2017	11/11/2019[†]	15/30	920	Migrant	2	1 + 1
U5344[‡] U5468[‡]	*592001	+2A	M	05/05/2017	16/07/2020	15/30	1167	Migrant	3	2 + 1
U5343	*588839	+2A	F	06/05/2017	30/09/2020	15/30	1243	Migrant	3	3
U5345	*588840	+2A	F	06/05/2017	12/11/2019[†]	15/30	920	Migrant	2	1 + 1
U5349	*592004	2A?	F	17/05/2017	12/08/2018	15/30	452	Migrant	1	1
U5355	*592005	+2A	M	17/05/2017	12/07/2017	15/30	56	?	-	-
U5350	*101609	2A	M	17/05/2017	19/05/2017	15/30	2	-	-	-
U5353	*592006	2A	F	17/05/2017	-	15/30	-	-	-	-
U5183	*588841	Ad	M	05/06/2017	22/10/2019[†]	15/30	869	Migrant	1 + 1	2
U5342	*592007	+2A	M	06/06/2017	31/10/2017	15/30	142	?	-	-
U5158	*592008	+2A	F	06/06/2017	15/10/2017	15/30	131	?	-	-
U5178	*588842	Ad	F	06/06/2017	08/02/2019	15/30	612	Migrant	1	2
U5621	*620875	Ad	F	09/11/2018	09/11/2018[†]	15/30	44	-	-	-
U5619	*620877	Ad	-	11/11/2018	12/10/2020	15/30	762	Migrant	2	2
200462	*586587	1A	M	19/08/2020		5/10	412[§]	Migrant	1	1
200461	*586592	Ad	F	26/08/2020		5/10	405[§]	Migrant	1	1
200460	*586593	1A	F	03/09/2020		5/10	398[§]	Migrant	1	1
200465	*586594	Ad	M	03/09/2020		5/10	398[§]	Migrant	1	1
200468	*586595	Ad	F	03/09/2020		5/10	398[§]	Migrant	1	1
201990	*586597	Ad	M	21/09/2020		5/10	380[§]	Migrant	1	1
201989	*586598	Ad	M	22/09/2020		5/10	378[§]	Migrant	1	1
201994	*586600	Ad	M	07/10/2020		5/10	364[§]	Migrant	1	1
201993	*108811	1A	M	08/10/2020		5/10	363[§]	Migrant	1	1
202977	*108815	Ad	M	18/11/2020		5/10	332[§]	Migrant	1	1

Brand of tracker: UvaBiTS (U); Ornitela (numbers). Age: Adult (Ad); 1 year (1A); 2 years (2A)
Ornitela settings were updated in 2020: 1 loc/min in French mountains at night
+ 1: incomplete tracking of route
[†] Logger has lost contact, but the bird may still be alive
[‡] First logger changed after one year of tracking
[§] Sample period stopped in October 2023

birds), which is accounted for by between individual variance. The *r* ranges from 0 to 1, with 0 indicating that all variance is individual, and 1 indicating that all variance is between individuals (Nakagawa and Schielzeth 2010). We estimated repeatability with the R package "rptR" (Stoffel et al. 2017), using the individual's ID as a random factor. Separate models were built for the spring and autumn migrations. We then calculated the 95% confidence intervals by bootstrapping 1000 estimates. We identified longitudes at which the birds crossed the latitudes 44, 40, 36°N (Vardanis et al. 2011), corresponding, respectively, to the Pyrenees, central Spain, and Gibraltar, however the latter was available only for birds that wintered in Morocco or Algeria. In the repeatability analysis, we used all individuals, even those with incomplete flight path tracking (n = 6 individuals) as the extraction was done on specific portions of the migration route. We finally compared the mean longitude of individuals at the latitude of 40°N to assess the variation between spring and autumn migration routes because this latitude did not correspond to any particular bottleneck and avoided therefore any overestimation of repeatability. The sample size available for such repeatability analyses were however small and therefore only very high repeatability values were expected to provide significant results.

Statistical analysis

Depending on independent variable distribution, we used linear mixed models (LMM) or general linear mixed models (GLMM) models. We compared variation in migratory behavior (duration, total migration distance, duration of stopover) between spring and autumn migration using LMM (normal error distribution) and stopovers (number of days) using GLMMs with a Poisson error distribution. All models used individual identity as a random intercept effect. The LMMs were fitted with the "lmer" function of the "lme4" R library (Bates et al. 2017), on pre- and post-breeding migration data. To assess the effect of capture date on migration departure, we applied the non-parametric Mann-Whitney U-test.

RESULTS

Timing and duration of migration

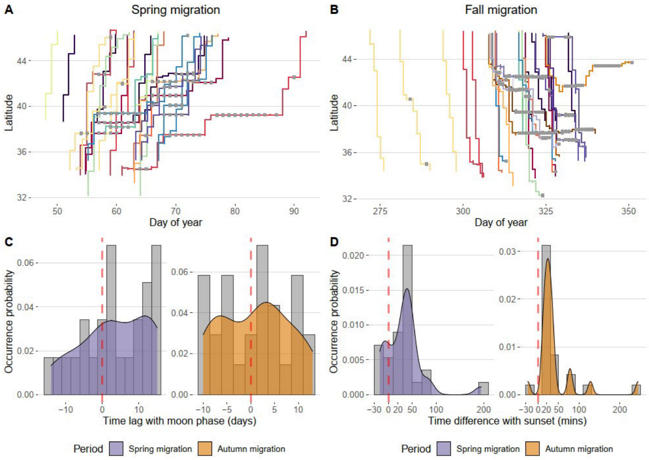
Out of the 32 GPS trackers that were fitted between 2012 and 2020, 27 provided locations (Table 1). There were no data from five loggers, or data only for a few days, which could have been caused either by logger failure or by the fact that fitted birds were not breeding in the study areas, i.e., were transient individuals that consequently were never in range for data downloading with the fixed antennas. The 27 GPS trackers yielded a total of 8,812,148 locations, with stone-curlew movements monitored for periods ranging from 44 days to over 5 years, depending on the individual. However, five additional loggers stopped sending data after a few months and did not allow the study of migration trips (Table 1). After excluding one resident bird, 73 migratory flight paths were extracted (60 of which were complete, or 82.2%). We also excluded an individual (ID-200462) that strayed during autumn and spring migration and took more than three months to return to the breeding site in spring. Of the complete routes, 33 were in spring and 27 were in autumn for 20 different individuals (Table 1).

Autumn migration started mainly in November, with departure ranging from 29 September to 27 November (mean: 7 November; Fig. 1B, Table 2). There was no effect of recent capture on departure date because the latter did not differ statistically between individuals that were caught and fitted in late summer or early autumn (n = 8), i.e., just before migration, and the others (LMM, $\beta = -3.33$, se = 13.29, n = 27, p = 0.81). There was no effect of sex on departure date either (LMM, $\beta = 0.95$, se = 6.97, N = 27, p = 0.89). The arrival dates at the wintering areas ranged between 2 October to 5 December (mean: 15 November; Fig. 1B, Table 2). Mean spring departure dates from the wintering grounds and arrival dates were, respectively, 29 February and 12 March (Fig. 1A, Table 2). For individuals, there were significant effects of departure date on arrival date both in autumn (LMM, $\beta = 1.00$, se = 0.14, n = 27, $p < 0.001$) and spring migrations (LMM, $\beta = 1.39$, se = 0.22, $p < 0.001$), but no sex effect nor interaction between sex and departure date (all p values > 0.74). There was no significant relation between arrival date in autumn and departure date the following spring (LMM, $\beta = 0.24$, se = 0.18, n = 26, p = 0.19; no sex effect, no significant interaction), i.e., individuals that arrived later did not depart either earlier or later (Fig. A1.2a). There was no significant relationship between departure date or arrival date in autumn migration and travelled distance (Fig. A1.2b). In spring, however, birds travelling shorter distances (i.e., wintering closer to the breeding site) arrived significantly earlier (10 days on average) to breeding sites, but this was true only for males because there was a significant interaction between sex and date (LMM, $\beta = 9.88$, SE = 4.20, p = < 0.05). There was no relationship between departure date and distance travelled in spring migration (Fig. A1.2c).

All individuals migrated exclusively at night, leaving their breeding or wintering areas on average 35.3 ± 41 min (range: -13.6–194) and 48.5 ± 51.9 min (-25.7–254), respectively, after sunset (Fig. 1D). Departure time was quite synchronized (Fig. 1D) but was unrelated to the moon phase (Fig. 1C). Stone-curlews reached their winter quarters (Morocco, Spain, or Portugal) by travelling on average 1475 ± 265 km in autumn migration and 1565 ± 270 km in spring migration (see Table 2, Fig. 2). The instantaneous flight speed ranged from 21.7 to 136 km/h in autumn migration (mean = 48.8) and 23.1 to 128 km/h in spring (mean = 41.4).

Spring migration duration was not significantly different compared to autumn migration (LMM, $\beta = 1.15$, se = 0.16, n = 60, p = 0.31). Comparing the spring and autumn migration of a given individual using paired tests indeed yielded a significant difference (paired t-test, = -2.17, df = 25, p = 0.039). On average, autumn migration was slightly shorter in duration and straighter, with fewer and shorter stopovers than spring migration (see Table 2).

Fig. 1. Temporal patterns of latitudinal movements for spring (a) and autumn journeys (b). The "plateau" with dots represents days the Eurasian Stone-curlews (*Burhinus oedicnemus*) stayed at a stopover. Colors distinguish individuals. The following figures represent the distribution of dates (Panel C) and departure times (Panel D) according to the nearest moon phase (C) and time of sunset (D).



Migration routes and stopovers during migration

Migration routes (see Fig. A1.3 and Fig. A1.4 for various examples), as described by the longitude at 40°N as a proxy of the route, did not differ between autumn and spring migrations, though some routes could be up to 80–130 km further to the east of central Spain in spring (LMM, $\beta = 0.81$, se = 0.51, n = 58, p = 0.11; no sex effect, no significant interaction). Stone-curlews showed relatively straight paths during autumn migration, with very few stopovers (Fig. 2, Table 2), except in the 2020 autumn migration in which 5 birds out of 10 used several stopover sites (Fig. 2C). Similarly, stopover duration was shorter in autumn (mean = 2.5 ± 2.4 days) than in spring but the difference was not significant (mean = 3.27 ± 2.88; GLM with Poisson error-distribution; Period*Sex effect: $\beta = 1.71$, se = 0.49, n = 92, p = 0.06; sex effect and period effect NS, p > 0.49). Distances between successive stopovers was on average 684 ± 574 km during autumn migration (21.3–1785 km) and 577 ± 460 km in spring (20.2–1845 km); the difference was not significant (LMM, Period*Sex effect: $\beta = 53.4$, se = 118.1, n = 108, p = 0.65; sex effect and period effect NS, p > 0.76).

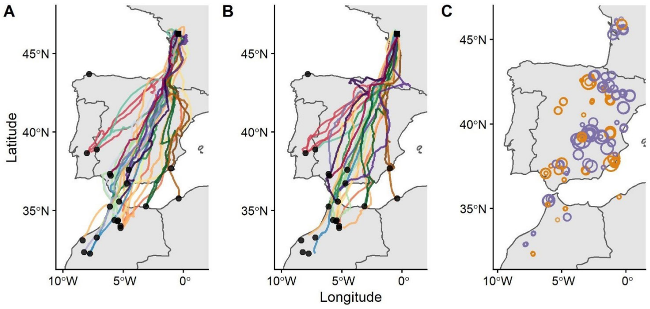
Wintering sites and home ranges

Migratory stone-curlews spent about 3 months (86 ± 32.5 days) on their wintering grounds, and in almost all cases returned to identical areas from year to year (Fig. 3). Main wintering areas detected included Morocco (12 birds, 57.14%), Algeria (1), Spain (6), and Portugal (2; Fig. 2A). A single individual remained

Table 2. Migration timing, duration, distance, speed and stopovers of Eurasian Stone-curlews (*Burhinus oedicnemus*), for different seasons, migration routes, and individuals (average values and SD are provided).

	Spring migration			Autumn migration		
	Mean (SD)	Min-Max	N	Mean (SD)	Min-Max	N
Departure date (days)	Feb 29 ± 9	Feb 10–April 1	33	Nov 7 ± 13	Sept 29–Nov 27	27
Arrival date (days)	March 12 ± 15	Feb 15–April 23	33	Nov 15 ± 14	Oct 2–Dec 5	27
Duration (days)	12 ± 9.59	2–32	33	8.37 ± 8.26	1–32	27
Total migration distance (km)	1565 ± 270	1147–2111	33	1475 ± 265	1080–2216	27
Migration ground speed (km/h)	59.6 ± 19.2	23.1–133	33	57.2 ± 17.2	21.7–138	27
Stopovers (number)	1.70 ± 1.74	0–6	33	1.33 ± 2	0–7	27
Stopover duration (days)	3.27 ± 2.88	1–14	56	2.5 ± 2.40	1–11	36

Fig. 2. Migration routes of adult Eurasian stone-curlews (*Burhinus oedicnemus*) tracked from central-western France for spring (Panel A) and autumn migration (Panel B) during 2015–2020. Only completed routes are represented and colors distinguish individual routes. On panel A and B, symbols refer to breeding and wintering areas (squares = breeding sites; circles = wintering sites). Panel C represents stopovers longer than one day (symbol size reflects the duration of stopovers, from 1 to 11 days) and colors differentiate between spring (purple) and autumn (orange).



sedentary, spending the whole non-breeding season very close to its nesting area (overlap in winter and summer home ranges ~78%). Its winter home range averaged 3.5 km² (70% kernel UD). The average winter home range size for migratory individuals was 2x larger, 6.17 ± 4.73 km² (0.01–24.4, median = 4.68), which was also larger than summer home ranges (2.55 ± 3.12 km²; LMM, effect: β = 2.99, se = 0.55, n = 76, $p < 0.05$; no sex effect nor interaction between sex and period) using the same parameters to calculate the 70% UD. The home range size did not differ on average between the three main wintering areas ($F_{1,35} = 0.742$, p = 0.53; Table A1.1). The cumulative distance of daily movements (day and night) in winter was 7.62 ± 4.12 km/day, similar for the resident bird (cumulative distance 5.56 km/day).

Variability and repeatability in individuals

Among individuals with repeated migratory information across years, we found that individual birds showed significant repeatability in autumn and spring migration despite relatively low sample sizes (Table 3). Autumn repeatability was particularly high for the departure date (0.753) and arrival date (0.714), although confidence intervals were sometimes large (Table 3). Spring migration repeatability in dates was also high (Departure = 0.531; Arrival = 0.957). Birds were also consistent in the choice of their trajectories. At latitudes of 40°N (central Spain; see Fig. 2) and 36°N (Gibraltar), repeatability values in route longitude were significant (ranging from 0.617 to 0.873; Table 3). This was not the case at a latitude of 44°N for autumn migration (100 km north of the Pyrenees; Table 3). At wintering sites, individuals tracked for several consecutive years showed a very high fidelity to wintering location (Fig. 3): home range (at 70% kernel UD) overlap between successive winters was 72.3 ± 18.9% (n = 9), and the mean core area (50%) overlap was 73.8 ± 23.01%.

DISCUSSION

These results provide detailed information on stone-curlew movements over the complete annual cycle, gathered in a suitable sample size (in terms of tracked individuals and the length of the study) to characterize the migration and wintering behavior of this continental declining population. Indeed, Mediterranean populations of the species had already been studied (Giunchi et al. 2015, Falchi et al. 2023). We did not detect any statistical effect of capture on migration behavior, as was found in a comparative study with GLS on shorebirds (Weiser et al. 2016). Our findings show that this French population complete autumn and spring migrations between their breeding sites in France (46°N) and their wintering areas in Spain, Portugal, Algeria, and Morocco (between 33°N and 39°N), with individuals migrating to geographically distinct areas. This population thus winters in areas also used partly by British stone-curlews, for which ring recoveries dated up to 2020 indicated 38 birds in Spain, 11 in Morocco, 4 in Portugal, 2 in Algeria, and 1 in Ghana (Green et al. 1997, Robinson et al. 2019). In the latter population however, most first-winter birds winter in West Africa (Green et al. 1997, Wernham 2002), but we did not tag fledglings in our study. We found high variation between individuals regarding all migration characteristics, but for certain characteristics, we detected medium (0.53) to high (0.96) repeatability in individuals. We did not observe significant differences between spring and autumn migration, in contrast to most other wader species.

Variation between stone-curlew individuals in choice of wintering area has already been suggested from one (Giunchi et al. 2015), and later, four stone-curlew populations from Italy (Falchi et al. 2023). Ring data from UK birds also suggested such a pattern (Thompson et al. 2004, Robinson et al. 2019). Many studies have demonstrated individual variation in migration strategies in terms of timing, routes, and staging sites in various shorebirds (Conklin et al. 2010, 2013) and in waders such as the Red Knot (Atkinson et al. 2007), Black-tailed Godwit (Lopes et al. 2013, Senner et al.

Fig. 3. Overlapping wintering home range estimates (70% threshold) of individual Eurasian stone-curlews (*Burhinus oedicnemus*) tracked for at least two complete winters between 2016 and 2019 (the inset map shows the location of the four individuals). Orange line = 1st winter; green line = 2nd winter; purple line = 3rd winter; blue line = 4th winter. Examples shown are for two individuals (left, wintering in Morocco; right, wintering in Portugal). Panels B, C and D show close home range sites and high fidelity, while panel A shows two distant sites during the first winter.

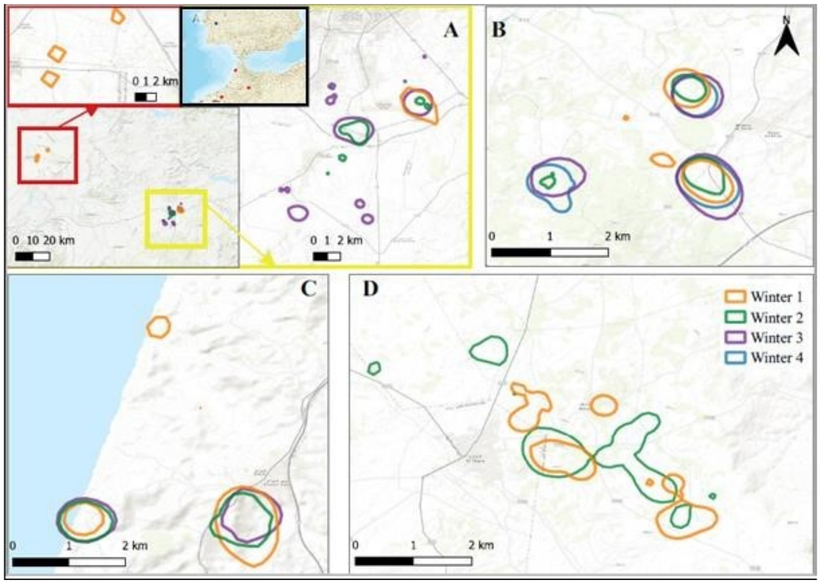


Table 3. Adjusted repeatability estimates and 95% confidence intervals for spring and autumn migration (2015–2020), including departure dates and arrival dates, spring and autumn crossing selected latitude (44°, 40°, 36°).

Period	Timing	N	Adjusted repeatability (*r*)	95% CI
Spring	Departure	36	0.531*	0.013 - 0.804
Autumn		35	0.753*	0.434 - 0.898
Spring	Arrival	36	0.957*	0.893 - 0.984
Autumn		35	0.714*	0.328 - 0.892
Spring	Latitude 44°	25	0.866*	0.589 - 0.971
Autumn		21	0.271	0 - 0.839
Spring	Latitude 40°	33	0.802*	0.515 - 0.93
Autumn		28	0.708*	0.285 - 0.901
Spring	Latitude 36°	22	0.873*	0.618 - 0.964
Autumn		15	0.617*	0.098 - 0.924

* Significant.

2018), Bar-tailed Godwit (Conklin et al. 2010, 2013), Eurasian Oystercatcher (Méndez et al. 2021), Northern Lapwing (Eichhorn et al. 2017), and Eurasian Curlew (Schwemmer et al. 2021, Pederson et al. 2022). Inter- or intra-individual variation may possibly be caused by variations in meteorological conditions experienced during migration, such as adverse winds, forcing birds to select safer but longer paths over land and sea (Liechti 2006). The high variability between individuals suggests that selective pressure is low for such traits (Verhoeven et al. 2019).

Waders are expected to show different migratory patterns between autumn and spring, not only because wind patterns differ, but also because of differential constraints in autumn, when birds need to save energy, and in spring, when the time available to breed is limited (Nilsson et al. 2013, Zhao et al. 2018, Duijns et al. 2019). Here we found that duration of the spring migration was slightly longer than autumn migration, conversely to expectations (but see (Zhao et al. 2018)). Grey plovers migrate at much higher speeds in spring compared to autumn, but spring migration lasts longer (although not significantly) because stopover-site sojourns are longer (Exo et al. 2019). In contrast, Whimbrels have a shorter migration in spring than in autumn because of shorter stopovers (Kuang et al. 2020). In a comparative analysis involving six different waders, spring migration was found to be shorter in duration than autumn migration, but only in smaller species (Zhao et al. 2018). The Eurasian Curlew, the largest species, showed shorter autumn migration than in spring (Zhao et al. 2018), as in our findings for the stone-curlew, but this was contradicted in another study (Pederson et al. 2022). Stone-curlews were shown here to migrate exclusively by night, as many other waders do (Newton 2023).

Stopover migration sites have been well studied in waders because of their potential conservation importance (Exo et al. 2019, Kuang et al. 2020). Because migration distances are rather short in the stone-curlew (and presumably well below the longest non-stop flights without refueling given body mass), stopover sites may not be as critical as in other species. As expected, stays at stopover sites were indeed very short in the stone-curlews we tracked (3 days) compared to 4–80 days in Little Ringed Plovers (Kasahara et al. 2020), 24–66 days depending on population and season in Whimbrels (Kuang et al. 2020), 21 days in Pacific Golden-Plovers (Johnson et al. 2020), and 20–145 days in Grey Plovers (Exo et al. 2019), for which inland routes had fewer and shorter stopover sites than coastal routes.

Navigation capacity has been studied in the stone-curlew regarding homing abilities (Orchan et al. 2016). When released in unknown sites, tested birds spent a few days before travelling back to their usual site. In several of the migratory routes we tracked, we also found that birds arriving close to the wintering grounds but not exactly on the wintering site (20–50 km from the final site) stayed for a few days and then travelled to the right locality (Fig. A1.3; see also Orchan et al. 2016). Navigation was also challenged when crossing the Mediterranean Sea or the high mountains of the Pyrenees. Stone-curlews reluctantly crossed mountain ranges, which has also been found in the Black-tailed Godwit (Senner et al. 2018). Interestingly, we found highly flexible behavior between individuals in migration routes, wintering sites, or stopover use; we detected medium (0.53) to very high (0.96) individual repeatability in these behaviors. Overall, constraints are higher in high Arctic breeding species and smaller species, a pattern that should enforce repeatability (i.e., within-individual consistency of behavior; (Kürten et al. 2022), and indeed, spring migration parameters were found to be more repeatable than autumn migration ones (Conklin et al. 2013, Schwemmer et al. 2021, Franklin et al. 2022) and higher repeatability in migration parameters was found in high-latitude breeders (Vardanis et al. 2011, Clausen et al. 2015, Tedeschi et al. 2020). Conversely, more variation in migration pattern is expected for populations with short migration routes (Nilsson et al. 2013, Falchi et al. 2023).

A similar pattern, i.e., high variability between individuals but consistency in individuals, has been found in other waders, such as Northern Lapwings for migratory behavior and wintering sites (Eichhorn et al. 2017), pre-breeding movements in Bar-tailed Godwit (Conklin et al. 2013), Sociable Lapwings for migration route, departure date, and stopover and wintering locations (Donald et al. 2021), and Eurasian Curlews for migration dates (Schwemmer et al. 2021, Franklin et al. 2022). We found significant and similar repeatability in departure and arrival dates for autumn migration as well as spring migration, in contrast to Eurasian Curlews, in which spring migration was more repeatable than autumn migration (Schwemmer et al. 2021). This may be related to the fact that selective pressure for the breeding timetable is likely to be less pronounced in temperate France than in the Arctic (aligned with snow melting), and more generally in high-latitude breeders (Vardanis et al. 2011, Clausen et al. 2015, Tedeschi et al. 2020). There was also repeatability in the stone-curlew migration routes (see also Vardanis et al. 2011) and wintering sites location. Winter site fidelity is rather a rule than an exception: such philopatry has been previously shown for stone-curlews (Piper 2011). Other wader species are also highly faithful to their wintering sites (Exo et al. 2019, Schwemmer et al. 2021). Differences between individuals but similar plasticity in individuals was interpreted mostly as learned behavior in a study on the Lesser Black-backed Gull (Brown et al. 2021), but our results are more in line with those obtained for the Eurasian Curlew (Schwemmer et al. 2021), which, conversely, suggest inherited behavior.

Consequences for conservation

Using five years of high-resolution GPS data, we were able to explore in detail the migratory and wintering patterns of a Eurasian Stone-curlew continental and temperate population, which is in strong decline (Gaget et al. 2019). In a Mediterranean population, departure date in autumn was shown to be triggered by negative temperatures, suggesting that an increasing proportion of birds may become resident (Falchi et al. 2023). The proportion of resident birds in our population is still modest, but increasing over the last 20 years, which means that conservation measures for the species should perhaps now also target wintering habitats.

Our findings showed very high differences between individuals in migration routes, strategies, and wintering sites, together with high to very high consistency in individuals. Migration for this population is of short duration, stopover sites are numerous and distributed throughout Spain, and are used for a very short time, which together suggest that migration is not a strong constraint for this population, at least in regard to what happens for high Arctic waders. We found that wintering home ranges were fairly small (per individual), which may suggest that food availability may not be a constraint. However, most wintering sites were found in agricultural areas. Habitat loss or habitat quality degradation in wintering sites may therefore be an issue because in at least half of the cases, stone-curlews wintered in areas of extensive agriculture. Iberian agricultural areas are changing very rapidly (Silva et al. 2018, Traba and Morales 2019) as are northern African and Sahelian areas (Augiron et al. 2015). Thus the quality of wintering habitats may not be an issue currently, though it may become one in the near future. Indeed, new potential threats for wintering stone-curlews may arise from fast development of photovoltaic plants, that currently occur in Spain and Portugal (Valera et al. 2022), which particularly affects steppic and semi-arid areas. Potential threat such as illegal killing in wintering areas, as has been shown for this species in the Middle East (Kittelberger et al. 2021), is also unlikely currently, none of the wintering areas identified so far being known as hotspots for illegal killing of birds. However, several GPS tagged birds, including one in our program, were killed in Algeria during migration by hunters. Therefore, the current population decline of this particular population in France appears not to result currently from wintering or stopover site availability (or quality), but rather to habitat quality problems in the breeding areas, as has already been suggested for this population (Gaget et al. 2019), in the UK (Hawkes et al. 2021), or in studies of species with similar habitats, e.g., the Little Bustard (Bretagnolle et al. 2018b) or Montagu's Harrier (Arroyo et al. 2002). Hence, conservation action should focus on breeding areas for the present, though attention should be given to two potential emerging issues: climate change that may increase the proportion of resident birds, and agriculture intensification (in particular, irrigation) in the Mediterranean area where birds spend the non-breeding season that may alter habitat quality for the species.

Author Contributions:

VB, ED, PL, and AM conceived the study, PL, ED, and VB analyzed the data, AV, SA, DC, LB, and AM captured the birds, AM and PL were in charge of data management, ED cured data, ED and VB analyzed data, ED, PL, and VB wrote a first draft, and all authors contributed to the final version.

Acknowledgments:

We would like to thank the landowners who allowed us to monitor stone-curlews in their fields, as well as all the fieldworkers who helped to spot and capture the birds and manage the network of antennas: Florent Bastianelli, Gaspard Bernard, Romain Bonnet, Pierrick Devoucoux, Marie Fretin, Elie Gaget, Méryl Gervot, Thomas Gouello, Matthieu Liaigre, Gildas Lemonnier and Vincent Rocheteau. We also thank Cécile Ribout for the molecular sexing of the birds. Finally, we are grateful to the Nouvelle-Aquitaine Regional Department of the Environment, Urban Planning and Housing (DREAL), the LISEA Biodiversity Foundation and the Réseau de Transport Electrique for their financial and technical support. A special mention to Catherine Ménard for her constant help, trust and support.

Data Availability:

Data are archived in MoveBank repository: https://urlz.fr/nI12.

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Editor-in-Chief: Alexander L. Bond
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Appendix 1

Figure A1.1 Location of captured sites (points) in Poitou-Charente within study area (A: SPA “Plaine de Niort Nord – Ouest”, B: LTSER “Zone Atelier Plaine et & Val de Sèvre”).

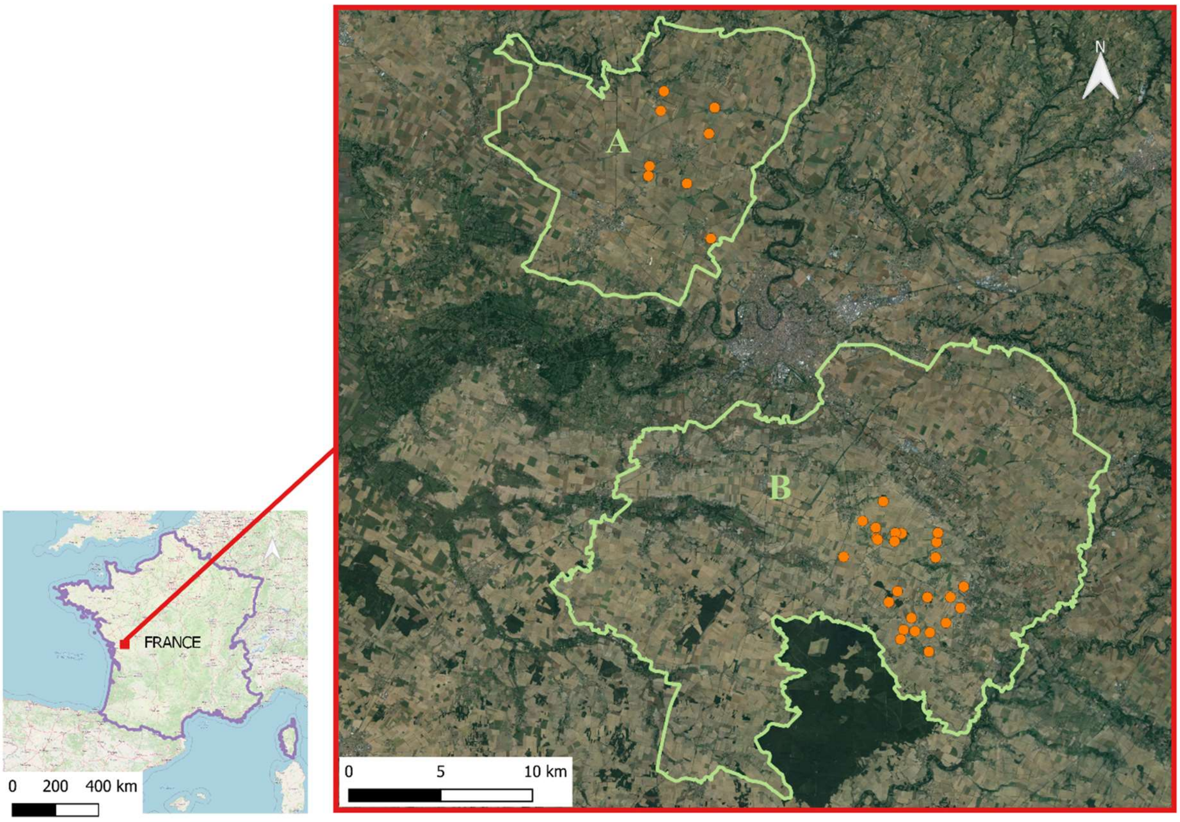
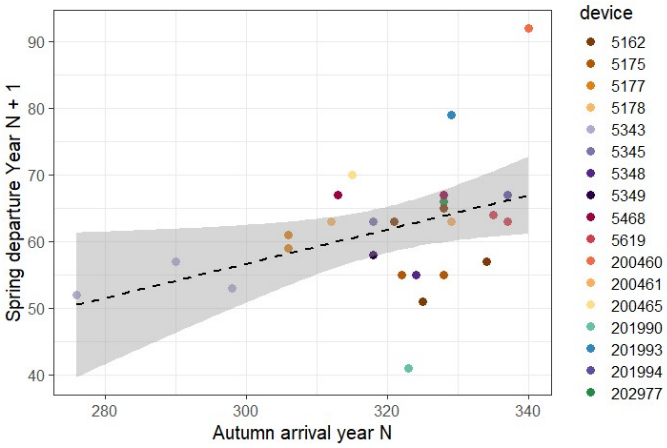
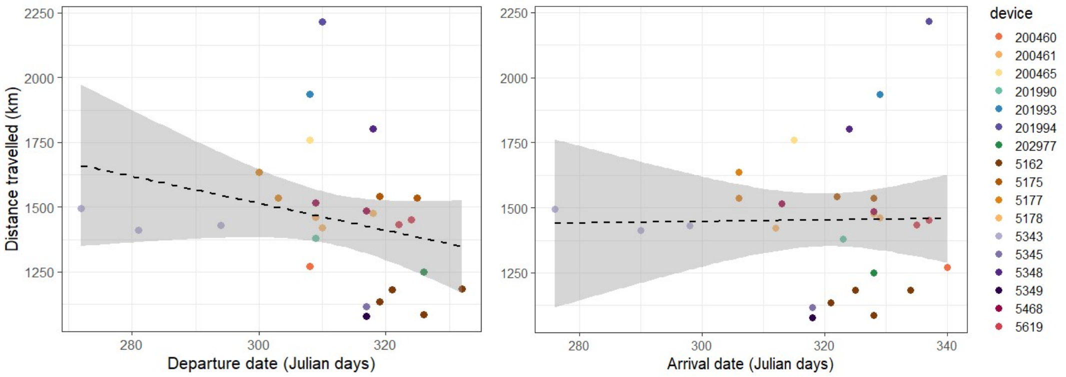


Figure A1.2.

a) Spring departure date versus autumn arrival date (n = 25). Days units are expressed in Julian days.



b) Total distance travelled (km) versus departure and arrival dates for autumn migration. Days units are expressed in Julian days.



c) Total distance travelled (km) versus departure and arrival dates for spring migration. Days units are expressed in Julian days.

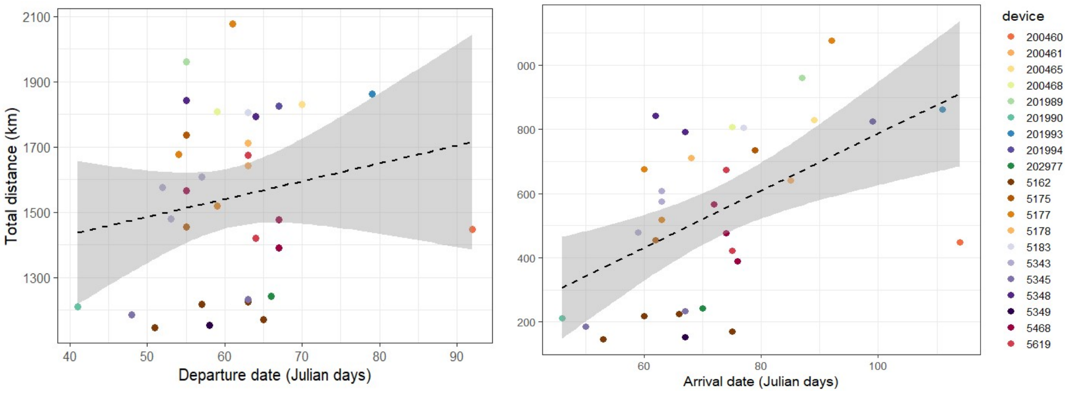


Figure A1.3: Two examples of birds arriving close to wintering areas (20 – 30 km), stayed for a few days to finally flight to the final wintering sites. An insert shows the location at larger scale.

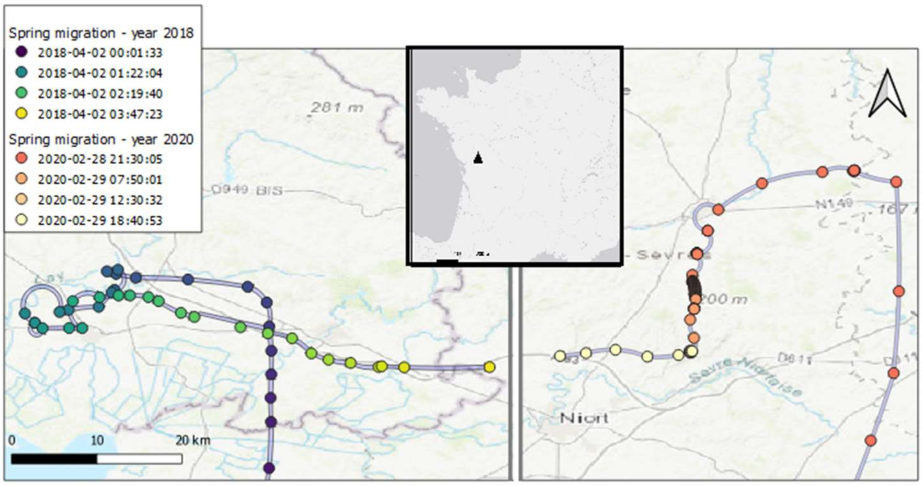
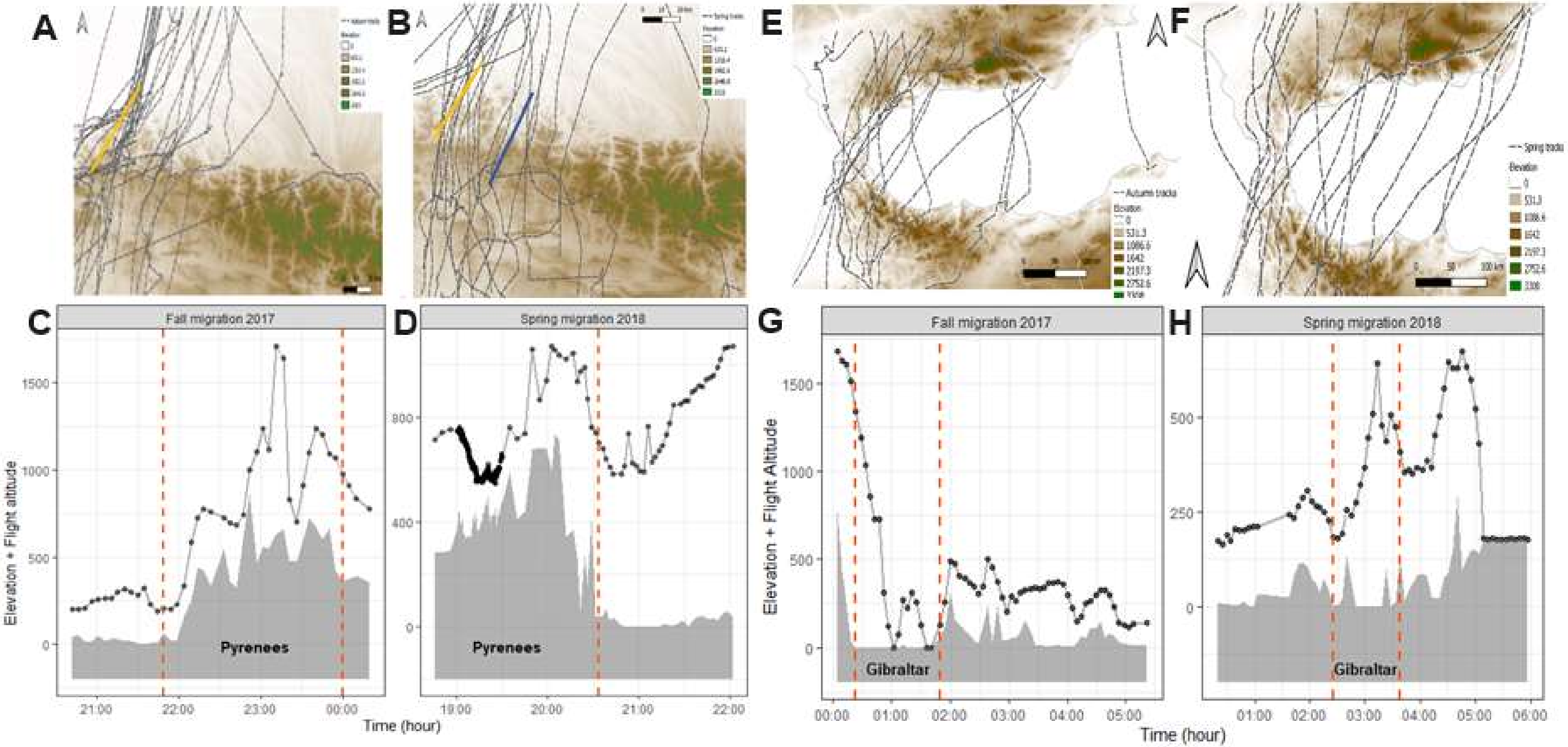


Figure A1.4: Migration routes of adult stone-curlews that crossed the Pyrenees in autumn (Panel A) and spring (Panel B) and the Gibraltar in autumn (Panel E) and in spring (Panel F) between 2017 and 2018. Selected example of flight altitude profile of two adult stone-curlews (Panel C and D: Pyrenees; Panel G and H: Gibraltar).



Tab A1.1. Among region differences in Stone-curlew home range sizes. Values presented are means ± *SE* with ranges in brackets.

Region	Number of birds tracked	95% kernel density (km²)	70% kernel density (km²)	50% kernel density (km²)
Spain	6	19.5 ± 20.4	4.75 ± 5.33	2.19 ± 2.5
Portugal	2	15.2 ± 4.39	7.28 ±7.69	3.16 ± 2.78
Morocco	12	27.9 ± 16.9	8.23 ± 4.41	2.93 ± 1.67
Algeria	1	2.34	0.82	0.4
All	21	23.6 ± 16.8	6.17 ± 4.73	2.78 ± 2.05