Broad-front migration leads to strong migratory connectivity in the lesser kestrel (*Falco naumanni*)

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Running head: *Migratory connectivity in the lesser kestrel*

Abstract

Aim: Migratory animals regularly move between often distant breeding and non-breeding ranges. Knowledge about how these ranges are linked by movements of individuals from different populations is crucial for unravelling temporal variability in population spatial structuring and for identifying environmental drivers of population dynamics acting at different spatio-temporal scales. We performed a large-scale individual-based migration tracking study of the lesser kestrel (*Falco naumanni*), an Afro-Palearctic migratory raptor, to determine the patterns of migratory connectivity of European breeding populations.

Location: Europe, Africa.

Methods: Migration data were recorded using different devices (geolocators, Argos PTTs, GPS loggers) from 87 individuals breeding in the three core European populations, located in the Iberian, Italian and Balkan peninsulas. We estimated connectivity by the Mantel correlation coefficient (r_M), and computed both the degree of separation between the non-breeding areas of individuals from the same population (i.e. the population spread) and the relative size of the non-breeding range (i.e. the non-breeding range spread).

Results: European lesser kestrels migrated on a broad-front across the Mediterranean Sea and Sahara Desert, with different populations using different routes. Iberian birds migrated to western Sahel (Senegal, Mauritania, western Mali), Balkan birds migrated chiefly to central-eastern Sahel (Niger, Nigeria, Chad), whereas Italian ones spread from eastern Mali to Nigeria. Spatial differentiation of non-breeding areas led to a strong migratory connectivity ($r_M = 0.58$), associated with a relatively high population (637 km) and non-breeding range (1149 km) spread.

Main conclusions: Our comprehensive analysis of the non-breeding distribution of European lesser kestrel populations revealed a strong migratory connectivity, a rare occurrence in long-distance avian migrants. The geographic conformation of the species' breeding and non-breeding ranges, together with broad-front migration across ecological barriers, promoted the differentiation of migratory routes and non-breeding areas. Strong connectivity could then arise because of both high population spread and broad non-breeding range.

Key words: bird migration, geolocators, GPS, non-breeding distribution, Sahel, satellite telemetry, spatial structure

1. INTRODUCTION

Migratory animals have been the subject of substantial research efforts tackling biogeographical aspects of migration due to their movements between often distant breeding and non-breeding ranges (e.g. Salewski & Bruderer, 2007; Louchart, 2008; Zink & Gardner, 2017; Winger, Auteri, Pegan & Weeks, 2019). Traditionally, biogeographic studies of migratory species, especially of birds, have been hampered by the difficulties of defining geographic ranges through the whole annual cycle. Recent technological advances in the study of bird migration (e.g. Bridge et al., 2011; Ruegg et al., 2014; Hobson & Wassenaar, 2018) have led to the identification of breeding/non-breeding ranges even of species that move between remote areas. This has allowed migratory patterns to be placed in a more coherent and revealing biogeographical perspective, emphasising the importance of migratory connectivity (e.g. Trierweiler et al., 2014; Finch et al., 2015; Finch, Butler, Franco & Cresswell, 2017).

Migratory connectivity measures the link between breeding and non-breeding areas (Webster, Marra, Haig, Bensch & Holmes, 2002) by comparing the spatial population structure between areas occupied during different phases of the annual cycle (Ambrosini, Møller & Saino, 2009; Cohen et al., 2018). ‘Weak’ or ‘diffuse’ connectivity occurs when individuals from different breeding areas spread through several non-breeding areas, therefore showing high inter-population mixing (Finch et al., 2017). ‘Strong’ connectivity arises instead when individuals from a given breeding area move to a specific non-breeding area and inter-population mixing is hence low. The mechanisms generating and affecting patterns of migratory connectivity may be diverse. These may include geographical constraints (Webster et al., 2002; Finch et al., 2017; Cohen et al., 2018) and population structure (Briedis & Bauer, 2018). The latter may be the case for example when differential migration patterns occur, i.e. when males and females or different age groups migrate at different times of the annual cycle and/or spend the non-breeding period in different areas (Briedis

& Bauer, 2018). It is therefore important to incorporate information about migratory behaviour in studies of migratory connectivity, particularly in those species showing differential migration (Briedis & Bauer, 2018).

Migratory connectivity involves both the spreading and mixing of breeding populations in the non-breeding areas (Finch et al., 2017). According to Finch et al. (2017), strong connectivity may arise from low population spread in the non-breeding areas and/or high non-breeding range spread. The population spread is defined as the mean of pairwise distances among non-breeding areas of individuals from different breeding populations and reflects the degree of separation in the non-breeding grounds of individuals from the same breeding population (Finch et al., 2017). The 'non-breeding range spread' is defined as the mean of the pairwise distances among non-breeding areas of individuals from all breeding populations and reflects the relative size of the non-breeding range (Finch et al., 2017). Understanding patterns of migratory connectivity and population differentiation in migratory behaviour is of pivotal importance to improve our understanding of ecological processes affecting population dynamics of migratory species (Briedis & Bauer, 2018; Kramer et al., 2018).

Based on a large migration tracking dataset (n = 87 individuals), we performed a continental-scale study of migratory connectivity in the lesser kestrel (*Falco naumanni*), a small (ca. 120 g) diurnal and colonially breeding trans-Saharan migrant raptor. The lesser kestrel is a species of European conservation priority that has suffered steep population declines and range contraction in the second half of the 20th century (Iñigo & Barov, 2010). It currently breeds across southern Europe, where populations have been partly recovering in recent years (Iñigo & Barov, 2010), North Africa, the Middle East, and Central Asia (Ferguson-Lees & Christie, 2001). During the boreal winter, it migrates to the Afrotropics (Ferguson-Lees & Christie, 2001), although some individuals (mostly adult males) remain close to breeding colonies (Negro, De la Riva & Bustamante, 1991). We focus on the whole European population, whose breeding range is fragmented in three main geographical areas, corresponding to the main southern European peninsulas (Iberian, Italian, and Balkan) (Iñigo & Barov, 2010; Bounas et al., 2018). Birds from Iberia (including those from the small population breeding in southern France) migrate to West Africa (Rodríguez, Negro, Bustamante, Fox, & Afanasyev, 2009; Catry et al., 2010; Limiñana, Romero, Mellone, & Urios, 2012; Pilard, Bourgeois & Sylla, 2017), whereas birds from the Middle East and Asia likely move to South Africa (Rodríguez, Negro, Bustamante et al., 2009; Rodríguez, Alcaide, Negro, & Pilard, 2011). The African non-breeding areas of central-eastern Mediterranean birds (Italian and Balkan regions) are currently unknown, due to the lack of sub-Saharan ring recoveries or migration tracking data (e.g. Spina & Volponi, 2008; Rodríguez, Negro, Bustamante et al., 2009; Bounas, Panuccio, Evangelidis, Sotiropoulos & Barboutis, 2016).

Our specific aims were to: 1) identify the non-breeding areas of birds from the central-eastern Mediterranean populations (Italy and the Balkans); 2) assess the different components of connectivity (inter-population mixing, population spread and non-breeding range spread; *sensu* Finch et al., 2017); 3) evaluate whether variation in migratory behaviour among populations from different breeding areas and differentiation of migratory routes affected connectivity patterns. Low migratory connectivity is relatively frequent among long-distance migratory bird species (Finch et al., 2017). Therefore, we predicted this to be the case in European breeding lesser kestrel populations, implying a relatively high degree of mixing in the non-breeding areas of birds from different breeding regions.

2. MATERIALS AND METHODS

2.1. Characteristics of the migration tracking dataset and general methods

Lesser kestrel migration tracking data have been previously reported from Iberia and southern France (geolocators, hereafter GLS: 20 individuals; Rodríguez, Negro, Bustamante, et al., 2009; Catry et al., 2010; Pilard et al., 2017; Argos Platform Transmitter Terminals, hereafter Argos PTTs: five individuals; Limiñana et al., 2012). We obtained migration data (either as original datafiles or from published graphs) from these studies for the individuals whose non-breeding area could be identified (n = 25 migration events).

We report new data for 69 migration events [GLS: Italy, n = 23, Greece, n = 6; remote-downloading archival GPS tags (GPS-UHF devices): Spain, n = 15; Italy, n = 12; France, n = 1; Argos PTTs: Bulgaria, n = 7; Italy, n = 1; Spain, n = 4] (see Appendix S1 in Supporting Information, Table S1.1). All devices were deployed on birds captured at or near their nest site (nestboxes or other cavities; e.g. Podofillini et al., 2018; Podofillini et al., 2019), mostly at the end of incubation or during the nestling phase. Birds were equipped with tracking devices when adults (i.e. at least two years old), except one Spanish individual that was tagged as a juvenile. Capture, handling and device deployment were carried out by experienced ornithologists according to recommended protocols aimed at ensuring animal welfare throughout the operations (e.g. Whitworth, Newman, Mundkur, & Harris, 2007). No individual was injured during capture or device deployment. All capture and device deployment activities were carried out under license from the relevant national/regional authorities (details in the ‘Acknowledgments’ section).

Overall, we analysed 94 migration events from 87 individuals (information on consecutive migration events was available for 7 individuals, see details in Table S1.1) breeding at 25 colony sites (eight in Spain, seven in Italy, four in Greece, three in France, two in Bulgaria, one in Portugal).

Birds breeding in different countries were assigned to three distinct geographical regions as follows: Portugal, Spain, France – Iberian peninsula; Italy – Italian peninsula; Bulgaria, Greece – Balkan peninsula. Birds from the small southern French population were considered as belonging to the Iberian core population (Bourgeois, Bonot & Lelong, 2016; Pilard et al., 2017). With the exception of a single individual, migration data from Bulgaria were collected from breeding birds partly originating from a re-introduction project involving Spanish birds (Gradev, Marin & Antolín, 2016). However, as their migratory behaviour was very similar to the other Balkan individuals, they were treated as belonging to the Balkan group. Indeed, removing data from these individuals did not qualitatively alter our conclusions concerning migratory connectivity (details not shown for brevity).

While GPS-UHF tags and Argos PTTs allowed accurate inference about migration routes (accuracy was generally within 50 m or 1.5 km, respectively; see paragraph 2.3), this information could not be obtained from GLS (e.g. Finch et al., 2015). This is because the latter devices have low accuracy (ca. 200-300 km in latitude; Lisovski et al., 2018) and show huge latitudinal uncertainty of location estimates around equinoxes, corresponding to migration periods of lesser kestrels and of most other landbirds moving between Europe and Africa (Lisovski et al., 2018). All spatial and statistical analyses were performed using R 3.3.3 (www.R-project.org) and QGIS 2.18 (qgis.osgeo.org).

2.2. GLS data collection and analysis

We deployed GLS (Mk5 and Mk7, Biotrack Ltd., UK) between 2014 and 2017 in Italy and Greece, using a backpack wing-loop harness made of braided nylon rope, as recommended by Rodríguez, Negro, Fox, & Afanasyev (2009). The total weight of devices (including harness) was ca. 2.5 g, corresponding to ca. 2.0% of the body mass of tracked individuals, i.e. well below the generally recommended tag weight limits for bird species (tag and harness weight should not exceed 5% of body mass; see Barron, Brawn, & Weatherhead, 2010). Geolocators were shown to have weak or no negative impact on breeding lesser kestrels (Rodríguez, Negro, Fox, et al., 2009). We retrieved GLS 1-2 years following deployment by recapturing birds (mostly by hand) during routine inspections of nest cavities/nestboxes (e.g. Podofillini et al., 2019). Details of GLS data analysis are reported in Appendix S2. Dates of post-breeding (autumn) migration end and pre-breeding (spring) migration onset were identified according to Liechti et al. (2015) as the first day of the first stationary period or the last day of the last stationary period (of at least 14 days) south of the Sahara, respectively. The geographic position of the non-breeding area was estimated as the centre of density (modal value) of all locations between the end of post-breeding migration and onset of pre-breeding migration (Liechti et al., 2015). Hence, the geographic position of the non-breeding area corresponds to the location that has been more frequently visited by birds during the non-breeding period [lesser kestrels may move between different non-breeding areas, as observed in satellite-tracked birds; see also Pilard et al. (2017)]. Migration routes were not reconstructed because of the uncertainties in latitudinal estimates around the equinoxes and because for most individuals only few reliable twilight events were identified during the migration periods (E. Rakhimberdiev, pers. comm.), preventing the application of advanced route reconstruction methods (e.g., Rakhimberdiev, Saveliev, Piersma, & Karagicheva, 2017). We also reanalysed the original geographic positions reported in Pilard et al. (2017) to compute the geographic position of the non-breeding area as detailed above.

2.3. Satellite tracking devices data collection and analysis

We deployed three models of solar-powered satellite tracking devices (hereafter, STDs) (Argos PTTs: 5 g PTT 100, Microwave Telemetry Inc., USA; and two remote-downloading dataloggers using the GPS system for location, GPS-UHF tags: 5 g Pica, Ecotone, Poland, and 4 g nanoFix-Geo+RF, PathTrack Ltd., UK) during 2012-2018, using a backpack Teflon harness. The overall mass of tag and harness was always below 4.0% (GPS-UHF) and 5.0% (Argos PTTs) of body mass of the tracked individuals (Limiñana et al., 2012; Cecere et al., 2018), which is within the generally recommended tag weight limits (see Barron et al., 2010). Argos PTTs were mostly programmed with a 8 h on/16 h off duty cycle (see Limiñana et al., 2012). We set GPS-UHF devices with a 17 h on/7 h off duty cycle during the residence period in breeding and non-breeding areas (one fix every 15 min) and one fix every 30 min during the expected migration months, with no off periods (sampling frequency could actually vary because our solar GPS-UHF tags adjusted sampling rate according to battery power; Cecere et al., 2018). Data from GPS-UHF devices were retrieved remotely the year after deployment using UHF base stations positioned near breeding colonies.

For Argos PTT data, we mostly relied on 0-3 location quality classes, which have an accuracy of ca. 1.5 km (see Limiñana et al., 2012 for details), while for GPS-UHF devices the expected accuracy of locations was 15-50 m (Cecere et al., 2018). A few unrealistic geographic locations (clearly reflecting Argos/GPS location errors) were removed based on visual inspection.

Onset/end dates of post- and pre-breeding migration were estimated based on visual inspection of movements and on net displacement values (Turchin, 1998). Date of onset of post-breeding migration was defined as the day when a clearly directional southward movement occurred, with no return (i.e. discarding all the post-breeding and pre-migratory movements). The geographic position of non-breeding areas was computed as detailed in paragraph 2.2.

2.4. Analysis of migratory connectivity

The extent of inter-population mixing was assessed by the Mantel correlation coefficient (r_M) between pairwise distance matrices of breeding sites and non-breeding areas (Ambrosini et al., 2009). The Mantel correlation coefficient was computed using the *mantel* function of the ‘vegan’ R package (Oksanen et al., 2017), and significance was assessed by randomization. Population spread, reflecting the relative geographic spread of a population on the non-breeding grounds (Finch et al., 2017), was assessed by computing mean (orthodromic) distances between non-breeding areas of birds from the same breeding region (Finch et al., 2017). Population spread was compared between birds from different breeding regions using a linear model of inter-individual distances, and significance was assessed by a randomization test (Manly, 1991) using the *lmperm* function of the 'permuco' R package (Frossard & Renaud, 2018). We also computed non-breeding range spread as the mean distance between all individual non-breeding areas of birds from all breeding regions (Finch et al., 2017). In these analyses, for those individuals with consecutive migration events, we only used data from the first migration event.

2.5. Calculation and analysis of migration-related variables

For each migration event, we obtained onset/end dates of both post- and pre-breeding migration, and computed duration of post-breeding migration (days), duration of stay in sub-Saharan non-breeding area (days), duration of pre-breeding migration (days), and minimum migration distance (km) (orthodromic distance between breeding site and non-breeding area). For individuals tracked with STDs and for both post- and pre-breeding migration, we further computed: migration track length (km) (sum of all distances between positions recorded on a migration track between onset and end, for all complete tracks), track straightness (minimum migration distance between location of onset and of end of the track divided by migration track length; Benhamou, 2004), migration speed (km/day) (migration track length/duration of migration), longitude at which the birds crossed the 25° N latitude (hereafter, longitude at 25° N), and the mean deviation (km) of a track from the orthodrome (hereafter, E-W deviation; computed as the mean longitudinal deviation of a track from the orthodrome based on 100 latitude values regularly positioned along the orthodrome; negative values: track westward of orthodrome; positive values: track eastward of orthodrome). The longitude at 25° N, which is approximately in the middle of the Sahara Desert (i.e. halfway between breeding and non-breeding areas), was computed to assess the geographic position at which the desert was crossed during migration.

Differences in migratory behaviour between birds from different breeding regions were assessed using linear mixed models (LMMs), including region (3-level factor) and sex as predictors, of the following response variables: onset/end dates of migration, duration of migration, duration of stay in non-breeding area, minimum migration distance, migration speed, migration track length, track straightness, longitude at 25° N, and E-W deviation. For some variables (duration of migration, migration speed, migration track length, track straightness, longitude at 25° N, E-W deviation), we also included season (autumn vs. spring, 2-level factor) as a further predictor. Whenever sample size allowed, we included in initial models 2-way interactions (region × sex, region × season, sex × season). In models of track length and straightness, to control for the variable frequency of data collection by different STDs, we included the number of locations/day during migration as a covariate. In all LMMs, bird identity was included as a random intercept effect to account for repeated measures of the same individuals (both between years and between seasons). In LMMs of migration onset, end, duration of migration, duration of stay in non-breeding areas, and speed, we included tracking device type (GLS, Argos PTT, GPS-UHF) as a further random intercept effect to control for heterogeneity among devices in the quality of the timing information that was obtained. Interactions were removed in a single step if non-significant ($p > 0.05$). Final models included all main effects and statistically significant interactions (if any). We fitted LMMs using the *lmer* function of the ‘lme4’ R library (Bates, Maechler, Bolker & Walker, 2014). Data from the single juvenile bird were excluded from the analyses of migration timing (migration timing of juvenile birds may largely differ from that of adults; Newton, 2008), but were considered for all analyses involving spatial variables. Statistical significance was set at $\alpha = 0.05$.

3. RESULTS

3.1. Geographic distribution of non-breeding areas and migratory connectivity

The non-breeding areas of birds from all breeding regions were located within the arid and semi-arid regions of the Sahelian belt, ranging between ca. 9° and 21° N (Fig. 1). Individuals from different breeding regions tended to migrate to distinct sectors of the Sahel (Fig. 1). As expected from previous studies, the non-breeding areas of Iberian birds were mostly located in the western Sahel (Senegal, Mauritania and western Mali). In contrast, most of the Balkan breeding birds spent the non-breeding season in central-eastern Sahel (Niger, Nigeria and Chad), whereas Italian lesser kestrels spread over a broad area of the central Sahelian belt, from eastern Mali (where they overlapped somewhat with Iberian birds) to Niger and Nigeria. A minority of individuals did not follow these general patterns: these were one bird from Iberia and one from the Balkans, both of which spent the non-breeding period in Burkina Faso, in a region mostly occupied by Italian birds, and an Italian individual migrating to Chad (Fig. 1).

There was a strong positive correlation between the longitude of the breeding sites and that of the non-breeding areas ($r = 0.83$, $n = 87$, $p < 0.001$). Migratory connectivity, as estimated by the Mantel correlation coefficient, was relatively strong ($r_M = 0.58$, $p_{rand} < 0.001$) compared to values reported in Finch et al. (2017), indicating that individuals from the same breeding region have non-breeding areas closer to each other than expected by chance (Fig. 1). The population spread of non-breeding areas was 637 ± 422 (SD) km, significantly different between regions ($F_{2,1474} = 32.6$, $p_{rand} < 0.001$). It was smaller for Iberian birds (575 ± 364 km), intermediate for Italian birds (700 ± 466 km), and larger for Balkan ones (958± 542 km) (Fig. 2; all pairwise comparisons were statistically significant, p_{rand} always < 0.001). The mean non-breeding range spread was 1149 ± 799 km.

3.2. Variation in migratory behaviour and routes

Descriptive statistics of post- and pre-breeding migration characteristics for each breeding region are reported in Tables 1 and 2. Most individuals departed for their post-breeding migration in the second half of September (18th to 22nd) and reached their non-breeding area at the beginning of October after 11-14 days of travelling (Table 1). Italian birds were significantly delayed compared to those from the other regions (Table 3). Birds spent ca. 160 days in the sub-Saharan non-breeding area (Table 1). Pre-breeding migration began in early March (Table 1), with Iberian birds starting migration on March 3rd, 13 days earlier on average than those from the other regions (Tables 1-3). As a consequence of significantly earlier pre-breeding migration onset and shorter minimum migration distance, Iberian birds also reached their breeding sites significantly earlier (March 18th) compared to Italian and Balkan ones (Tables 1-3).

The duration of pre-breeding migration did not significantly vary among birds from different regions, birds taking on average 18-23 days to complete their northward journey (Tables 1, 4). Pre-breeding migration lasted significantly longer (by ca. 7 days) than post-breeding migration (Tables 1, 4). Moreover, birds migrated at a significantly slower pace in spring than in autumn (255 vs. 376 km/day) (Tables 1, 4). Both the minimum migration distance and track length significantly differed among birds from different regions, being greater for Balkan birds, shorter for Iberian ones, and intermediate for Italian ones (Tables 2-4). Track length was also significantly greater in spring than in autumn (4012 vs. 3644 km, respectively), which was mainly because birds tended to move southward during the non-breeding stay in the Sahel (Table S1.2).

In autumn, birds migrated over a broad front across the Mediterranean Sea and the Sahara Desert (Fig. 3). The longitude at 25° N was clearly differentiated between birds from different breeding regions (Fig. 3, Tables 2, 4). The pattern for spring migration was similar, but there was a tendency, especially for Iberian and Italian birds, to cross the Mediterranean over relatively narrower sea stretches (the Alboran Sea and the Strait of Sicily, respectively) (Fig. 3), with no clear evidence of funneling of migration tracks along coastlines or concentration at migratory 'bottlenecks' (Fig. 3). Iberian birds migrated across the Sahara Desert as well as along the Atlantic coast during both autumn and spring (Fig. 3). Track straightness and E-W deviations did not significantly vary among birds from different regions (Tables 2, 4). The vast majority of tracks to non-breeding areas was rather straight, although a few individuals made considerable eastward detours (Fig. 3). Spring migration tracks were less straight and showed marked westward detours (Fig. 3, Tables 2, 4). As a consequence of spring westward detours, pre-breeding tracks were significantly more westerly (by 3.1° longitude at 25 °N) than post-breeding ones (Fig. 3, Tables 2, 4). Overall, there was a very strong correlation between the longitude of the breeding site and the longitude at which birds crossed the 25° N parallel, both during the post-breeding ($r = 0.93$, $p < 0.001$, $n = 40$) and the pre-breeding migration ($r = 0.86$, $p < 0.001$, $n = 30$). The correlation was similarly strong if the second half of the journey was considered (correlation between longitude at the 25° N and that of non-breeding areas; post-breeding migration, $r = 0.92$, $p < 0.001$, $n = 40$; pre-breeding migration, $r = 0.89$, $p < 0.001$, $n = 30$).

The migratory behaviour of males and females was remarkably similar (Tables 3, 4). Significant sex differences in migratory behaviour were detected for a few variables only: males began their post-breeding migration ca. 7 days later than females, and, at least among Italian birds, reached their non-breeding areas significantly later (Tables 3, 4). Moreover, males performed a significantly straighter migration compared to females (Tables 3, 4). No significant sex differences in the position of non-breeding areas were detected (Table S1.3).

4. DISCUSSION

4.1. Spatial segregation of non-breeding areas and migratory connectivity

Our survey of migratory connectivity of European lesser kestrel populations provided for the first time a comprehensive overview of the sub-Saharan non-breeding areas of this species of conservation priority (Iñigo & Barov, 2010). Indeed, despite of one century of bird ringing in Europe, no information on the African non-breeding areas of central-eastern Mediterranean populations was available until now (see Introduction). We found that lesser kestrels breeding in the three southern European regions (Iberian, Italian and Balkan peninsulas) migrated to different sectors of the Sahelian belt. Such spatial segregation of non-breeding areas originated from broad-front migration across the Mediterranean Sea and the Sahara Desert (Fig. 1). Accordingly, the degree of inter-population mixing was low, indicating a relatively strong migratory connectivity (as quantified by a Mantel correlation value of 0.58). Indeed, Finch et al. (2017) reported that only seven out of 28 species had a Mantel correlation value greater than 0.50. We emphasize that our estimate of migratory connectivity should be highly reliable because the sample of tracked individuals is very large compared to previous analyses summarized in Finch et al. (2017) and because birds were sampled at several breeding sites spanning the entire European range.

Overall, the population spread was ca. 650 km and the non-breeding range spread was 1150 km, i.e. relatively high values among the migratory bird species studied to date (Finch et al., 2017; the population spread observed in the present study is above the modal value shown in Finch et al. 2017). In addition, population spread significantly increased eastwards, as birds from Iberia migrate to a relatively smaller non breeding-range than those from the Balkans. This pattern may originate because of geographic constraints on migration routes of Iberian birds due to the proximity of the Atlantic coast, implying that those migrating birds cannot disperse over the Sahel as much as those from Italy and the Balkans, as well as by geographic differences in resource abundance (e.g.

orthopterans, the main prey of the lesser kestrel; Zwarts, Bijlsma, van der Kamp, & Wymenga, 2009) among Sahel sectors, with western Sahel receiving much more rainfall and having a greater primary productivity than the central Sahel (Anyamba & Tucker, 2005). The western Sahel may thus sustain a higher population density compared to the central Sahel, where most of the Italian and Balkan birds spend the non-breeding season.

Our estimate of the non-breeding range spread mirrors the almost geographically unconstrained non-breeding areas of the lesser kestrel, spanning over 5000 km in longitude, and located in the widest portion of the African continent. Hence, the high population spread is associated with a relatively high non-breeding range spread to reduce the mixing of European breeding populations in the African non-breeding range, resulting in a strong migratory connectivity.

4.2. Migratory connectivity, routes and detours

Satellite-tracking data revealed that lesser kestrels largely migrated over a broad front across the ecological barriers (Mediterranean Sea and Sahara Desert) rather than concentrating at migratory ‘bottlenecks’ as many other soaring-gliding raptors (e.g. buzzards, eagles) (Bildstein, 2006). Some western Iberian birds were a partial exception to this pattern, as they tended to congregate in the surroundings of the Strait of Gibraltar, especially during spring migration, likely because of the geographical constraints to migration routes imposed by the Atlantic coast. The non-converging migration routes of birds breeding in the three different regions, which was testified by the strong association between the longitude of breeding site and the estimated longitude halfway through their migratory flights across the ecological barriers, argues for a key role of broad-front migration and spatial route segregation in determining the strong migratory connectivity we have highlighted. Such a connectivity pattern is similar to that reported for another migration tracking study of an Afro-Palearctic migratory raptor, the Montagu’s harrier (*Circus pygargus*) (r_M = 0.56-0.60)

(Trierweiler et al. 2014). However, the individuals tracked by Trierweiler et al. (2014) were from a far more restricted breeding range than ours.

Some migratory tracks showed evidence of conspicuous detours, especially during desert crossing, in birds from all three populations. This is a common feature for raptors migrating across the Sahara, and constitutes a response to both local winds and large-scale atmospheric circulation patterns (e.g. Klaassen et al., 2010; Vansteelant, Shamoun-Baranes, Manen, Diermen, & Bouten, 2017). While a detailed analysis of the individual responses to weather conditions *en route* is beyond the scope of this study, previous studies of migratory raptors (including the lesser kestrel; Limiñana, Romero, Mellone, & Urios, 2013) have suggested that detours result from initial wind drift, which is subsequently partly offset by overcompensation flight path segments (Limiñana et al., 2013; Vansteelant et al., 2017). Wind circulation patterns over ecological barriers (Kemp, Shamoun-Baranes, Van Gasteren, Bouten, & Van Loon, 2010) suggest that birds experience intense westward crosswinds at the onset of spring migration south of the Sahara, which tend to displace them from their track direction (i.e. N-NE), whereas in autumn they can mostly fly with moderate eastward crosswinds over the Mediterranean, and mostly with tailwinds over the Sahara. Broad-scale seasonal wind patterns may thus explain the significantly lower track straightness and greater track length in spring than in autumn, and the fact that spring migration is considerably slower and longer-lasting (a feature shared by other raptors, see review by Schmaljohann, 2018). The few wide detours observed during autumn migration above the desert may result from occasional strong eastward winds.

4.3. Migratory connectivity, genetic population structure and population dynamics

The current genetic structure of animal and plant species has been strongly affected by the geographic location of Pleistocene glacial refugia (Hewitt, 2000; Schmitt, 2007). Within refugia, populations could have diverged in many traits (Schmitt, 2007), including migratory behaviour

(Turbek, Scordato, & Safran, 2018). Although glacial refugia of the lesser kestrel are not well defined (Finlayson, 2011), its current fragmented breeding range overlays the distribution of Eurasian refugia (Hewitt, 2000). The strong migratory connectivity we have found, coupled with high breeding philopatry (e.g. Alcaide, Serrano, Tella, & Negro, 2009), are thus expected to reduce gene flow and reinforce isolation (Webster et al., 2002). However, microsatellite analyses revealed only a weak genetic structuring among European lesser kestrel populations, with clear evidence for past, severe, and prolonged population bottlenecks (Bounas et al., 2018).

Our findings may provide a basis for future studies assessing the ecological drivers of European lesser kestrel population trends (e.g. Sherry, 2018). Ecological conditions in the non-breeding areas can significantly influence population trends and inter-annual survival of Afro-Palearctic migratory birds (Ockendon, Johnston, & Baillie, 2014; Beresford, Sanderson, Donald, Burfield, Butler, Vickery, & Buchanan, 2018). Non-overlapping migration routes and non-breeding distributions among birds breeding in different regions may led population trends of lesser kestrels breeding in different European regions to be differently affected by African climatic variability or by environmental changes taking place in different non-breeding areas and migration routes. The interannual rainfall variability of the Sahel area is known to affect population growth of lesser kestrels. High rainfall is associated with increasing population size (Morganti, Ambrosini, & Sarà, 2019), likely due to high invertebrate (mainly orthopteran) prey availability improving survival of first-year birds (Mihoub, Gimenez, Pilard, & Sarrazin, 2010). Variation in decadal rainfall trends over different sectors of the Sahel region, suggesting a change in the west-to-east rainfall gradient (e.g. Nicholson, Fink, & Funk, 2018), may thus variably influence population trends of the different European lesser kestrel populations.

4.4. Inter-population and sex differences in migratory behaviour

Apart from migratory routes, the migratory behaviour of birds from different breeding regions mainly differed because of migration distance, with birds from the Balkans making the longest migrations while those from Iberia making the shortest ones. The timing of migration was broadly similar in all three populations, although the onset of autumn migration was delayed among Italian birds and the onset of spring migration was earlier among Iberian ones. An earlier onset of migration by Iberian birds may be related to the more favourable ecological conditions in the non-breeding areas of the western Sahel compared to those of the central Sahel, which may trigger earlier departure and earlier arrival on the breeding grounds (e.g. Robson & Barriocanal, 2011), likely via positive effects on pre-migratory fuelling or body condition during the non-breeding season. Sex differences in migratory behaviour were weak, except for significantly later post-breeding migration onset of males compared to females, mostly evident among Italian birds, and significantly straighter migration in males. Delayed post-breeding male migration may be explained by sex differences in annual moult scheduling, as females start moulting when incubating, which males do to a much lesser extent (Podofillini et al., 2019). Sex differences in track straightness may reflect a sex-specific susceptibility to wind conditions during migration and/or sex differences in stopover behaviour (Morganti et al., 2011).

5. CONCLUSIONS

Our large-scale study unraveled the non-breeding areas and migratory routes of the core of the European lesser kestrel breeding population, highlighting that a strong spatial structuring, unrelated to population genetic structuring documented so far, is retained throughout the entire annual cycle. Long-distance migratory birds have suffered marked population declines in recent decades, which can be partly explained by their greater sensitivity to climatic and environmental changes occurring in breeding, migration, and non-breeding areas compared to year-round resident avian species (Sanderson, Donald, Pain, Burfield, & van Bommel, 2006; Møller, Rubolini, & Lehikoinen, 2008). However, assessing the relative importance of ecological conditions experienced during different annual cycle phases on population dynamics is a challenging task, due to the limited availability of detailed information on the spatio-temporal distribution of long-distance migrants (Sherry, 2018). Characterizing migratory connectivity is therefore a crucial step for elucidating the relative importance of spatially and temporally variable environmental conditions on different populations of migratory taxa, as well as for assessing the resilience of migratory species to spatially variable climatic changes.

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Biosketch

Maurizio Sarà is a zoologist based at the University of Palermo, with wide-ranging interests in the conservation and biogeography of Mediterranean vertebrates. **Diego Rubolini** is an ecologist at the University of Milano. He has broad interests in the ecology, evolution and genetics of avian migration.

Author Contributions: M.S., J.G.C. and D.R. conceived the study; all co-authors contributed to field data collection; M.S., S.B., S.P., U.M., J.G.C., P.P. and D.R. analysed the data; M.S. and D.R. wrote the manuscript with significant input from J.G.C., J.B., and U.M. All the authors reviewed the manuscript.

Conflict of interest

The authors declare no conflict of interest.

Data availability statement

The dataset used for the analysis of migratory connectivity is reported in Table S1.1. Datasets used for the analyses of migratory movements will be uploaded on Dryad once the manuscript is accepted for publication. Raw tracking data (from GLS, GPS-UHF, and Argos PTT devices) are available from the corresponding authors on request.

Table 1. Summary statistics of the migration phenology and migration speed of lesser kestrels from the three main European breeding regions. Mean values are shown together with their standard deviation (round brackets). Square brackets: minimum and maximum values, sample size (number of datapoints, number of individuals). For variables expressed as day of year, day 1 = January 1.

Variables	Breeding region		
	Iberia	*Italy*	*Balkan*
Post-breeding migration			
Onset (day of year)	261 (14) [232 – 297; 44, 41]	265 (10) [245 – 289; 36, 34]	263 (8) [249 – 279; 13, 11]
End (day of year)	273 (13) [251 – 313; 44, 41]	275 (10) [261 – 298; 36, 34]	276 (8) [260 – 287; 13, 11]
Duration (days)	12 (8) [3 – 38; 44, 41]	11 (4) [5 – 22; 36, 34]	14 (7) [7 – 29; 13, 11]
Speed (km/day)	373 (155) [177 – 670; 24, 21]	318 (91) [206 – 558; 13, 13]	423 (95) [266 – 535; 7, 5]
Pre-breeding migration			
Onset (day of year)	61 (17) [36 – 109; 35, 33]	75 (15) [34 – 114; 32, 30]	70 (10) [57 – 84; 12, 10]
End (day of year)	78 (21) [44 – 117; 34, 32]	94 (18) [50 – 133; 31, 29]	94 (13) [67 – 108; 9, 8]
Duration (days)	18 (12) [3 – 50; 34, 32]	20 (10) [8 – 44; 31, 29]	23 (13) [5 – 41; 9, 8]
Speed (km/day)	234 (114) [98 – 476; 20, 18]	246 (123) [141 – 476; 9, 9]	294 (286) [139 – 723; 4, 3]
Duration of stay in non-breeding area (days)	153 (24) [101 – 201; 35, 33]	166 (18) [123 – 210; 32, 30]	160 (14) [141 – 181; 12, 10]

Table 2. Summary statistics of migration track characteristics and minimum migration distance of lesser kestrels from the three main European breeding regions. The E-W deviation represents the deviation (in km) to the east (positive values) or west (negative value) of a track compared to the minimum migration distance line (orthodrome) (see paragraph 2.5). Mean values are shown together with their standard deviation (round brackets). Square brackets: minimum and maximum values, sample size (number of datapoints, number of individuals).

Variables	Breeding region		
	Iberia	*Italy*	*Balkan*
Post-breeding migration			
Track length (km)	3347 (386) [2545 – 3906; 25, 22]	3770 (547) [2936 – 4634; 13, 13]	3945 (307) [3546 – 4280; 7, 5]
Track straightness	0.86 (0.09) [0.7 – 0.96; 25, 22]	0.82 (0.1) [0.6 – 0.93; 13, 13]	0.85 (0.03) [0.82 – 0.9; 7, 5]
Longitude at 25° N (°)	-6.91 (4.71) [-12.07 – 3.41; 25, 22]	9.6 (5.08) [2.5 – 22.77; 13, 13]	21.54 (4.6) [16.89 – 29.85; 7, 5]
E-W deviation (km)	17 (182) [-302 – 401; 25, 22]	175 (257) [-79 – 863; 13, 13]	334 (153) [37 – 501; 7, 5]
Pre-breeding migration			
Track length (km)	3661 (506) [2854 – 4716; 20, 18]	4203 (586) [3479 – 5219; 9, 9]	4339 (696) [3616 – 5143; 4, 3]
Track straightness	0.80 (0.09) [0.63 – 0.94; 20, 18]	0.75 (0.09) [0.63 – 0.88; 9, 9]	0.83 (0.10) [0.72 – 0.96; 4, 3]
Longitude at 25° N (°)	-9.22 (4.22) [-14.68 – -2.71; 20, 18]	5.34 (4.5) [0.37 – 14.4; 9, 9]	18.04 (6.61) [9.94 – 26.12; 4, 3]
E-W deviation (km)	-134 (214) [-477 – 217; 20, 18]	-210 (221) [-497 – 199; 9, 9]	-59 (320) [-461 – 271; 4, 3]
Minimum migration distance (km)	2946 (350) [2107 – 3639; 45, 42]	3098 (261) [2413 – 3570; 36, 34]	3481 (236) [3045 – 3812; 13, 11]

Table 3. Linear mixed models of the effects of breeding region and sex on migration onset/end, duration of stay in non-breeding area, and minimum migration distance of European lesser kestrels. Denominator degrees of freedom for F-tests were estimated according to the Kenward-Roger's approximation. Raw mean values for each region are shown in Tables 1 and 2. Estimated marginal means (EMMs) are reported (with associated standard errors) for statistically significant effects; region abbreviations: IB = Iberian, IT = Italian, BA = Balkans; sex: F = female, M = male. Different superscript letters associated with EMMs denote statistically significant comparisons ($p < 0.05$) from *post hoc* tests. Two-way interactions were not significant (all p-values > 0.08) and were removed from the models.

Predictors	F	d.f.	p	EMM
Post-breeding migration onset				
Breeding region	4.07	2, 81	0.020	IB: 264 (5)^{a}; IT: 271 (5)^{b}; BA: 262 (5)^{ab}
Sex	5.99	1, 81	0.017	F: 262 (4); M: 269 (5)
Post-breeding migration end				
Breeding region	6.12	2, 79	0.003	-
Sex	5.47	1, 79	0.022	-
Breeding region × sex	4.17	2, 80	0.019	F - IB: 274 (5)^{a}; IT: 275 (5)^{a}; BA: 272 (5)^{a} M - IB: 274 (5)^{a}; IT: 293 (6)^{b}; BA: 277 (8)^{ab}
Pre-breeding migration onset				
Breeding region	7.17	2, 68	0.001	IB: 61 (4)^{a}; IT: 75 (5)^{b}; BA: 74 (6)^{ab}
Sex	0.01	1, 68	0.99	-
Pre-breeding migration end				
Breeding region	7.01	2, 64	0.002	IB: 78 (5)^{a}; IT: 96 (6)^{bc}; BA: 98 (8)^{c}
Sex	0.19	1, 65	0.66	-
Duration of stay in non-breeding area				
Breeding region	2.17	2, 68	0.12	-
Sex	0.83	1, 68	0.37	-
Minimum migration distance				
Breeding region	10.57	2, 82	< 0.001	IB: 2960 (50)^{a}; IT: 3104 (55)^{a}; BA: 3452 (95)^{b}
Sex	0.09	1, 82	0.76	-

Table 4. Linear mixed models of the effects of breeding region, season and sex on migration duration, speed and track characteristics of European lesser kestrels. Denominator degrees of freedom for F-tests were estimated according to the Kenward-Roger's approximation. Raw mean values for each region/season are shown in Tables 1 and 2. Estimated marginal means (EMMs, accounting for other model effects) are reported (with associated standard errors) for statistically significant effects; region abbreviations: IB = Iberian, IT = Italian, BA = Balkans; season: POB = post-breeding; PRB = pre-breeding. Different superscript letters associated with EMMs denote statistically significant comparisons ($p < 0.05$) from *post hoc* tests. Two-way interactions were not significant (all p-values > 0.10) and were removed from the models.

Predictors	F	d.f.	p	EMMs
Duration				
Breeding region	0.76	2, 71	0.47	-
Season	36.05	1, 92	< 0.001	POB: 13 (1); PRB: 20 (1)
Sex	0.01	1, 61	0.91	-
Speed				
Breeding region	2.02	2, 29	0.15	-
Season	16.39	1, 45	< 0.001	POB: 376 (44); PRB: 255 (46)
Sex	0.96	1, 35	0.33	-
Track length				
Breeding region	4.15	2, 36	0.024	IB: 3547 (90)^a; IT: 3918 (141)^a; BA: 4020 (212)^a
Season	17.23	1, 41	< 0.001	POB: 3644 (88); PRB: 4012 (98)
Sex	3.48	1, 34	0.07	-
Locations/day	0.41	1, 46	0.52	-
Track straightness				
Breeding region	0.93	2, 34	0.40	-
Season	9.78	1, 44	0.003	POB: 0.85 (0.01); PRB: 0.79 (0.02)
Sex	5.94	1, 34	0.020	F: 0.80 (0.01); M: 0.85 (0.02)
Locations/day	0.28	1, 42	0.60	-
Longitude at 25° N				
Breeding region	123.72	2, 33	< 0.001	IB: -7.9 (0.8)^a; IT: 7.7 (1.1)^b; BA: 19.7 (2.0)^c
Season	9.43	1, 43	0.004	POB: 8.0 (0.8); PRB: 5.0 (1.0)
Sex	0.35	1, 34	0.56	-
E-W deviation				
Breeding region	2.45	2, 29	0.10	-
Season	23.70	1, 46	< 0.001	POB: 146 (37); PRB: -103 (43)
Sex	1.44	1, 34	0.24	-

Figure legends

Figure 1. Migratory connectivity of lesser kestrels from the three main European breeding regions (Iberia, yellow lines; Italy, green lines; Balkans, blue lines). Lines connect breeding sites (white dots) and non-breeding areas (see Methods). The current European breeding distribution range is shown in blue-green, whereas the dark-grey areas show the non-European breeding range (modified from Iñigo & Barov, 2010 and http://datazone.birdlife.org/species/factsheet/lesser-kestrel-falco-naumanni/distribution, accessed March 2019). Sample size per region (number of individuals and number of connections): Iberian, n = 42 and 45; Italian, n = 34 and 36; Balkan, n = 11 and 13.

Figure 2. Boxplot of the population spread (pairwise distances between non-breeding areas of individuals from the same breeding region) of European lesser kestrel populations (sample size per region: Iberian, n = 42 individuals; Italian, n = 34; Balkan, n = 11). The midline shows the median value and the box the interquartile range, whereas whiskers are computed as 1.5 × interquartile range, and dots represent the outliers.

Figure 3. Post-breeding (upper panel) and pre-breeding (lower panel) migration tracks of lesser kestrels from the three main European breeding regions (Iberia, yellow lines; Italy, green lines; Balkan, blue lines). The horizontal dashed line denotes the 25° N parallel. Sample size per region (number of individuals and number of tracks recorded by solar-powered satellite tracking devices): post-breeding migration, Iberian, n = 22 and 25; Italian, n = 13 and 13; Balkan, n = 5 and 7; pre-breeding migration: Iberian, n = 18 and 20; Italian, n = 9 and 9; Balkan, n = 3 and 4.