ORIGINAL ARTICLE

Inter and intra-population variability of the migratory behaviour of a short-distance partial migrant, the Eurasian Stone-curlew *Burhinus oedicnemus* (Charadriiformes, Burhinidae)

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Abstract

Migratory behaviour in birds shows a remarkable variability at species, population and individual levels. Short-distance migrants often adopt a partial migratory strategy and tend to have a flexible migration schedule that allows a more effective response to extreme environmental variations. Weather seasonality and environmental heterogeneity have been reported as significant factors in the diversification of migratory behaviour for Mediterranean migrants, but relatively few studies investigated the migration patterns of non-passerine birds migrating within the Mediterranean basin. In this study, we investigated the migratory strategy of 40 Eurasian Stone-curlews *Burhinus oedicnemus* tagged with geolocators and GPS-GSM tags and belonging to continental and Mediterranean populations of the Italian peninsula. The proportion of migrants was higher in continental populations, but we observed a significant variability also within Mediterranean populations. All birds spent the winter within the Mediterranean basin. Continental Stone-curlews departed earlier in spring and later in autumn and covered longer distances than those from Mediterranean areas. The speed of migration did not change between seasons for continental birds, while Mediterranean individuals migrated faster in spring. The likelihood of departure for autumn migration of GPS-tagged birds increased when temperatures were near or below 0 °C suggesting that Stone-curlews tend to delay departure until weather conditions worsen abruptly. As a consequence of global warming in the Mediterranean, the frequency of migratory birds in the considered populations might decrease in the near future. This could affect the distribution of species throughout the year and should be taken into account when targeting conservation measures.

Keywords Bird migration · Short-distance migrant · Weather conditions · Partial migration

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Zusammenfassung

Unterschiede im Zugverhalten eines Kurzstreckenziehers innerhalb von und zwischen Populationen: der Triel (*Burhinus oedicnemus*, Charadriiformes, Burhinidae)

Das Zugverhalten von Vögeln zeigt bemerkenswerte Unterschiede auf Art-, Populations- und Individuen-Ebene. Kurzstreckenzieher verfolgen häufig eine partielle Zugstrategie und haben in der Regel eine flexible Zeitplanung, die eine effektivere Reaktion auf extreme Umweltveränderungen ermöglicht. Die jahreszeitlichen Wetterschwankungen und die unterschiedlichen Umgebungsbedingungen werden als wichtige Faktoren für die Differenzierung des Zugverhaltens von Zugvögeln im Mittelmeerraum genannt, aber nur relativ wenige Studien haben sich mit den Zugmustern von Nichtsperlingsvögeln, die innerhalb des Mittelmeerraums wandern, befasst. In dieser Studie untersuchten wir die Zugstrategien von 40 mit Ortungs- und GPS-GSM-Sendern versehenen Trielen (*Burhinus oedicnemus*) von kontinentalen und mediterranen Populationen auf der italienischen Halbinsel. Der Anteil der Zieher war in den kontinentalen Populationen höher, aber auch innerhalb der mediterranen Populationen wurde eine erhebliche Bandbreite festgestellt. Alle Vögel überwinterten im Mittelmeerraum, wobei die kontinentalen Triele im Frühjahr früher und im Herbst später abflogen und größere Entfernungen zurücklegten als die Vögel aus den Mittelmeergebieten. Die kontinentalen Vögel zogen unabhängig von der Jahreszeit mit gleicher Geschwindigkeit, während die Vögel des Mittelmeerraums im Frühjahr schneller zogen. Die mit GPS-Sendern versehenen Vögel brachen bei Temperaturen nahe oder unter 0 °C mit höherer Wahrscheinlichkeit zum Herbstzug auf, was darauf schließen lässt, dass Triele dazu neigen, den Aufbruch hinauszuschieben, bis sich die Wetterbedingungen abrupt verschlechtern. Als Folge der globalen Erwärmung im Mittelmeerraum könnte die Anzahl der ziehenden Vögel in den hier untersuchten Populationen in der nahen Zukunft abnehmen. Dies könnte sich auf die Verteilung der Arten über ein gesamtes Jahr hinweg auswirken und sollte bei der Planung von Bestandserhaltungsmaßnahmen berücksichtigt werden.

Introduction

The extent and the pattern of migration may vary strongly among different taxa and even within the same taxon (Dingle and Drake 2007). Migratory behaviour in birds, in particular, shows a remarkable variability at species (Schmaljohann 2018; Anderson et al. 2020), population (Monti et al. 2018a, 2018b; Phipps et al. 2019) and individual levels (Shamoun-Baranes et al. 2017a; Tedeschi et al. 2020). One of the most extreme forms of intra-population variation in migratory behaviour is partial migration, where only a fraction of individuals are migrants (Chapman et al. 2011, 2014). This seems to be the most common strategy in birds (Chapman et al. 2011), especially among short-distance migrants (Pulido et al. 1996; Newton 2008). Besides intra-population heterogeneity in migratory strategy, short-distance migrants also show considerable variability in migratory behaviour, mainly due to the effect of environmental factors in modulating the phenology of migration (Berthold 1996; Pulido and Widmer 2005; Both et al. 2010; Newton 2012). This is especially true for post-breeding migration as birds do not have the urgency to get to wintering grounds first and in time (McNamara et al. 1998; Nilsson et al. 2013). Due to the relative proximity between breeding and wintering grounds, short-distance migrants can also optimize their departure schedules by selecting weather conditions that allow them to minimize energy expenditure throughout the trip (Alerstam and Lindström 1990; Lehikoinen et al. 2004; Rubolini et al. 2007; Knudsen et al. 2011; Nilsson

et al. 2013). This leads to more flexible migration schedules for short-distance than for long-distance migrants (Pulido and Widmer 2005; Newton 2008; Pulido and Berthold 2010; Monti et al. 2018b) and allows the former to respond more effectively to extreme environmental variations, like those due to climate change (Jenni and Kéry 2003; Gordo 2007).

Weather seasonality and environmental heterogeneity at regional and local scales are significant factors in the diversification of migratory behaviour at inter and intra-population levels for some species migrating within the Mediterranean region (Pérez-Tris and Tellería 2002; García de la Morena et al. 2015). Moreover, the ongoing increase in temperature recorded in this area due to global warming (Mariotti et al. 2015) can affect migration timing of short distance migrants (e.g., Birtsas et al. 2013) and might even lead to the complete suppression of their migratory behaviour (Gordo 2007; Morganti 2015). Relatively few studies, however, have investigated migration patterns and the role of environmental factors in modulating migratory behaviour of non-passerine birds migrating within the Mediterranean basin (but see Birtsas et al. 2013; García de la Morena et al. 2015; Monti et al. 2018a; Alonso et al. 2019).

The Eurasian Stone-curlew *Burhinus oedicnemus* (Charadriiformes, Burhinidae, hereafter, Stone-curlew) is a steppe bird whose European populations are mainly concentrated in the Mediterranean area (Vaughan and Vaughan-Jennings 2005; Delany et al. 2009; Keller et al. 2020). In Italy the species is relatively widespread in Sardinia, Sicily and in the Southern part of the peninsula, while it is scarce,

although locally common, along the riverbanks and in farmlands in the Centre and the North of the peninsula (Brichetti and Fracasso 2004; Biondi and Pietrelli 2015).

The species is of European conservation concern (BirdLife International 2021) but information on the status of its populations is limited (Gaget et al. 2019). Available information suggests that the migratory behaviour of the Stone-curlew should be rather variable at intra- and inter-population level throughout its range (Cramp and Simmons 1983; Green et al. 1997; Vaughan and Vaughan-Jennings 2005; Giunchi et al. 2015), but relatively little is known about its movements. Investigating the migratory strategies of different populations, the geographical range of their movements and the degree of migratory connectivity is an important contribution for understanding the factors affecting population trends (Webster et al. 2002; Taylor and Norris 2010; Finch et al. 2017). Furthermore, understanding how migration phenology is influenced by proximate meteorological factors can help to understand how a species would react to the ongoing climate change (Gill et al. 2014; Haest et al. 2018, 2019; Burnside et al. 2021; Linek et al. 2021).

In this study we aimed at: (i) investigating the spring and autumn migratory strategies of Stone-curlews belonging to four Italian populations, two from the North and two from the center of the peninsula and (ii) performing a preliminary evaluation of the possible role of exogenous factors in modulating the phenology of autumn migration.

Regarding the migratory strategies applied by Stone-curlews, we expected that: (i) the northern populations would have a higher proportion of migrants than the southern ones, as reported for other Palearctic migrants (Newton and Dale 1996; Newton 2008; Linek et al. 2021) and suggested for the Stone-curlew (Delany et al. 2009; Biondi and Pietrelli 2015); (ii) Stone-curlews should use a time-minimization strategy during spring migration and an energy-minimization strategy during autumn migration (Alerstam and Lindström 1990; Kokko 1999; Nilsson et al. 2013), with a spring migration faster than the autumn one in all populations, as reported for several bird species, including waders (Zhao et al. 2017; Schmaljohann 2018); (iii) the breeding latitude should affect the timing of departure, as already observed in long-distance migrants where northern populations tend to depart later in both autumn and spring than birds from southern populations (Conklin et al. 2010; Briedis et al. 2016; Neufeld et al. 2021).

When evaluating the possible effect of exogenous cues on the birds' migratory choices, we hypothesised that the timing of autumn migration of tagged Stone-curlews was significantly affected by weather variables and expected that: (i) northern populations should anticipate their departure compared to southern populations, with a quite variable migration timing, such as other short-distance migrants that usually show a quite flexible migratory schedule (Pulido and Widmer 2005; Newton 2008; Pulido and Berthold 2010; Monti et al. 2018b); (ii) this variability in migration timing should be particularly high in autumn, when there is no compelling need to reach the wintering sites (Shamoun-Baranes et al. 2006; Nilsson et al. 2013); (iii) meteorological variables, such as wind conditions (Liechti 2006; Grönroos et al. 2012), temperature (Burnside et al. 2021), and atmospheric pressure (Dänhardt and Lindström 2001) would significantly affect migratory departures. Low temperatures, in particular, should significantly increase the likelihood of migratory departure, given (1) their negative effect on the availability of invertebrates (Eggleton et al. 2009; Abram et al., 2017) which are the main food supply for the Stone-curlew (Amat 1986; Green et al. 2000; Giannangeli et al. 2004; Giovacchini et al. 2017), and (2) the low resting/basal metabolic rate of the Stone-curlew (Duriez et al. 2010; Gutiérrez et al. 2012), which could make the thermoregulation process in cold conditions rather costly.

Methods

Study areas

The study was carried out on four Italian areas, two located in the continental biogeographical region (https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3), Taro river (Parma Province, Northern Italy, 44.74° N 10.17° E; $n = 9$) and Piave river (Treviso Province, Northern Italy, 45.80° N 12.28° E; $n = 12$), and two in the Mediterranean biogeographical region, Grosseto Province (Southern Tuscany, Central Italy, 42.60° N 11.22° E; $n = 10$) and Viterbo Province (Northern Latium, Central Italy, 42.35° N 11.83° E; $n = 10$) (Fig. 1). According to the Köppen-Geiger climate classification, which is based on the relationship between climate and vegetation (Köppen 2011; Chen and Chen 2013), Taro and Piave areas are within a mild temperate, fully humid zone with warm summer (warmest month average temperature < 22 °C and at least four months with temperatures ≥ 10 °C), while Grosseto and Viterbo areas are within a mild temperate zone with dry and hot summer (warmest month average temperature ≥ 22 °C) (data obtained using the R-package 'kgc' 1.0.02, Bryant et al. 2017). Birds were captured during the breeding period (March-July) from 2013 to 2019 using different methods (i.e., mist nets, fall traps, dip nets). All birds were measured according to standard ringing procedures (Busse and Meissner 2015) and molecularly sexed according to Griffiths et al. (1998). Biometric measures and sex were not available for birds belonging to Viterbo population.
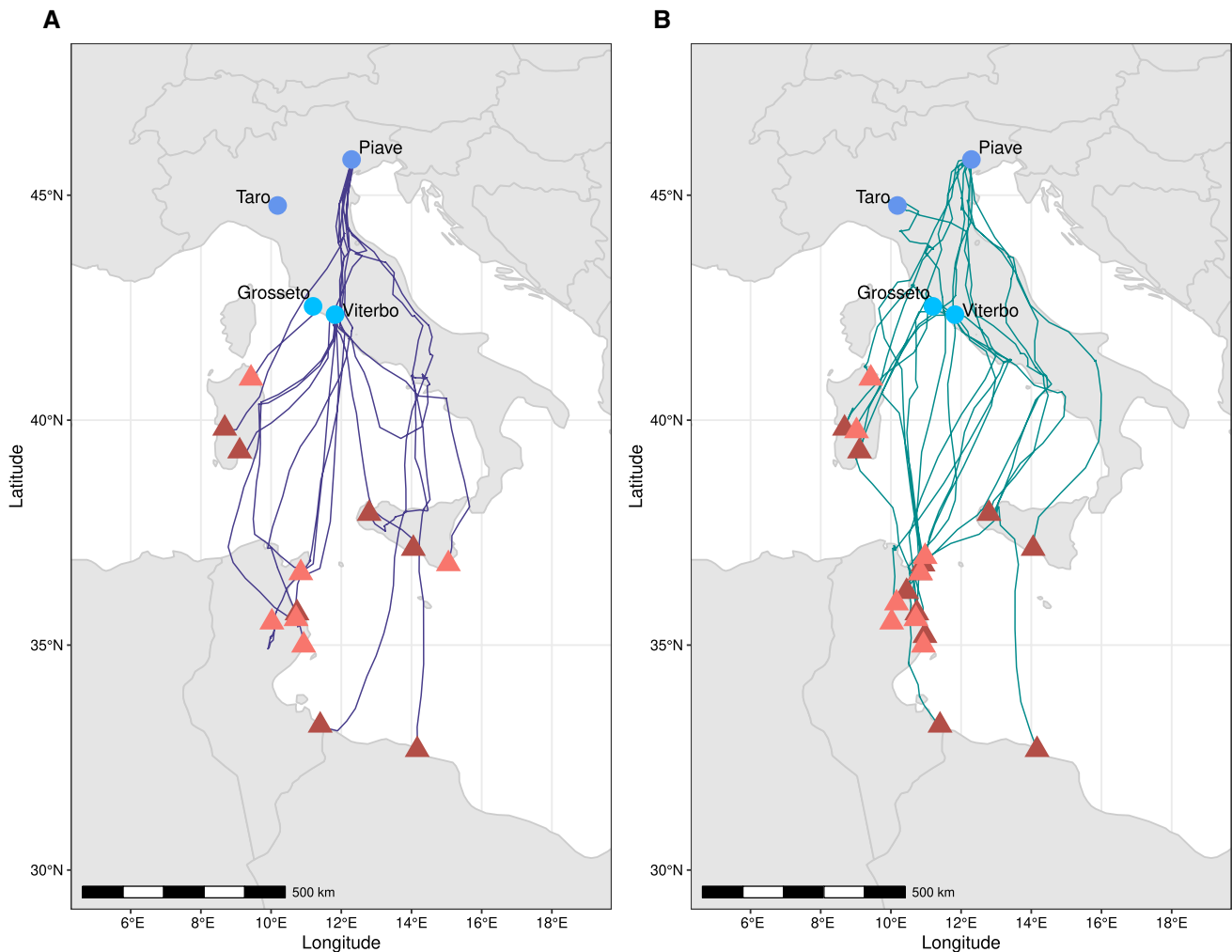
Fig. 1 Capture areas (dots), migration tracks and winter locations (triangles) of Stone-curlews equipped with GPS in Italy in the period 2012–2019. **A** Autumn migration ($n = 14$ individuals); **B** spring migration ($n = 19$ individuals). Darker symbols: continental popula-tions; lighter symbols: Mediterranean populations. For the Taro population, autumn migration was not available due to a temporary failure of the tags

Tracking data

Two types of tracking devices were used throughout the study period: geolocators and solar powered GPS tags. Geolocator data were collected in the years 2010–2011 only for the Taro population and were already published (see Giunchi et al. 2015 for details). These data were taken into account solely for comparing the proportion of migrants and residents from the four populations. GPS devices (GPS-UHF and GPS-GSM) were used in all populations in the period 2012–2019 (see Supplementary Table S1 for details). Part of the tracks considered in this study were already published in Giunchi et al. (2015) and in Cerritelli et al. (2020). The GPS were fitted on birds using a Teflon ribbon leg-loop (Rappole and Tipton 1991) or backpack harness (Viterbo population only). The weight of the tags plus the

harness corresponded to 3–4% of the bird's body weight (average bird weight = 475.4 g ± 37.3 SD, $n = 23$; average tag weight = 17.2 ± 2.3 g, $n = 24$). The weight of birds tagged in the Viterbo province was not available. The weight of the tags was less than recommended 5% of the body weight (Barron et al. 2010), but slightly above the recently suggested 3% limit (Geen et al. 2019). We have not had the opportunity to adequately test the impact of tags and cannot rule out the possibility that weight of the devices might have an effect on the migratory behaviour of tagged animals (Geen et al. 2019). However, we can assume that the impact was similar in the different populations, and therefore should not have affected most of the results reported in the paper.

Since the number of birds in each population followed for more than one year was relatively small, we randomly selected a single track for each season whenever more than

two tracks were available for a given individual to avoid pseudoreplication (Hulbert 1984) and simplify the analysis.

To minimize possible bias inherent in using subjective criteria (Cerritelli et al. 2020), we objectively identified departure and arrival dates in both breeding and wintering areas and stopovers through the segmentation method implemented in the package 'segclust2d' 0.2.0 (Patin et al. 2020) in R 4.0.2 (R Core Team 2020). This method allows to find similar segments in function of the speed and tortuosity (i.e., low variability for limited periods), corresponding to stationary phases, and cluster them in a common class, corresponding to a given state. Two parameters had to be set to carry out the analysis (Patin et al. 2020): a minimum segment length corresponding to the minimum time that a certain behavior could be considered stationary (L_{min}) and the maximum number of states (M). The optimal number of segments (K) and of states (M) are then chosen by means of model selection according to the Bayesian information criterion (BIC). Track segmentation was performed in two steps. In the first step, aimed at identifying the onset and the end of migration, we considered for each individual a tracking period ranging from 20 days before the presumed departure to 20 days after the presumed arrival, as inferred by the visualization of the tracks. The track was regularized (Patin et al. 2020) using 'adehabitatLT' 0.3.25 R-package (Calenge 2006) at 1 fix every 60 or 180 min to obtain the best trade-off between the maximum number of tracks available for the analyses and the minimum time lag between fixes (Supplementary Table S1). The tracks were segmented by setting the L_{min} so that the minimum time of stationarity was 12 h, the maximum number of states $M = 3$ (residency in breeding and wintering areas and migration states).

In the second step of the segmentation process, we used the migratory tracks identified in the previous step to identify the stopover periods. This analysis was performed on the tracks of 14 individuals which had at least 1 fix/90 min. The tracks were regularized according to the original duty cycle (Supplementary Table S1) and then segmented by considering a minimum time of stationarity of 6 h with three states (rest at stopover, foraging at stopover, migration). Stopovers were not identified using the segmentation method for six birds (Supplementary Table S1, individuals marked with an asterisk), as the duty cycles of their tags included switching off the instrument for 8 h during the day. For these birds, we considered as stopovers the group of fixes collected during at least 12 h and spaced < 4 km apart, i.e., the third quartile of the distribution of the distances calculated among locations identified as stopovers for the remaining birds using the clustering-segmentation method (median = 2.1 km, first-third quartile = 0.7–4.0 km, min–max = 0–17.7 km).

After the identification of migratory and stopover periods, we calculated: the total migration distance as the sum of distances between all fixes, excluding movements in stopover areas, the straightness index, i.e., the ratio between the straight distance between wintering and breeding site and the total distance travelled by the birds (Batschelet 1981), the number of stopovers, the time spent in stopovers, the total migration length (including the stopover period) and the time spent flying. All distance measurements were performed by means of the orthodromic Vincenty ellipsoid method using the R-package 'geosphere' 1.5–10 (Hijmans 2019). Every location was classified as nocturnal (from sunset to sunrise) or diurnal considering nautical crepuscule, by means of the R-package 'amt' 0.1.2 (Signer et al. 2019) in order to verify whether this species migrates mostly during the night (Vaughan and Vaughan-Jennings 2005).

Regional weather data

The centroids of breeding areas for each individual were calculated and the weather data recorded in each location were extracted from the European Centre for Medium-Range Weather Forecasts European Reanalysis v5-Land data (ECMWF ERA5-Land; spatial resolution $0.1° \times 0.1°$; temporal resolution 1 h). As the sample size of tracked birds was relatively small, we considered a small set of variables which are known to affect the likelihood of departure (see e.g., Dänhardt and Lindström 2001; Liechti 2006; Conklin and Battley 2011; Grönroos et al. 2012; Duijns et al. 2017; Burnside et al. 2021) to avoid data dredging. We considered the period starting about 25 days before the departure of the first bird, i.e., from 1 October until the departure of all birds from the breeding areas. The variables included in the analysis were (Supplementary Table S2): (1) the daily average of the northward component of the wind speed (10 m above the ground; Vwind, m/s), (2) the daily minimum temperature (2 m above the ground; Tmin, °C), (3) the difference between the minimum temperature of the day and that of the previous one (ΔTmin, °C) and (4) the difference between the daily average of the sea surface atmospheric pressure of the day and that of the previous one (ΔPatm, hPa). The correlation among these variables, assessed with the Spearman correlation coefficients was always well below 0.5. Photoperiod was not included in the model because its effect on migration timing is well known (Gwinner 1990; Berthold 1996; Gwinner and Helm 2003) and the aim of our analysis was to assess the effect of proximate meteorological variables in modulating the start of migration in a time window when day length is permissive for migration.

Statistical analyses

We initially tested if the proportion of migrants and residents differed in the four populations including in the analysis both birds tagged with geolocators and those tagged with GPS. We used a Firth's bias-reduced penalized-likelihood logistic

regression model as implemented in the R-package 'logistf' 1.24 (Heinze et al. 2020), with migration strategy (presence or absence of migration) as binary dependent variable and population (four-levels factor: Taro, Piave, Grosseto, Viterbo) as independent variable. Model significance was assessed using the likelihood ratio (LR) test. We considered three planned contrasts, i.e., continental versus Mediterranean populations, Taro vs Piave population and Grosseto vs Viterbo population.

The analysis of the migratory behaviour was performed by comparing birds from the Mediterranean region (one from Grosseto population and eight from Viterbo population), with birds from the Piave ($n=9$) and Taro ($n=2$) populations, as representative of the continental region. We used standard linear models (LM) with departure or arrival date (Julian day, $1=1$st of January) as dependent variable and region as predictor to investigate the relationship between timing of migration, season and area. Data from the two migratory seasons were analysed separately. To verify if this species is a nocturnal migrant and if this behaviour changes between seasons and regions, the proportion of migratory fixes recorded during the night was compared between seasons (two-levels factor: autumn vs spring) and regions (two-levels factor: continental region vs Mediterranean region) using a Generalized Linear Mixed Model (GLMM) with binomial error distribution and bird ID as random intercept. A Linear Mixed Model (LMM) was used to test whether the distance travelled was affected by the migratory season, the breeding region and by their interaction and to investigate the relationship between speed of migration, season and area of origin. To take into account the effect of different duty cycles in LMM, we included a weight variable in LMM of distance and speed: a weight of 1 was assigned to the animals with a duty cycle of 60 min during migration, whereas a weight equal to 0.66 was assigned to the two animals with a duty cycle of 90 min. In all LMM models, bird ID was included as a random intercept.

(G)LMM were fitted using the package 'lme4' 1.1–26 (Bates et al. 2015). Significance of fixed effects was tested by means of the likelihood ratio (LR) test. Model fit, overdispersion and collinearity were checked by means of the packages 'performance' 0.6.1 (Lüdecke et al. 2021) and 'DHARMa' 0.3.3.0 (Hartig 2020). 95% confidence intervals were estimated using the package 'parameters' 0.6.1 (Lüdecke et al. 2021). Adjusted R^2 was reported for every linear model. Conditional and marginal R^2 for the linear mixed models was calculated according to Nakagawa et al. (2017) using the package 'MuMIn' 1.43.17 (Bartoń 2020).

The possible effect of the considered meteorological variables on the start of migration of the Stone-curlew was investigated by means of the non-parametric Cox proportional hazard model (Moore 2016). This model describes the probability per unit of time that an event occurs as a function of the baseline hazard and a set of covariates (fixed or time dependent). The models were fitted using the R-package 'survival' 3.2–11 (Therneau 2020; Therneau and Grambsch 2000). Data were clustered by bird ID and robust variance was estimated using a jackknife approach (Therneau 2020; Therneau and Grambsch 2000). The predictors included in the two models were the breeding region (two-levels factor: continental region vs Mediterranean region) and four time-dependent covariates (Vwind, ΔPatm, Tmin and ΔTmin; Supplementary Table S2). The breeding region was included in the model to take into account the difference in migratory length among the populations belonging to the two areas (see Results). Model selection was performed according to the corrected Akaike Information Criterion (AICc; Burnham and Anderson 2002) using the 'MuMIn' package (Bartoń 2020). We considered all combinations of the three time-dependent predictors while keeping the stratum covariate fixed. Given the relatively small available sample size, we reduced model complexity by not considering any interaction and by limiting the maximum number of terms to three (intercept included). The model with the lowest AICc value was used for inferences, provided that the null model was not included in the set of models within two units from the best one (Burnham and Anderson 2002). For each model, we calculated the Akaike weight w_i, representing the probability of the model given the data (Burnham and Anderson 2002). Model significance was tested using the Robust Score (RS) test while goodness-of-fit was evaluated by means of model concordance (Therneau 2020; Therneau and Grambsch 2000). RS test, model concordance, covariate coefficients and estimated hazard ratios of departure after 1 SD increase of the variables included in the model were reported for all models within two units from the best one (Burnham and Anderson 2002). Model assumptions were checked according to Therneau and Grambsch (2000) using the package 'survminer' 0.4.9 (Kassambara et al. 2021).

All statistical analyses were performed with R (version 4.0.2) (R Core Team 2020). All geographical analyses and plots were carried out using QGIS 3.4 (QGIS Development Team 2020).

Results

Migration strategy

The proportion of migrants differed significantly among populations ($\chi^2=18.9$, $df=3$, $P=0.0003$, Firth's bias-reduced penalized-likelihood logistic regression model, LR test; Supplementary Fig. S1), with migratory birds being more common in continental than in Mediterranean populations ($\chi^2=7.4$, $P=0.007$). The proportion of migrants was not different between the two continental populations (Taro

vs Piave: $\chi^2 = 2.1$, $df = 1$, $P = 0.1$), while it was unexpectedly different among the two Mediterranean populations, being significantly higher in Viterbo than in Grosseto population ($\chi^2 = 9.8$, $df = 1$, $P = 0.002$).

Migration routes, speed and timing

From the 20 GPS-tagged Stone-curlews identified as migrants, we reconstructed a total of 33 migratory tracks: 14 in autumn and 19 in spring. Migration turned out to be rather short in both seasons (on average less than 1000 km covered in less than 5 days; Table 1). Migrant Stone-curlews spent their wintering period within the Mediterranean basin (Fig. 1), i.e., in Sardinia ($n = 4$), Sicily ($n = 3$), Tunisia ($n = 12$) and Libya ($n = 1$).

All birds followed a straight and direct migratory route (most straightness indexes > 0.80) both in autumn and in spring (Table 1). The only exceptions to this pattern were TK2343 (Piave population) that showed a clear detour during autumn migration leading to a relatively low straightness index (0.59; Supplementary Fig. S2A) and GR06 (Grosseto population) which showed a moderate detour during spring migration just before arriving at the breeding site (0.67; Supplementary Fig. S2B).

The departure and arrival dates showed a high degree of variability in both migratory seasons, ranging from the last week of October to the end of December/early January in

autumn, and from early February to early April in spring (Table 1). The continental populations departed on average 25 days earlier for autumn migration than the Mediterranean ones and delayed by about 10 days the onset of spring migration when compared with the Mediterranean populations, leading to significant differences in departure and arrival dates between the two areas (autumn departure: $F_{1,12} = 9.3$, $P = 0.01$, adjusted $R^2 = 0.39$; autumn arrival: $F_{1,12} = 8.3$, $P = 0.014$, adjusted $R^2 = 0.36$; spring departure: $F_{1,17} = 5.2$, $P = 0.035$, adjusted $R^2 = 0.19$; spring arrival: $F_{1,17} = 7.4$, $P = 0.015$, adjusted $R^2 = 0.26$; LM, Fig. 2A). As expected, most of the migratory movements took place at night, especially during autumn migration when the proportion of nocturnal locations tended to be higher than in spring ($\chi^2 = 7.2$, $df = 1$, $P = 0.007$; GLMM, LR test; Supplementary Fig. S3). No differences were observed in the proportion of nocturnal locations between regions ($\chi^2 = 0.099$, $df = 1$, $P = 0.8$), with all tracked birds showing comparable nocturnal migratory movement.

Migration length only differed between regions of origin ($\chi^2 = 12.3$, $df = 1$, $P = 0.0004$; LMM, LR test), with individuals from continental populations covering longer distances than the Mediterranean ones (Fig. 2B). No differences in migration lengths were observed between the two migratory seasons ($\chi^2 = 0.42$, $df = 1$, $P = 0.5$) and individuals from different populations travelled similar distances during both migrations ($\chi^2 = 0.30$, $df = 1$, $P = 0.6$).

Table 1 Summary statistics of individual autumn and spring migratory tracks of 20 migrant Stone-curlews equipped with GPS in Italy in the period 2012–2019

	Autumn migration ($n = 14$) Median (IQR) Range	Spring migration ($n = 19$) Median (IQR) Range
Departure date	25 Nov (22 Nov–3 Dec) 25 Oct–31 Dec	3 March (28 Feb–4 Mar) 8 Feb–10 Apr
Arrival date	2 Dec (27 Nov–6 Dec) 28 Oct–2 Jan	8 Mar (2 Mar–21 Mar) 9 Feb–12 Apr
Migration length (km)	3.3 (2.2–6.0) 1.1–17.5	4.3 (1.4–8.1) 0.5–12.3
Time spent flying (days)	1.4 (1.1 –2.0) 0.7–2.7	1.1 (0.9–2.4) 0.5–3.3
Time spent in stopovers (days)	1.9 (0.9–3.8) 0.4–14.8	2.7 (0.6–6.2) 0—9.9
Number of stopovers	2 (2–3) 1–4	2 (1–5) 0–7
Total migration distance (km)	956.5 (798.9–1160.6) 252.2–1601.0	977.0 (794.2–1206.6) 350.4–1641.8
Migration speed (km/day)	279.0 (230.8–409.2) 86.7–525.0	306.9 (139.4–645.4) 38.5–1320.8
Actual speed (km/day)	709.2 (584.8–852.9) 360.2–954.2	736.7 (514.9–963.9) 389.4–1401.5
Straightness index	0.90 (0.85–0.93) 0.59–0.98	0.90 (0.83–0.92) 0.66–0.95

Migration speed was calculated as the total distance travelled divided by the migration length, whereas the actual speed of migration was the result of the total distance travelled between successive stopovers divided by the number of travelling days
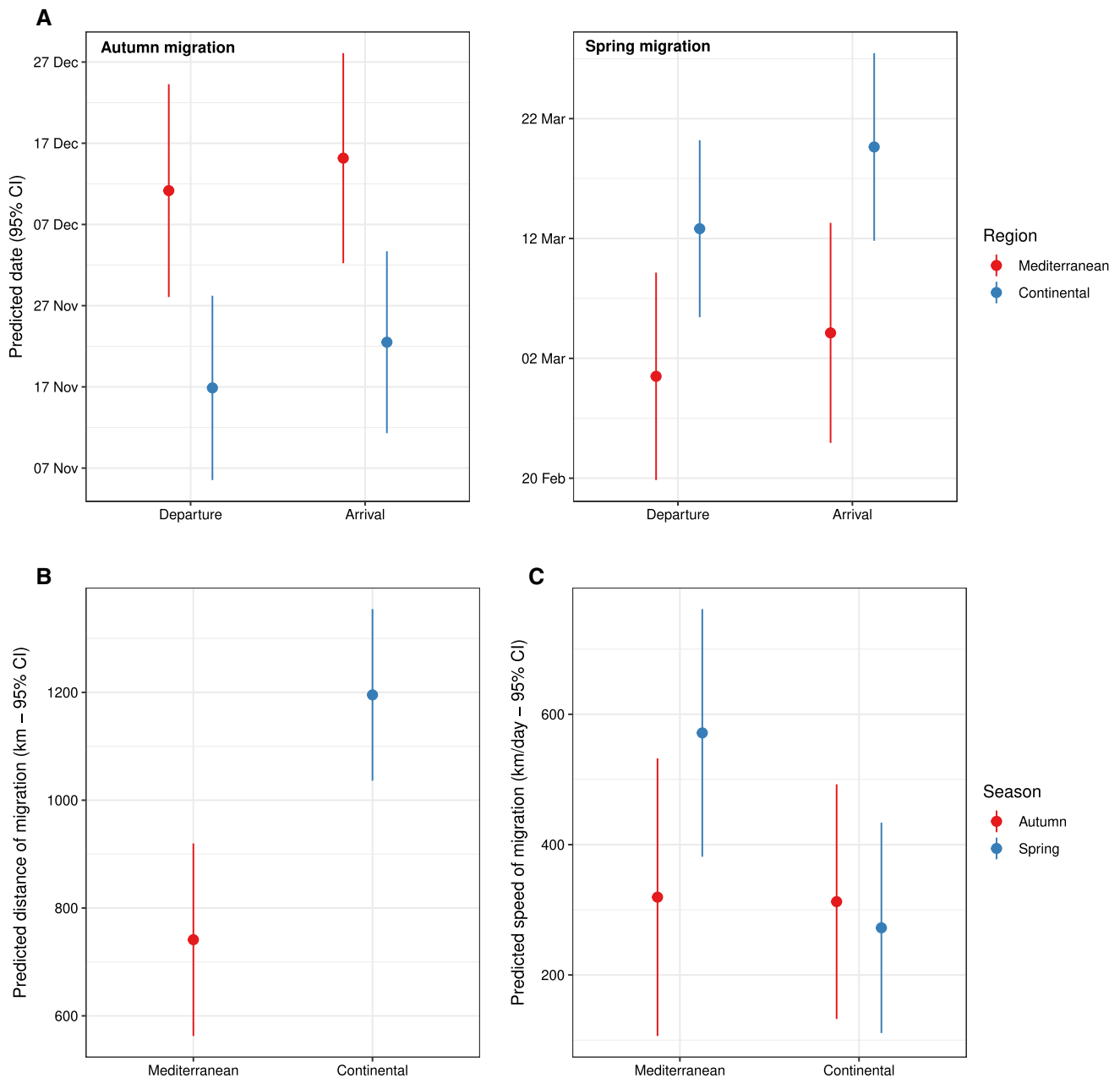
Fig. 2 Plot of effects of the breeding region and migratory season on the main migratory parameters. **A** Departure and arrival of autumn (upper left panel) and spring (upper right panel) migration of Stone-curlews equipped with GPS in Italy in the period 2012–2019. Results from the linear models with the departure or arrival date (Julian day, 1 = 1st of January) as dependent variable and region as predictor. Departure and arrival dates were significantly different between the two regions both in autumn and in spring, with the continental populations departing earlier than the Mediterranean ones in autumn and delaying departure in spring. **B** Migration distance recorded in Stone-curlews equipped with GPS in Italy in the period 2012–2019. Birds from the Mediterranean populations migrated longer distances in the spring than the autumn. Results from a linear mixed model with season (two-levels factor: autumn vs spring), region (two-levels factor: continental region vs Mediterranean region) and their interaction as predictors and bird ID as random intercept. SD of the random intercept = 239.9, conditional $R^2 = 0.88$, marginal $R^2 = 0.42$, number of observations = 33, number of birds = 20. **C** Speed of migration recorded in Stone-curlews equipped with GPS in Italy in the period 2012–2019. Birds from the Mediterranean populations migrated faster in the spring than the autumn, but this was not the case for continental populations where migration speeds were similar between seasons. Results from a linear mixed model with season (two-levels factor: autumn vs spring), region (two-levels factor: continental region vs Mediterranean region) and their interaction as predictors and bird ID as random intercept. SD of the random intercept = 201.6, conditional $R^2 = 0.66$, marginal $R^2 = 0.18$, number of observations = 33, number of birds = 20

The total duration of migration was rather short, often less than 5 days, and the median duration of active flight was about 1 day only (Table 1). The number of stopovers was rather variable in both seasons but usually it did not exceed two (Table 1); in two cases (birds VT42A, VT873), the individuals did not stop at all during spring migration, while we recorded seven stopovers for bird T25 for the same migration. Median stopover length was < 3 days, even though in some cases birds could stop for more than 1 week. The median of the total migratory speed was 300 km/day but active flight migration segments were often covered at more than 700 km/day (Table 1).

The migratory speed was not cohesive among populations and seasons ($\chi^2 = 5.1$, $df = 1$, $P = 0.02$; LMM, LR test): while individuals from continental populations kept a similar migratory speed rate between seasons, the Mediterranean population was generally migrating faster in spring than in autumn (Fig. 2C).

Effects of meteorological variables on the start of autumn migration

The analysis on the effects of meteorological factors on the start of autumn migration was performed on 14 birds (eight from the continental region and six from the Mediterranean region). The most supported model among the considered set included the daily minimum temperature (Tmin) and the daily averaged northward wind component (Vwind) (Table 2). The effect of temperature seems to be particularly strong, as this is the only covariate included in the second model, still within two units from the best one (Table 2). Both models were highly significant and have a high coefficient of concordance. As expected, the likelihood of departure increased when both Tmin and Vwind decreased, meaning that birds tended to depart when they were experiencing low temperatures and favourable wind conditions (wind blowing southward, i.e., tailwind conditions) (Fig. 3).

Table 2 Comparison of non-parametric Cox proportional hazard models developed to identify the meteorological variables affecting the likelihood of starting autumn migratory movements by Stone-curlews equipped with GPS in Italy in the period 2012–2019

Model	k	logLik	ΔAICc	w_i	Concordance	RS test	Tmin	Vwind
Vwind + Tmin	3	− 15.6	0.0	0.36	0.80 ± 0.08	10.2, $p = 0.006$	$\beta = -0.29 \pm 0.07$ $z = -4.0$, $p < <0.0001$ HR = 0.75 (0.65–0.86)	$\beta = -0.44 \pm 0.17$ $z = -2.5$, $p = 0.01$ HR = 0.65 (0.46–0.91)
Tmin	2	− 17.7	1.6	0.17	0.84 ± 0.06	9.8, $p = 0.002$	$\beta = -0.28 \pm 0.06$ $z = -4.4$, $p < <0.0001$ HR = 0.75 (0.66–0.85)	
Tmin + ΔTmin	3	− 16.8	2.4	0.11				
ΔTmin + Region	3	− 16.8	2.5	0.10				
Vwind + ΔTmin	3	− 17.1	3.0	0.08				
Tmin + Region	3	− 17.6	4.1	0.05				
Tmin + ΔPatm	3	− 17.7	4.3	0.04				
ΔTmin	2	− 19.1	4.3	0.04				
Vwind + Region	3	− 18.2	5.2	0.03				
ΔTmin + ΔPatm	3	− 18.9	6.6	0.01				
Vwind	2	− 20.6	7.3	0.01				
Vwind + ΔPatm	3	− 20.3	9.5	0.00				
Region	2	− 22.0	10.2	0.00				
Region + ΔPatm	3	− 20.9	10.6	0.00				
ΔPatm	2	− 23.2	12.5	0.00				
Null model	1	− 25.2	14.2	0.00				

Concordance (± SE), model significance [Robust Score (RS) test], model coefficients ($\beta \pm$ SE) and relative significance, estimated hazard ratio (HR) of departure after 1 SD increase of the variables included in the model (95% coefficient intervals) are reported only for models within two units from the best model. Predictors included in the models: *Vwind* daily averaged northward wind component (m/s), *Tmin* daily minimum temperature (°C), *ΔTmin* difference between the minimum temperature of the day and that of the previous one (°C), *ΔPatm* difference between the average sea level atmospheric pressure of the day and that of the previous one (hPa), *k* number of parameters, *logLik* log-likelihood, *ΔAICc* difference in AICc between a given model and the model with the lowest AICc, *w_i* Akaike weights. Number of observations = 802; number of birds = 14
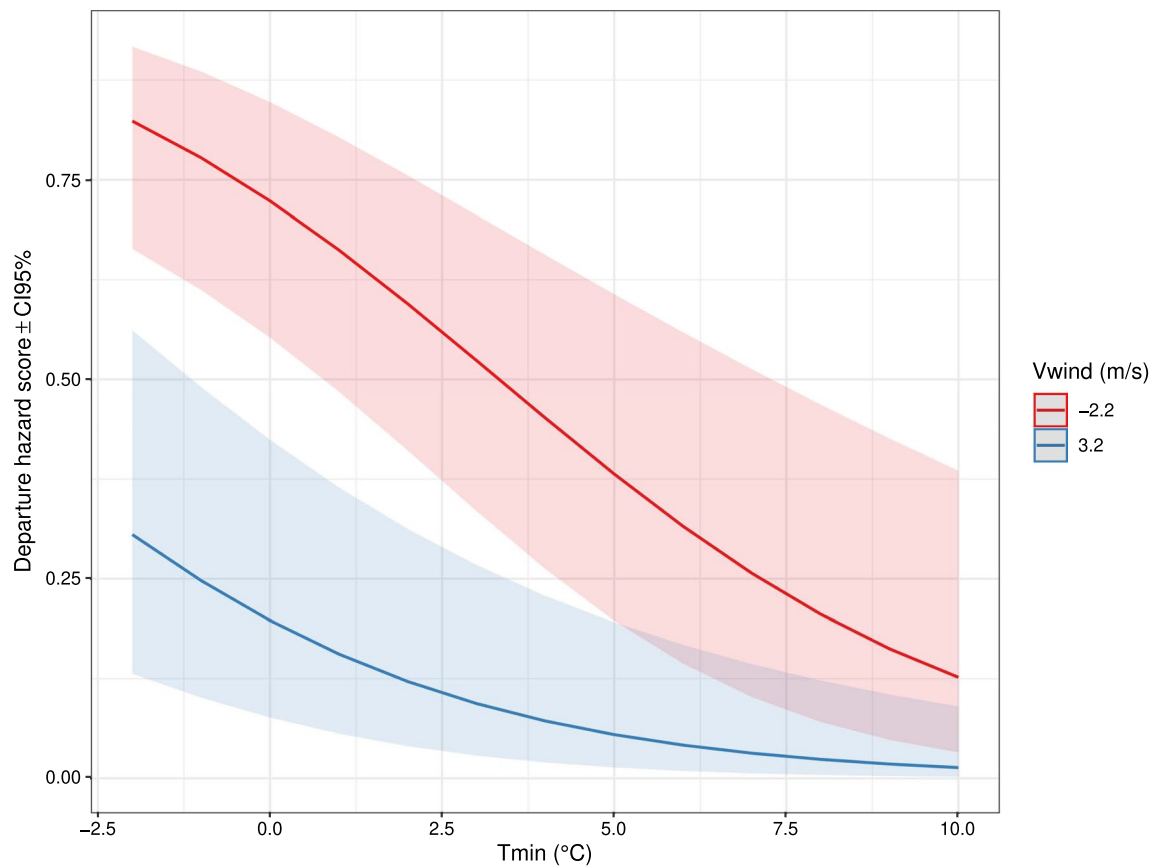
Fig. 3 Plot of the effects of daily minimum temperature (Tmin) and daily averaged northward wind component (Vwind; negative values indicate North to South flows) on the likelihood of departure (departure hazard score) for autumn migration of Stone-curlews equipped with GPS in Italy in the period 2012–2019. Results from the best Cox proportional hazard models (see Table 2 for further details). Number of birds = 14

Discussion

This study reports one of the few detailed investigations of the migratory behaviour of a Mediterranean migrant and the first for the Stone-curlew. Most of the studied populations were partially migratory, with short distance movements within the Mediterranean basin. Interestingly, our results highlight the significant intra- and inter-population variability of the migratory behaviour, which is not fully explained by breeding latitude and suggest that temperature and wind conditions modulate the timing of autumn migration.

Migration strategy

Three of the four considered populations were found to be partially migratory. This result is not surprising as partial migration is a fairly common strategy among short-distance migrants (Pulido et al. 1996; Newton 2008). The analysis of the proportion of migrating individuals showed significant interpopulation variability, as recorded for other migratory species in the Mediterranean basin (García de la Morena

et al. 2015; Monti et al. 2018a, b). Individuals belonging to continental populations (Taro and Piave) were more likely to undertake migration than populations belonging to the centre of the peninsula, in agreement with our expectations based on data from other Palaearctic migrants (Newton and Dale 1996; Newton 2008) and with what has been previously suggested for the Stone-curlew (Brichetti and Fracasso 2004; Biondi and Pietrelli 2015). The proportion of migrants was not different between the Piave and Taro populations, but the Taro population was the only one in which all tagged birds were found to be migrants. The relatively small number of birds tagged in the Taro could at least partly explain these results, as resident birds were probably rare, while an effect of the low accuracy of the geolocators used in the Taro population seems unlikely (see Giunchi et al. 2015 for details). Since individuals from the Taro population were tagged earlier than those from the Piave population, however, we cannot exclude that the small difference in the proportion of residents in the two populations could be interpreted as an ongoing change in the migratory strategies of the northern populations of the species, as recently observed for other

birds migrating over short distances (Doswald et al. 2009; Pautasso 2012; Ambrosini et al. 2016; Tellería et al. 2016; Podhrázský et al. 2017). The difference in the proportion of migrants between the two southernmost populations (Viterbo and Grosseto) was unexpected, as their respective breeding areas are very close to each other (about 57 km) and subject to comparable climatic conditions. It should be noted, however, that of all the birds followed for at least 2 years ($n=6$ for Viterbo and $n=7$ for Grosseto and Piave populations), only two birds changed their migratory strategy (one from Viterbo and one from Grosseto). Although the sample size is relatively small, this finding seems to indicate that the observed variability between populations is not primarily caused by individual inter-annual variability in migratory behaviour. We could speculate that this result could be due to intrinsic differences between tagged individuals possibly related to their sex and age, which are known to influence the migration strategy of birds (Gauthreaux 1982; Terrill and Able 1988; Newton 2008; Chapman et al. 2011; Hegemann et al. 2019). We did not record the sex of Viterbo birds, but data collected on the remaining populations did not show a consistently different pattern in the migration strategy of males and females (data not shown). Furthermore, all birds considered in this study were adults (> 1 year old). Interestingly, the only exception was the single migrant in the Grosseto population, which migrated when it was one year old and then became resident for the next two years of monitoring. This suggests that age and/or competitive ability may indeed play a role in modulating the migratory behaviour of Stone-curlews, as observed in other partial migrants (see Newton 2008; Chapman et al. 2011; Hegemann et al. 2019 for references), but it is not very helpful in understanding the unexpected migratory propensity of Viterbo birds. It cannot be excluded that this result is due to genetic differences between the two populations, even though previous genetic analyses (not including the Viterbo population) suggested that the gene flow between Italian Stone-curlew populations is significant (Mori et al. 2017). Alternatively, it could be hypothesised that the resources available in the Viterbo area during the non-breeding season are more limited than in the Grosseto area, e.g., due to a more widespread use of intensive agricultural practices, thus leading a higher fraction of individuals to migrate (Cox 1985; Boyle 2008; Jahn et al. 2010). Beyond the possible explanations, this result highlights a high local variability in the migration strategy of this species that deserves further investigation.

Migration routes, speed and timing

Most birds followed a relatively straight and direct route both in autumn and in spring. Migratory movements were limited within the Mediterranean basin, but wintering sites showed a wide latitudinal range (from Sardinia to Libya) compared to the latitudinal range of breeding areas and to the scale of migratory movements. The large overlap of wintering sites between continental and Mediterranean populations indicates a telescopic migration, i.e., populations that are allopatric during the breeding period overwinter in sympatry (Newton 2008; Borras et al. 2011; Arizaga and Tamayo 2013). This pattern suggests a weak connection between breeding and non–breeding areas (migratory connectivity, Webster et al. 2002) which can have significant implications for the conservation of the species (Cresswell 2014; Finch et al. 2017). In this regard, it is interesting to observe that all tagged migrant Stone-curlews spent the winter season in areas that probably already hosted resident populations of the species (Delany et al. 2009; Brichetti and Fracasso 2004; Tinarelli et al. 2009; Hume and Kirwan 2020).

Our data were only partially in agreement with the expectation that total migration speed should be higher in spring than in autumn (Kokko 1999; Nilsson et al. 2013; Zhao et al. 2017; Schmaljohann 2018). Spring migration was indeed faster only for Mediterranean Stone-curlews, whereas no difference was observed for continental birds. Population variability in the difference in overall migration speed between seasons has been observed in other species (see e.g., Vansteelant et al. 2015; Schmaljohann 2018). The variability recorded in this study was relatively small, so we might assume that Stone-curlews did not significantly change their migration strategies in different seasons, given the short migration distance. Some data collected on shorebirds of different sizes also seemed to suggest that the seasonal difference in migration speed tended to be smaller for larger species (Zhao et al. 2017). It cannot be ruled out, however, that Stone-curlews do indeed adopt different strategies in spring and autumn, but no difference in migratory speed could be detected for continental birds due to the effect of unfavourable weather conditions encountered en route that may have delayed or interrupted the migratory journey (see e.g., Newton 2008; Shamoun-Baranes et al. 2010, 2017b). This effect might have been less relevant for Mediterranean individuals, because the greater proximity between the wintering and breeding areas might allow them to better adjust their timing of migration in function of weather conditions they expect to find en route and in the area of arrival (Lehikoinen et al. 2004; Rubolini et al. 2007; Møller et al. 2010; Knudsen et al. 2011). In this regard, it is interesting to note that birds from both areas tended to migrate during the day more frequently in spring than in autumn, as indicated by the significantly lower fraction of migratory fixes recorded during the night in spring. This extension of nocturnal migration into the daytime, which has been recorded for other nocturnal migrants especially when crossing ecological barriers (Newton 2008; Adamík et al. 2016; Malmiga et al. 2021), might suggest a tighter migratory schedule in spring and therefore seems to be in agreement with a time-minimization strategy.

Even though the latitudinal range of migratory movements was quite small, we observed a significant effect of breeding latitude on the timing of migration. Continental birds departed significantly earlier than Mediterranean ones in autumn while the opposite occurred for spring migration. The earlier autumn departure of animals breeding at higher latitudes is in contrast to what has been observed in long-distance migrants (Conklin et al. 2010; Briedis et al. 2016; Neufeld et al. 2021), but seems to confirm the expected effect of meteorological variables and the likely depletion of food resources in influencing the migratory timing of this species (see below). The pattern observed for arrival dates was the same as that observed for departure dates probably because the difference in the migration distance between the two areas was quite small. Interestingly, all autumn departures occurred after the end of primary moult estimated using data from the Taro population (17th October $\pm$ 14 days SD, Giunchi et al. 2008). This indicates that at southern latitudes animals have sufficient time to complete the moulting of the remiges before migrating and do not need to suspend the moult as appears to be the case at northern latitudes (see Giunchi et al. 2008 for details).

The timing of migration was quite variable as both autumn and spring departures occurred over a period of two months. This variability is in line with the observed flexibility of the migratory schedule of short-distance migrants (Pulido and Widmer 2005; Newton 2008; Pulido and Berthold 2010; Monti et al. 2018a) which are often characterized by a sort of "relaxed migratory systems" (see Monti et al. 2018a), but has also been observed in long-distance migratory shorebirds (e.g., Black-tailed Godwit *Limosa limosa*, Senner et al. 2019). Contrary to the expectations (Shamoun-Baranes et al. 2006; Nilsson et al. 2013) and to what has been observed in other shorebird species (e.g., Sociable Lapwing *Vanellus gregarius*, Donald et al. 2021), the variability of departure dates was comparable between autumn and spring. The wide interval of departures observed in both seasons could be at least partially due to a different timing of migration between age or sex classes (differential migration, Ketterson and Nolan 1993; Newton 2008). We cannot exclude an effect of sex, as the sex of some of the tracked birds was not available while the effect of age seems rather unlikely as all tracked birds were adults (> 1-year old).

Effects of meteorological variables on the start of autumn migration

The analysis of the meteorological proximate factors affecting the timing of migration suggests that departure dates are affected in particular by temperature and wind conditions. As expected, birds tended to depart in tailwind conditions (Åkesson and Hedenström 2000; Liechti 2006; Gill et al. 2014; but see Eikenaar and Schmaljohann 2015;

Schwemmer et al. 2021), but the greatest effect on the probability to start autumn migration is due to the daily minimum temperature, probably for its negative effect on the availability of invertebrates (Eggleton et al. 2009; Abram et al. 2017) and on the cost of thermoregulation for a species with a low resting/basal metabolic rate (Duriez et al. 2010; Gutiérrez et al. 2012). The effect of temperature on migratory departure has been documented in several long- and short-distance migrants (e.g., Xu and Si 2019; Klinner and Schmaljohann 2020; Linek et al. 2021). In a medium-distance steppe migrant, the Asian Houbara *Chlamydotis macqueenii*, the effect of temperature was stronger in spring rather than in autumn, as departure decisions were less repeatable for temperature in autumn rather than in spring (Burnside et al. 2021). Unfortunately, this pattern cannot be verified in our species, as the small sample size available and the latitudinal spread of wintering areas did not allow robust modelling of the effect of temperature on the onset of spring migration. In addition, the lack of a significant number of repeated migration tracks did not allow an estimation of the repeatability of individual migration timing.

The relatively large increase in the probability of departure when temperatures were near or below 0 °C might suggest that Stone-curlews may tend to delay departure until winter conditions worsen abruptly (Haila et al. 1986; Newton 2008). This strategy could be effective at the considered latitudes, because the relatively mild environmental conditions combined with the short migration distance could allow for a relatively relaxed timing of the start of migration. This seems to be supported by the wide time interval of autumn departures, some of which occurred even in the second half of December. According to this hypothesis, it can be predicted that the frequency of migratory birds in the considered populations will decrease in the near future due to the effect of global warming in the Mediterranean (Gordo 2007; Morganti 2015). This could consequently modify the present distribution of the species throughout the year and should be taken into account when targeting conservation measures, as the ecological needs of the Stone-curlew could change between breeding and non-breeding seasons.

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