ORIGINAL ARTICLE

Spatio-temporal migratory patterns, habitat crossing and within-individual movement repeatability of Central Mediterranean European Rollers *Coracias garrulus*

Flavio Monti[1] · Sebastian Cannarella[2] · Davor Ćiković[3] · Vesna Tutiš[3] · Jelena Kralj[3] · Carlo Catoni[2] · Sanja Barišić[3]

Abstract

Populations of long-distance migratory species may exhibit dissimilarities in the leeway of scheduled annual migration programs, the routes they follow and their convergence at ecological barriers. The aim of this study was to fill the current geographical gap, spanning over 1,100 km longitudinally between southern France and eastern Austria, in the pan-European assessment of the migration ecology of the European Roller *Coracias garrulus*, and contribute to completing the puzzle of spatio-temporal patterns of migration, stopover and wintering at the Western-Palearctic scale for this species. We utilized high-resolution GPS tracking data from adult Rollers breeding in Italy and Croatia, tracked on their intercontinental seasonal journeys between 2018 and 2022 and modelled the variation of migratory components both at individual and population levels. Rollers from the Central Mediterranean exhibited a clockwise spring migration loop, following a Central African migration route and wintering across a wide longitudinal belt spanning from Namibia to Mozambique. Northern savannah zones were used as long stopovers, both in autumn (Chad/Sudan) and spring (Central African Republic/Cameroon). The probability of movement was significantly higher during the night and in spring. Migration speed varied according to season (> in spring) and the habitat crossed (sea > desert > rainforest > savannah). Individuals tracked in successive years showed high consistency of key migratory parameters and partial winter home ranges overlap, in contrast with the large variability of migratory parameters at the population level. This work bridges the current geographical gap of Roller migration ecology at the European level and helps meet conservation needs at the scale of the species' flyway, with new ecological information valuable for the implementation of International Single Species Action Plans (ISSAP) dedicated to the Roller.

Significance statement

Tracking studies help to disentangle intraspecific variation in migratory strategies and wintering destinations among populations, as well as investigate individual-level decisions taken *en route* across seasonal journeys. By GPS tracking the intercontinental migration of adult Rollers we found that spatio-temporal components of migratory and flight strategy largely depend on extrinsic factors such as daytime, season and the habitat they traversed, and vary at population level. In contrast, within-individual consistency in migratory and wintering patterns emerged across years. Our findings emphasize the need for effective conservation strategies at the flyway scale.

Introduction

Migratory landbird species have suffered and are still experiencing serious population declines (Sanderson et al. 2006; Vickery et al. 2014). The new European Breeding Bird Atlas (EBBA2; EBCC 2022), a comprehensive dataset providing the most up-to-date information on the distribution and abundance of birds in Europe, shows a drastic reduction

in the distribution and size of populations of many species since the 1980s. This process did not occur evenly, with change patterns varying across biogeographic regions. For example, a net loss of species has been documented particularly in the Mediterranean, which was the most affected region. To effectively conserve migratory landbird populations during the full annual cycle, it is important to identify limiting factors and potential drivers that influence population dynamics at various spatial and temporal scales (Newton 2004; Marcacci et al. 2023). To address this point, it is essential to have in-depth knowledge of their spatio-temporal distribution throughout the year, since migratory birds rely on widely separated sites. Most of the Western-Palearctic migratory landbirds spend over half of the year travelling and wintering in Africa (Zwarts et al. 2009, 2023). Only by operating at the entire flyway scale through international cooperation and shared commitment could allow for targeting long-lasting conservation outcomes, to secure the future of migrant landbirds (e.g., AEWA; Marcacci et al. 2023). The first step towards this goal is to clearly identify birds' migratory routes, key staging sites attended *en route* across seasonal journeys as well as their breeding and wintering grounds (e.g., Jiguet et al. 2019a, b). Different populations of the same species may express dissimilarities in the leeway of scheduled annual migration programs, face different conservation threats and/or have particular requirements at non-breeding quarters (e.g., Rodríguez-Ruiz et al. 2019). Thus, tracking studies are necessary to investigate intraspecific variation in migratory patterns and wintering destinations among populations (Finch et al. 2015, 2017), as well as to assess their migratory connectivity (i.e. the the degree to which individuals from the same breeding site migrate to the same wintering site; Webster et al. 2002; Trierweiler et al. 2014). All this information aids in detecting threats and areas of high conservation concern for the species within its distribution range. Moreover, information gathered at the population level plays a significant role in the development, and regular update of International Single Species Action Plans (ISSAPs), aimed at *i*) producing practical conservation recommendations for target species at the flyway scale (e.g., Kovacs et al. 2008; Brown 2015; Fisher et al. 2018; Kiss et al. 2020) and *ii*) ultimately leveraging connections with decision-makers and stakeholders to implement evidence-based conservation plans into legislation (e.g., Marcacci et al. 2023).

A recent pan-European assessment of migratory strategies of a near-threatened declining long-distance migrant, the European Roller *Coracias garrulus* (hereafter "Roller"), revealed weak to moderate migratory connectivity and differences in migratory patterns between Roller populations from eight countries along a longitudinal gradient, from Portugal to Cyprus (Finch et al. 2015). This and previous studies (Emmenegger et al. 2014; Catry et al. 2014; Rodríguez-Ruiz

et al. 2014) showed how Rollers from different breeding populations partially mix during the non-breeding season, with wintering grounds located across a wide belt within the Greater African subequatorial savannas and mixed woodlands bioregion. To get there, individuals follow different migratory routes, depending on their breeding sites. Individuals from different populations exhibit as well a variation in the orientation of the migratory direction, having clockwise (e.g. spring migration displaced to the west compared to autumn migration) or counterclockwise (*vice versa*) loop migration (Finch et al. 2015).

As data were not available at that time, some Roller populations from the Central-Mediterranean area, namely from the Italian peninsula and Balkan countries, were not included in the pan-European assessment, resulting in a broad geographical gap spanning over 1,100 km longitudinally between southern France and eastern Austria. These populations, like many others in Europe, experienced drastic declines in the past but are now gradually recovering thanks to proactive management actions (e.g., Barišić et al. 2018; Monti et al. 2019). As part of a long-term monitoring program, GPS tracking devices were fitted to adult Rollers breeding in Italy and Croatia since 2018 to collect information on their movement ecology throughout the annual cycle. This study aims to fill the current geographical gap in knowledge and contribute to completing the puzzle of spatio-temporal patterns of migration and wintering of Rollers at the Western-Palearctic scale. Specifically, we were interested in investigating the orientation of the migratory direction, identifying new routes across Africa and detecting any specificities in terms of migration speed, stopover patterns and habitat use across seasons. Here, we present a detailed analysis of migration patterns and wintering ecology of central-Mediterranean Rollers, by GPS tracking the intercontinental migration of adult Rollers from Italy and Croatia. We also analyse migration and flight strategy across habitats, home range estimates in winter and first data on within-individual repeatability in migratory and wintering patterns.

Materials and methods

Capture and tracking techniques

Between 2018 and 2021, we trapped 24 adult Rollers (13 in Italy and 11 in Croatia) in their nest-boxes during the incubation or nestling period (May–June). For 11 individuals (Italy: 6 males; Croatia: 3 females and 2 males), we were able to gather migration and wintering data the following year, upon their return to the breeding grounds, using a base station that allows automatic wireless radio downloading. It was not possible to record data blind because our study

involved focal animals in the field. In Italy, we tagged Rollers with 3.5 g GPS loggers Gipsy-Remote XS (Technosmart Europe srl, Rome, Italy), while in Croatia, we used NanoRadio Tag-3 (Milsar Technologies, Cluj, Romania) of the same weight/size. Loggers were mounted as a backpack harness (i.e. looped around the bird's wings, with loops crossing on the sternum, and the device positioned on the animal's back) using a 2-mm-wide Teflon harness. The mass of the tracking device never exceeded 3% of the bird's body mass (percentage of body mass range: 2.2–2.8%, mean body mass 144.94 ± 11.47 g SD; $n = 20$). Each bird was measured and ringed with a metal ring in Italy and with both metal and plastic rings (black with yellow 3-letter inscription) in Croatia. We assessed the sex of the bird by visual inspection of morphological characters, which in the case of Italian birds, was confirmed by molecular analyses (e.g., Griffiths et al. 1998). Devices were programmed to collect daytime GPS position every 30 min and provided data on instantaneous flight speed (m/s) and altitude (m above ground level). However, the frequency of acquisition of the positions varied according to the state of the battery, sometimes resulting in non-uniform daily relocations and depending on individual birds and periods (Supplementary file1: Table S1).

Tracking data processing

GPS positions were imported into QGIS (v. 3.6.1) and projected to the Universal Transverse Mercator (UTM) coordinate system for all spatial analyses. Following Limiñana et al. (2008) and Rodríguez-Ruiz et al. (2014), the onset of autumn and spring migration was defined as an abrupt change in movement patterns and indicated by a southward (or northward) movement of > 100 km/day without a return flight towards the north (or the south), in autumn and spring respectively (for further details see Rodríguez-Ruiz et al. 2014, 2019; Berger-Geiger et al. 2022). Following Rodríguez-Ruiz et al. (2014), the end of autumn migration was identified as the day when the bird stopped displacement of > 100 km/day for longer than 10 days, after crossing the Equator. The end of spring migration was defined as the first GPS position at the destination (breeding area), as Rollers arriving at the breeding grounds usually do not prospect around, but rather show restricted movements in the immediate surroundings of about a 1 km radius, of the area subsequently used for breeding (Monti et al. 2023). A stopover site during migration was defined as an area where a bird displaced less than 20 km in at least 24 h, following Strandberg et al. (2008) and Rodríguez-Ruiz et al. (2014). We also separated track segments travelled in different geographic areas through QGIS Geoprocessing Tools to extrapolate instantaneous flight speed (converted to km/h) and altitude information of GPS locations over different habitat matrices during migrations. According to the major terrestrial

ecoregions (source: https://geospatial.tnc.org/; Fig. 1), we distinguished between the following habitats: sea, desert, Northern savannah (north of the Equator), rainforest and Southern savannah (south of the Equator).

For the winter period, individual home ranges and core areas were estimated for each bird as the 95% (hereafter "HR") and 50% (hereafter "CA") Utilization Distribution (UD) respectively, using the fixed kernel density estimation (KDE) with reference bandwidth (*href*) in the R package *adehabitatHR* (Calenge 2006). As an alternative metric for literature comparison, we also computed the Minimum Convex Polygon (MCP) encompassing all GPS locations obtained for each bird (Worton 1989). Overlap analyses of each individual's space use estimate (HR, CA and MCP) between consecutive years were run through QGIS Geoprocessing Tools. To infer the overlap of wintering grounds between populations (Croatia *vs* Italy), we computed population-level MCPs encompassing the winter locations of each individual belonging to the same population and then calculated the overlap percentage of the generated MCPs between the two populations.

Statistical analyses

Due to the limited sample size and the non-normal distribution of data for certain parameters, non-parametric tests were used. In particular, to investigate differences between populations in migration timing (onset of autumn and spring migration), duration and stopover use we used the non-parametric independent 2-group Mann–Whitney U test. Differences between migration seasons (autumn and spring) in distance travelled and total duration, number of stopovers and duration of stay, were tested with two-tailed Wilcoxon signed rank tests, on complete journeys only. In these cases, to avoid pseudoreplication related to repeated journeys by the same individual, we arbitrarily selected the first migratory track per individual, for each season. Data are reported as mean $\pm$ standard deviations (SD).

To investigate migratory strategy, we analyzed movement activity data using generalized linear mixed models (GLMMs; Zuur and Ieno 2016). The analyses were conducted in two steps. First, we wanted to explore whether Rollers exhibited seasonal or daily variation in movement activity. For this purpose, we distinguished between stationary (instantaneous flight speed < 5 km/h) and travelling (instantaneous flight speed > 5 km/h) GPS locations. These were categorized based on the daytime period. We distinguished between "day" (from 6:00 to 18:00) and "night" (from 18:00 to 6:00) since sunrise and sunset oscillate around 6:00 and 18:00 respectively, across the route and seasons (NOAA Solar Calculator: https://gml.noaa.gov/grad/solcalc/), thus including transitory light conditions in both categories. A preliminary data exploration suggested that

Fig. 1 Migratory routes of Central-Mediterranean European Rollers. Tracks recorded by GPS loggers between breeding sites in Italy and Croatia and the wintering grounds in southern Africa. White and yellow dots are for GPS locations during autumn and spring migrations, respectively. Black and red lines represent autumn and spring migration tracks, respectively. Blue triangles and the white-shaded polygon show wintering GPS locations and MCP at the population level, respectively. The base map represents the major terrestrial ecoregions (source: https://geospatial.tnc.org/): main habitat categories as follows: desert and xeric scrubland in pink, tropical and subtropical grasslands, savannas and shrublands in light green, tropical and subtropical moist broadleaf forest in green, flooded grasslands and savannas in light yellow, Mediterranean forests, woodlands and scrub in pale orange, temperate broadleaf and mixed forests in light blue, and white for seas. The Roller is by Alessandro Troisi ©
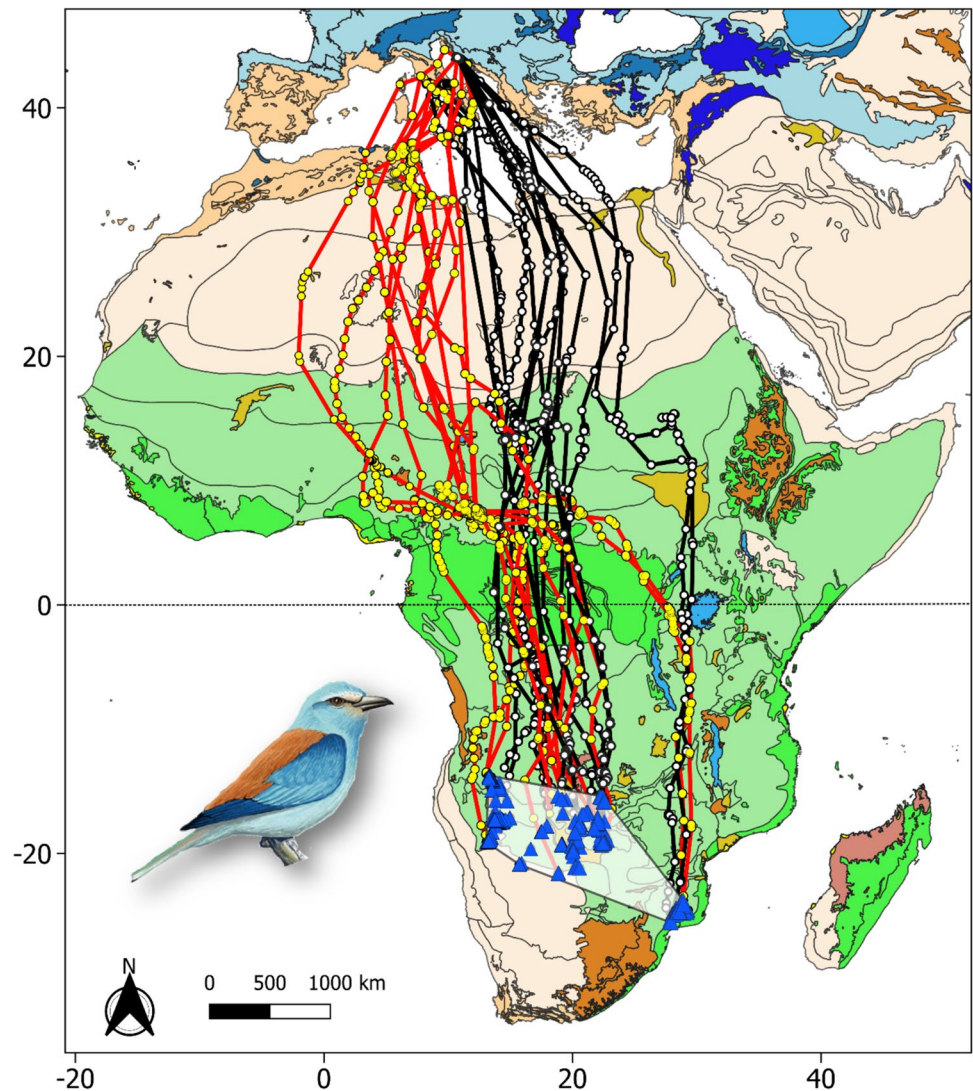
multicollinearity was found between daytime and habitat type (r <|0.5|). For this reason, these two predictor variables were tested in separate models. The probability of activity (stationary = 0 *vs* travelling = 1) was set as the response variable and modelled in relation to daytime (categorical: day vs night) and season (categorical: autumn *vs* spring) and their interaction, with a binomial distribution (link: logit) (Zuur et al. 2009).

Then, we focused on the subset of "travelling" locations and fitted models to investigate the general differences in instantaneous flight speed values across different habitats (categorical: sea; desert; Northern savannah; rainforest; Southern savannah) and seasons, without their interaction due to multicollinearity (r >|0.5|) of these two predictors. Speed was modelled with tweedie errors, as it is customary with continuous, 0 + variables. In all models, we included 'individual' as a random effect. For each model set, we fitted candidate models comprising all potential combinations of predictors, including also the null model, because each combination could represent a distinct a priori hypothesis. The model selection used Akaike's Information Criterion corrected for small sample sizes (AICc). Models were selected if they had ΔAICc ≤ 2, and if their AICc value was lower than that of any simpler alternative (Harrison et al. 2018). Therefore, we obtained either a set of top-ranked models or a single best model for each response variable. Inference about the effects of predictors was made using the best model: we estimated coefficients and 95% confidence intervals (CIs) of predictors, assessing whether 95% CIs overlapped "0" to identify informative predictors. GLMMs and model selections were performed in R 4.3.1, using the function *glmmTMB::glmmTMB* (Brooks et al. 2017) for fitting models and *dredge::MuMIn* (Bartoń 2020) for model selection. Best models were validated through visual inspection of residuals through the 'DHARMa' package (Hartig 2022).

Plots for the top-ranked models were obtained using package "effects" version 4.2–0 (Fox 2003; Fox and Weisberg 2019).

Regarding repeatability, as it can depend both on inter-individual variation and on levels of intra-individual consistency (e.g. individual consistency relative to other individuals; Patchett et al. 2022), we decided to investigate both within-individual repeatability and population variation in migratory components. Within-individual repeatability was tested for individuals tracked for two consecutive years ($n=6$ tracks from three males). In particular, we tested consistency in: i) departure date from the breeding site, ii) stopover duration and iii) number of stopover sites in both seasons, iv) total migration duration during both seasons, v) arrival date at the first wintering area and vi) arrival at the breeding site. We also tested for repeatability in the vii) latitude and viii) longitude of non-breeding locations, as well as ix) the total distance covered in both seasons. For timing components, departure and arrival dates were expressed as Julian days, calculated starting from 01 January of the same year. The latitude and longitude of winter locations were calculated as the median coordinates of the month of January when adult Rollers likely remain at a single location. For stopover evaluation (number of stops and total duration), we followed the definitions provided by Rodríguez-Ruiz et al. (2014). All repeatability models were run using the "*rpt*" and its functions of the R package "*rptR*" (Nakagawa and Schielzeth 2010), which provided mean ($\pm$ SE) R estimates, 95% confidence intervals obtained from 1000 bootstrap iterations and p-values. This package uses a linear mixed model framework where the groups compared for repeatability are specified by a random effect (i.e., in this case, we used the individual as a random intercept). Confidence intervals were estimated within the *rpt* function by running 1000 bootstraps. The significance of repeatability was estimated by a likelihood ratio test within the *rpt* function (Nakagawa and Schielzeth 2010). As in other studies, the sample size of the repeated individual tracks was low, thus we approach results with caution (e.g., Wellbrock et al. 2017; Patchett et al. 2022).

As pointed out by Patchett et al. (2022) in their study on repeatability in migratory components of Cyprus wheatears *Oenanthe cypriaca*, it is important to provide levels of variation at the population level to investigate individual consistency relative to other individuals. Accordingly, we report separate estimates of the migratory components for the Italian and Croatian Rollers, but also for the Central Mediterranean Roller population (by pooling the two datasets). Specifically, we calculated the range between the minimum and maximum values for each migratory component as a descriptor of population-level variation, as well as the mean, standard deviation and median for each parameter. This approach was also applied to arrival at wintering grounds and spring departure and arrival.

Results

Our final dataset comprised fourteen tracks of autumn migration and thirteen of spring migration, along with thirteen wintering events, provided by eleven individuals (5 birds from Croatia and 6 from Italy; Table S1). Three birds (two males from Croatia and one from Italy) were tracked for two consecutive years, thereby providing multiple seasonal tracks (Table S1). In total, this equated to six tracks of repeatedly tracked males. The GPS data collection of the device of a bird (#KA2377) ceased at some point in the second year, during the spring migration, allowing only a partial analysis of this track. Similarly, GPS data collection of another bird (#H212223) stopped during its autumn migration, thus providing an incomplete track and hampering the detection of its wintering locality as well as the spring migration route. All birds exhibited a clockwise (westerly) spring loop (Fig. 1; Table S1). The mean longitudinal difference between autumn and spring routes was -6.96 $\pm$ 3.4° (range from -13.7° to -3.6°) and did not differ between populations (Independent 2-group Mann–Whitney U test: U $=$ 11.5; $P=$ 0.832; $n=10$).
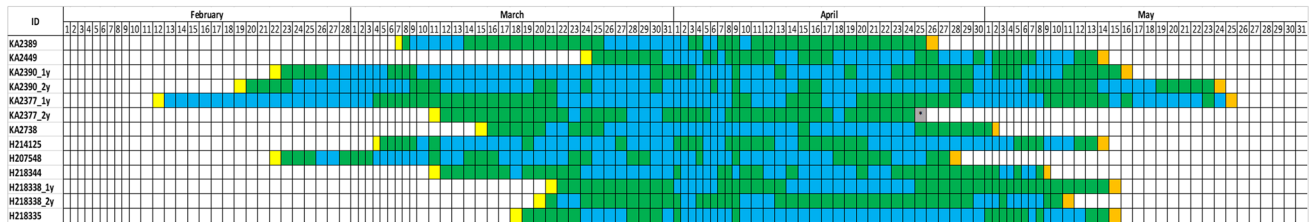
Autumn migration

All Rollers commenced their autumn migration in September (range: 01/09–20/09), with 81.8% initiating within the first decade of the month. Birds followed an eastern route in autumn compared to spring (clockwise) across the Mediterranean Sea, the Sahara desert, the rainforest of central Africa to their wintering grounds located in southern Africa. Rollers crossed the Mediterranean Sea at various crossing points, reaching Africa between Libya and Egypt. On the southbound migration, all birds made use of several stopovers (mean number: 4.5 $\pm$ 1.8 stops). Time spent at stopover was on average 46.7 $\pm$ 14.6 days and represented ca. 63% of the total autumn migration duration. In one case, a Croatian Roller had short consecutive stops in Greece a few days after migration started, while two Italian Rollers stopped for less than one week in Libya. All birds made a protracted stop in Sahelian sub-Saharan savannah habitats in Chad or Sudan, usually between the second half of September and October (Fig. 2). Subsequently, after crossing the tropical rainforest of central Africa, Rollers made several shorter stops in sub-Saharan Africa in November while approaching their final winter destination (Fig. 2a). The total migration distance (including stopovers) covered in autumn was lower (7670 $\pm$ 417.3 km; $n=10$) than in spring (8497.5 $\pm$ 670.4 km; $n=10$). More specifically, the mean total migration distance for Croatian rollers was 7831.2 $\pm$ 442.6 km in autumn and

a)
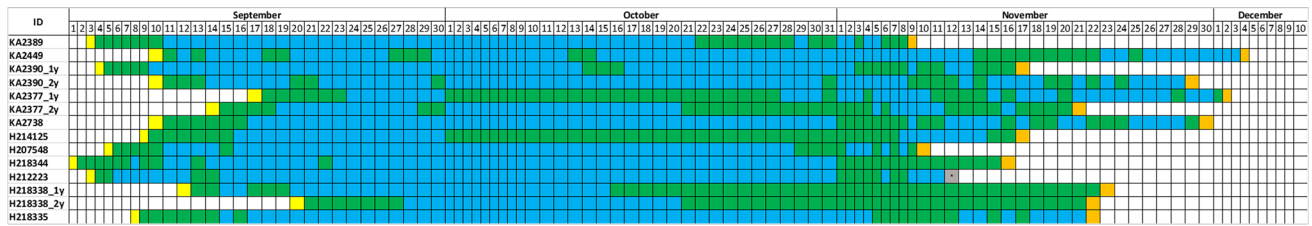
b)

Fig. 2 Migration phenology of Central Mediterranean Rollers tracked with GPS loggers between 2018–2022. **a**) Autumn migration phenology and **b**) spring migration phenology. The onset of migration (yellow), travel days (green), stopovers (blue) and arrival at winter and/or breeding grounds (orange) are represented for each individual (ID column). Grey squares with an asterisk indicate cases of GPS tracking ceasing, thus providing incomplete data. For individuals tracked over consecutive years, the year of reference is reported (1y = first; 2y = second)

8539.4 ± 685.2 km in spring, while for Italian rollers was 7508.9 ± 362 km and 8455.6 ± 7733.1 km in the same seasons, respectively. These differences were significant between seasons (Wilcoxon signed rank test: $Z = -2.599$, $p = 0.009$, $n = 10$), but not between populations (independent 2-group Mann–Whitney U test: $U = 40$; $P = 0.45$; $n = 20$).

Winter

Rollers arrived at their winter destinations between November and December (range: 02/11–04/12; Table S1; Fig. 2a). Winter quarters were predominantly situated in central-southern Africa, mostly between Botswana, Zambia and Zimbabwe, for individuals from both populations (Figs. 1, 3), but also in Angola-Namibia and Namibia-Botswana. A Croatian Roller (#KA2390) ended up in Mozambique for two consecutive years, representing the easternmost wintering locality of this study. In both years, this bird followed an extremely eastern autumn route but in spring exhibited a large longitudinal spread, following a route across central Africa, consistent with other Central-Mediterranean Rollers (Table S1).

The mean loxodromic distance between nest sites and the outermost location reached during the winter period was 7164.3 ± 2986.8 km. The winter range of tracked individuals (cumulative MCP of all locations) covered an area of $1,171,679.52$ km^2, spanning from $-14.7°$ to $-24.9°$ latitude and from $+16.4°$ to $+34.07°$ longitude (Fig. 3). Wintering grounds of Rollers from the two populations partially overlapped in northern Botswana (population MCPs overlap: 11.52%; Fig. 3), with two Italian and four Croatian Rollers wintering there. However, without including the individual wintering in Mozambique, this overlap rises to 17.89%. Individual home range sizes varied among individuals (Table 1). On average, home ranges and core areas were 92458.3 ± 143961.8 km^2 and 21529.3 ± 33994.8 km^2, respectively. The mean MCP was 22026.6 ± 33994.8 km^2. The winter period lasted approximately three and a half months (mean: 108.3 ± 8.3 days).

Spring migration

There was considerable variation among individuals in the onset of spring migration (Table S1). Departure from wintering locations occurred between 12/02 and 24/03 (Fig. 2b). During northbound migration, birds followed a western route compared to autumn. Initially, this migratory bout resembled that of autumn migration. After crossing the rainforest, birds made a slight westward directional shift to reach savannah habitats between the Central African Republic and Cameroon and/or Nigeria (Fig. 1). There, Rollers made repeated stops in various areas over ca. 25 days, between March and April (Fig. 2b). Subsequently, birds embarked on crossing over the two major ecological barriers, the Sahara desert and the Mediterranean Sea. Although the Mediterranean Sea was crossed from different points (along the coasts of Algeria, Tunisia and Libya), six out of ten individuals stopped in northern Tunisia (stopover duration range: 1–7 days), as the last stopover before embarking on the sea crossing. Rollers

Fig. 3 Locations of both Italian (white dots) and Croatian (red dots) Rollers, wintering in central-southern Africa. The solid line represents the total MCP encompassing all winter locations. The light red and withe MCPs are for Croatian and Italian Rollers' locations, respectively, while the green MCP indicates the common wintering areas (overlap: 11.5%) between the two populations. Names of the countries where GPS locations felt within are reported on the map
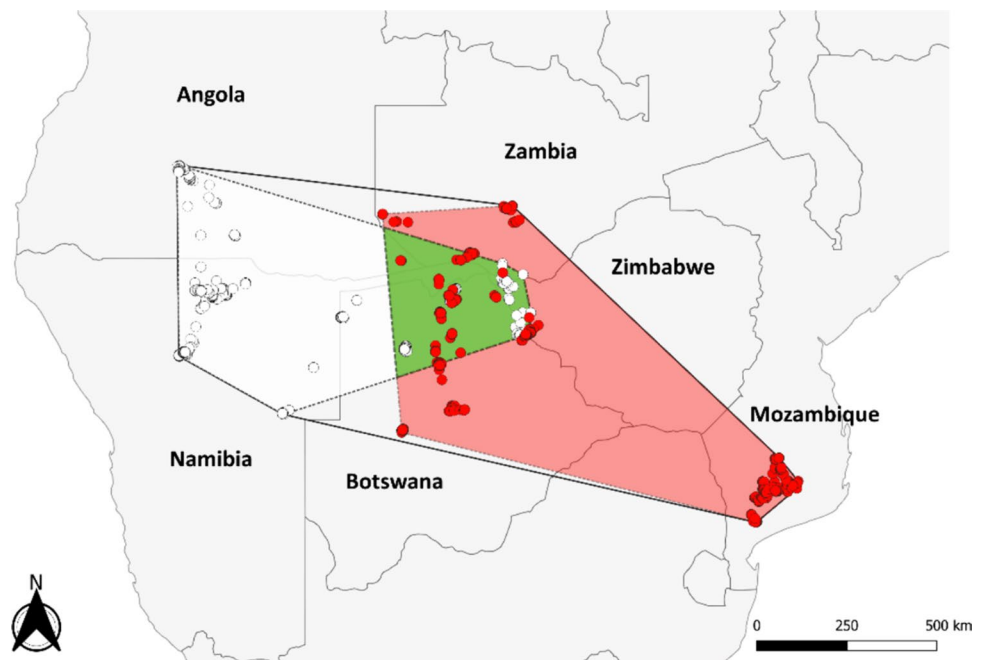
Table 1 Home range estimates of Central-Mediterranean European Rollers tracked between 2018–2022 and wintering in southern Africa. For each winter event is reported: the home range (UD 95%), core area (UD 50%), Minimum Convex Polygon (MCP) and the total number of fixes for the referred period (see Table 1). Estimates are reported in km² and for home ranges and core areas computed through the *adehabitatHR package* (Calenge 2006) with reference bandwidth (*href*)

ID	Home range	Core area	MCP	Number of fix
KA2389	300421	85245.7	58486.24	113
KA2449	27161.5	5475.1	4713.39	393
KA2390	21419.1	4872.9	9212.03	324
	11311.3	1899.5	7042.32	294
KA2377	844.2	204.0	1030.57	118
	488304.8	105903.7	101064.23	266
KA2738	454.9	79.5	351.71	205
H214125	33223.9	7733.9	4678.73	368
H207548	125205.4	25794.5	65072.06	1072
H218344	42376.6	8872.8	15378.67	117
H218338	21156.1	3757.7	4556.07	39
	30926.2	8526.8	9204.8	76
H218335	99152.7	21515.3	5555.36	277
Mean	*92458.3*	*21529.3*	*22026.629*	*281.7*
SD	*143961.8*	*33994.8*	*31773.0893*	*263.9*

arrived at their breeding quarters between the end of April and May (range: 26/04–24/05; Fig. 2b).

Overall, birds made slightly more stopovers in spring (mean number: 6.65 ± 2.3 stops) than in autumn, but the total time spent at stopovers (mean: 35.1 ± 15.5 days) was lower than in autumn, comprising ca. 54.6% of the total spring migration duration. Consequently, spring migration was faster than autumn migration, although neither the number nor the total time spent at stopovers differed significantly between the two migratory periods (Wilcoxon signed rank test; number of stops: $Z = -1.787$, $p = 0.074$, $n = 10$; stopover duration: $Z = -1.530$, $p = 0.126$, $n = 10$), nor between the two populations (Croatia vs Italy: Independent 2-group Mann–Whitney U test; number of stops: $U = 43.5$, $P = 0.619$, $N = 20$; stopover duration: $U = 37$, $P = 0.325$, $N = 20$). Total migration distance in spring did not differ between populations ($U = 12$, $P = 0.917$, $n = 10$).

Habitat crossing

Overall, we collected 7140 GPS locations (91.86% stationary and 8.14% travelling; Supplementary file2). The probability of movement was significantly higher during the night and in the spring season (Table 2; Fig. S1a: first model selection). Speed analysis revealed that Rollers travelled faster over sea and desert habitats, had intermediate speeds over rainforest habitats and exhibited lower values in savannah habitats, regardless of whether they were encountered north or south of the Equator. Rollers also travelled faster during the spring season (Table 2; Fig. S1b: second model selection). The maximum speed and altitude were reached over the desert at 113.4 km/h and 4,112 m a.g.l., respectively. Average speed estimates and mean altitude per habitat and daytime are provided in Table S2.

Table 2 Parameters estimated from top-ranked GLMMs predicting the probability of movement activity in relation to daytime and seasons (first model selection) and of speed values (km/h) in relation to overflown habitats and seasons (second model selection): variance of random intercepts (σ2), predictors' coefficient estimates (β), and their 95% confidence intervals (CIs). An asterisk marks coefficients whose CIs do not include "0"

Model ranknig	Response variable	Predictor	β coefficient	95% CI
1	Probability of movement activity $\sigma 2$ *Individual* $= 0.04388$ *(best model)*	Intercept	-3.065	-3.270; -2.859
		Day_night: night	1.003	0.822; 1.184*
		Season: spring	0.372	0.189; 0.554*
2	Probability of movement activity $\sigma 2$ *Individual* $= 0.04422$ *(second best model)*	Intercept	-3.049	-3.271; -2.827
		Day_night: night	0.977	0.744; 1.210*
		Season: spring	0.338	0.075; 0.602*
		Day_night: night * Season: spring	0.062	-0.292; 0.418
1	Speed $\sigma 2$ *Individual* $= 0.2688$ *(best model)*	Intercept	2.620	2.212; 3.028
		Habitat: N_savannah	-2.490	-2.769; -2.211*
		Habitat: rainforest	-0.804	-1.269; -0.338*
		Habitat: S_savannah	-1.602	-1.913; -1.291*
		Habitat: sea	0.98967	0.478; 1.500*
		Season: spring	0.37309	0.177; 0.568*

Within-individual repeatability and population variation in migratory components

Estimates of within-individual repeatability in migratory routes, timing and winter home ranges between consecutive winters were possible for only three males (two from Croatia and one from Italy; Fig. 4). However, in these repeatedly tracked Rollers, we found high consistency ($r > 0.8$; $p < 0.05$) in the total distance covered and related stopover duration in autumn (Table 3). The duration of spring migration and related time spent at stopovers were also highly repeatable. The repeatability index was significant for the longitude of the wintering ground as well (Table 3). Regarding the spring departure, a male postponed it by approximately one month

in the second year, while the other two males exhibited extremely high consistency for this parameter (Table S1). However, the duration of autumn migration and arrival at wintering sites were not repeatable ($r < 0.2$; $p = 1$), as these values differed between tracking years. It is important to note that these results should be regarded as provisional due to the extremely small number of individuals and journeys.

Regarding winter home ranges, birds were generally faithful to their wintering ground in all cases, returning to the same key area used in the previous year. However, they also explored different sites between years, as indicated by the relatively low mean home range overlap (overlap: $HR = 19.4 \pm 17.2\%$; $CA = 12.10 \pm 15.06\%$; $MCP = 15.73 \pm 14.2\%$; $n = 3$). This pattern was already
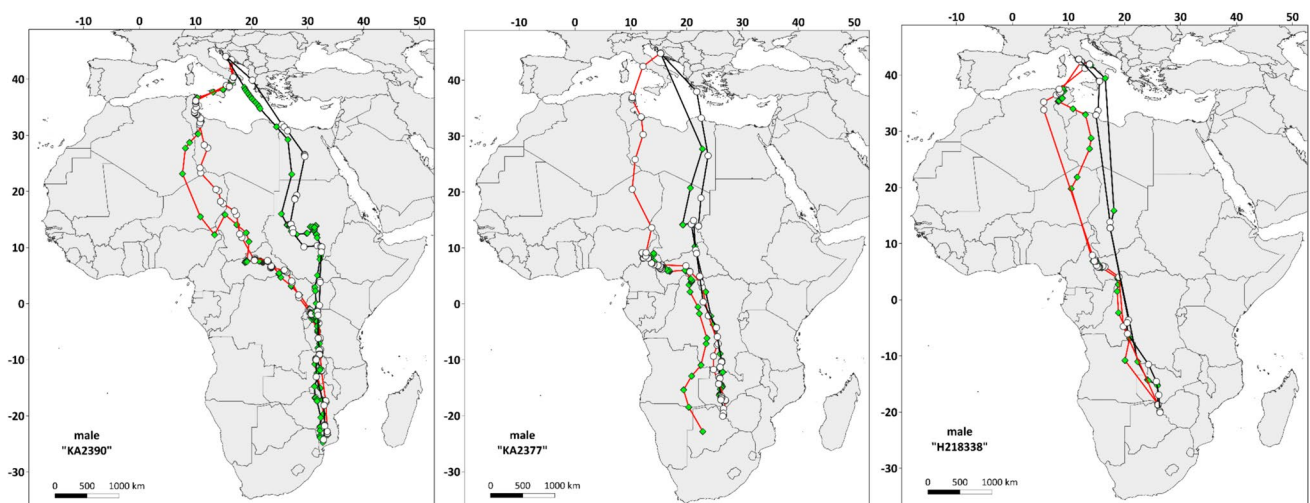
Fig. 4 Migration routes of three repeatedly tracked adult male Rollers. From left to right: "KA2390", "KA2377" and "H218338" (see Table S1). Black and red lines represent autumn and spring migration routes, respectively. White dots show GPS locations during the first year of tracking, while green squares during the second year. Spring migration of "KA2377" is interrupted in the second year of tracking (last fix on 25/04/2022). Latitude and longitude (at intervals of 10°) are reported on the left and upper side of each box, respectively

Table 3 Repeatability (r) of spatio-temporal migratory components for six tracks belonging to three adult European Rollers. The sample size is the number of individuals that were tracked for two consecutive years, expressed for each of the migratory components. The repeatability score r ranges from 0 to 1 with a score of 1 indicating high similarity between years. The p-value tests if r is significantly different from zero. Numbers in bold are significant. Repeatability estimates were computed using the R package "*rptR*" (Nakagawa and Schielzeth 2010), which provided mean ($\pm$SE) R estimates, 95% confidence intervals obtained from 1000 bootstrap iterations and *p*-values

Migratory component	N	Repeatability "Individual"			
		R	SE	CI	*p*
Departure_breeding	3	0.545	0.342	0–0.965	0.243
Arrival_winter	3	0	0.278	0–0.8721	1
Duration_autumn	3	0.199	0.322	0–0.923	1
Departure_wintering	3	0.567	0.345	0–0.967	0.226
Arrival_breeding	2	0.44	0.367	0–0.982	0.402
Duration_spring	2	0.941	0.227	0–0.945	**0.033**
Autumn_stop_dur	3	0.935	0.243	0–0.996	**0.012**
Spring_stop_dur	2	0.923	0.248	0–0.998	**0.035**
N_stop_autumn	3	0.481	0.342	0–0.956	0.29
N_stop_spring	2	0.7	0.367	0–0.991	0.143
Winter_Lat	3	0.754	0.33	0–0.982	0.099
Winter_Lon	3	0.908	0.247	0–0.995	**0.021**
Distance_covered_AUT	3	0.871	0.285	0–0.993	**0.036**
Distance_covered_SPR	2	0.659	0.361	0–0.999	0.158

evident when comparing individual home range estimates between years (Table 1).

At the population level, the timing of migration was considerably less variable in autumn than in spring (Table 4). Departures from breeding sites in autumn were confined to a period of 19 days (from 1st to 20th September), whereas departures from wintering sites in spring occurred over a total span of 40 days (from 12th February to 24th March). The corresponding figures for arrival dates at the wintering (in autumn) and breeding sites (in spring) were ca. 30 days, for each. Population variability in autumn migration duration spanned a period of 22 days (but less than 2 weeks in Italian Rollers). This variability was even higher in spring (54 days) at the population level, although it was mostly due to Croatian Rollers (for Italian Rollers, it was only 19 days). Population variability was also evident in stopover usage, both in terms of the number of stopovers and the time spent, in both autumn and spring (Table 4). In all cases, Croatian Rollers contributed more to these variability estimates than Italian Rollers, which, in contrast, exhibited reduced variation in the duration and timings of migratory components (Table 4).

Discussion

In the Western Palearctic, Rollers migrate through three major migratory flyways/routes: western, central and eastern, with populations expressing different clockwise or counterclockwise migration strategies (Finch et al. 2015). In the west, Rollers from the south and central Iberia (e.g., Portugal, central and southeast Spain) follow a westerly route along the Atlantic coast of West Africa (Catry et al. 2014; Rodríguez-Ruiz et al. 2014), while those from northeast Spain and southern France cross the Mediterranean Sea and fly directly across the Sahara desert (Emmenegger et al. 2014; Rodríguez-Ruiz et al. 2014). In the east, Rollers cross the Mediterranean Sea at various crossing points before entering Africa, following a central-eastern route (Finch et al. 2015). Our results show that Central Mediterranean Rollers migrate to Africa using a clockwise loop migration, via a central route passing through the Italian and/or Balkan Peninsula, entering Africa via Libya or Egypt then towards central Africa until sub-Saharan wintering grounds located in central-southern Africa. This route, which covers ~7000 km on average, is straighter than that followed by Rollers from the western Mediterranean (e.g., Catry et al. 2014). Previous studies showed how Rollers from Iberia adopt alternative strategies, including west–east detours to reach Lake Chad as a stopover in autumn. This detour is particularly pronounced for Portuguese and southwestern Spanish populations which enter Africa by following a western route along the Atlantic Coast (Catry et al. 2014; Rodríguez-Ruiz et al. 2014) before turning east towards Chad. Similarly, Rollers from southwestern France initiate their autumn migration heading in a straight southern direction, to then abruptly turn eastward once in the Sahelian zone to circumvent the Gulf of Guinea and reach the western Lake Chad basin (e.g., Emmenegger et al. 2014). In our case, we did not record any detour in autumn, as the migration routes of Central Mediterranean Rollers followed a straight southern direction, with important staging site located on the way.

At the European level, different populations show a variation in the orientation of the migratory direction, having clockwise or counterclockwise loop migration. From the west towards the east, the migratory pattern seems to reverse from counterclockwise to clockwise to counterclockwise. Populations from Portugal, central and southeast Spain show counterclockwise migration (Rodríguez-Ruiz et al. 2014; Finch et al. 2015). Eastward from approximately the prime meridian, populations show clockwise migration (NE Spain; Rodríguez-Ruiz et al. 2014; France, Austria and Montenegro; Finch et al. 2015). Further eastward from approximately 19°W, Rollers again show counterclockwise migration (Hungary and Romania: http://satellitetracking.eu; Latvia and Cyprus: Finch et al. 2015).

Table 4 Population variation of migratory components for adult Central Mediterranean Rollers. N is for the number of tracks providing data for the related parameter. Values from repeatedly tracked individuals were averaged before computing means and median at the population level. Range values include all data. Estimates are shown for the whole population and for Croatia and Italy, separately

Migratory component	Population	n	Population variation		
			Mean ± SD	Median	Range
Departure from the breeding site	all	14	09/09 ± 5	10/09	01/09–20/09
	Croatia	7	10/09 ± 5	10/09	03/09–17/09
	Italy	7	08/09 ± 6	09/09	01/09–20/09
Autumn stopover duration (d)	all	13	46.7 ± 14.6	51	22–65
	Croatia	7	52.1 ± 11.9	57	32–65
	Italy	6	41.3 ± 16.2	50	22–57
Autumn stopover number (n stops)	all	13	4.5 ± 1.8	5	1–9
	Croatia	7	6 ± 1.1	6.5	4–9
	Italy	6	3.5 ± 1.6	4	1–5
Arrival at the wintering site	all	13	22/11 ± 8	22/11	02/11–04/12
	Croatia	7	22/11 ± 9	29/11	02/11–04/12
	Italy	6	18/11 ± 5	19/11	10/11–25/11
Duration of autumn migration (d)	all	13	73.5 ± 6.3	73.5	63–85
	Croatia	7	76.4 ± 7.1	77	67–85
	Italy	6	70.7 ± 6.3	75	63–76
Total distance autumn migration (km)	all	13	7667.7 ± 543.4	7493.1	7165.5–9147.1
	Croatia	7	7831.5 ± 609.3	7611.8	7220.9–9147.1
	Italy	6	7503.8 ± 560.4	7473.3	7165.5–8119.1
Duration of wintering (d)	all	13	108.3 ± 8.3	109	82–118
	Croatia	7	105.6 ± 10.5	105.5	82–118
	Italy	6	111 ± 5.2	107	104–118
Departure from the wintering site	all	13	07/03 ± 13	11/03	12/02–24/03
	Croatia	7	04/03 ± 14	07/03	12/02–24/03
	Italy	6	11/03 ± 10	14/03	22/02–21/03
Spring stopover duration (d)	all	12	35.1 ± 15.5	34.5	15–64
	Croatia	6	37.6 ± 20.2	31	16–64
	Italy	6	32.6 ± 10.6	38	15–41
Spring stopover number (n stops)	all	12	6.65 ± 2.3	7.5	2–10
	Croatia	6	6.2 ± 2.5	7.5	3–10
	Italy	6	7.1 ± 2.3	8	2–9
Arrival at the breeding site	all	12	12/05 ± 9	15/05	26/04–25/05
	Croatia	6	13/05 ± 9	15/05	26/04–25/05
	Italy	6	10/05 ± 6	11/05	28/04–15/05
Duration of spring migration (d)	all	12	64.6 ± 17.9	58.5	48–102
	Croatia	6	68 ± 25.4	51	48–102
	Italy	6	61.3 ± 18.2	59	52–71
Total distance spring migration (km)	all	12	8582.8 ± 826.4	8398.6	7742.2–11,059.6
	Croatia	6	8708.1 ± 981.4	8726.2	7820.2–11,059.6
	Italy	6	8457.5 ± 730.9	8071	7742.2–9262.5

In this sense, we found that the southbound migration route for Central Mediterranean Rollers is similar and partially overlaps with that followed by eastern Roller populations in autumn (e.g., Hungary, Latvia and Romania), although in spring the former turns clockwise while the latter counterclockwise. Eastern Rollers migrate via Arabia in spring, across the Horn of Africa and along the Arabian Peninsula before returning to Europe (http://satellitetracking.eu; Finch et al. 2015). While Central Mediterranean Rollers turn westward in spring, crossing the Sahara in the vicinity of the Ahhagar mountains and finishing in Libya or Tunisia before sea crossing. The case of the Croatian Roller (#KA2390) wintering in Mozambique for two consecutive years represented the most eastern wintering locality recorded in our study. Based on our knowledge, Mozambique has not been previously recorded as winter quarters for Rollers breeding in Europe (http://satellitetracking.eu; Finch et al. 2015). In both years, the bird was consistent in

following the same routes in both autumn and spring. Even though this bird followed a more eastern autumn route, in spring it followed a route across central Africa, as all the other Central Mediterranean Rollers. This bird also stayed the shortest at the winter quarters in both years (Table S1). Based on the described migratory patterns, at least three Roller metapopulations should exist in Europe (e.g. Western/counterclockwise, Central/clockwise, Eastern/counterclockwise), with expected genetic structuring. However, the most recent work on Roller genetics (Nebel et al. 2018) recorded no substructuring within the European haplogroup, indicating possible extensive gene flow among populations in the past. Further studies to shed light on the possible underlying reasons for the difference in migration routes and loop systems are needed.

Departure for autumn migration occurred in a narrow time window (within the first decade of September) for most individuals, although ranges in departure dates spanned ~ 20 days at the population level. A previous study showed that the departure date of autumn migration in Rollers from Italy and Croatia was not influenced by the breeding outcome (success *vs* failure) (Monti et al. 2023), suggesting that despite more time available in the case of failed breeders, Rollers did not advance autumn migration, possibly because of stringent genetic traits related to departure dates. However, differences between breeding populations have been recorded. For example, Rodríguez-Ruiz et al. (2014) found interannual differences in departure dates, spanning from July to September, among three sampled populations in Spain. Similarly, Portuguese populations tended to depart earlier, in August (Catry et al. 2014), possibly to compensate for the long detour to reach the Lake Chad basin in time to exploit the trophic resource booms (e.g., high arthropod abundance) associated with seasonal rainfall patterns (e.g., Cox et al. 2011; Nwaogu et al. 2019). It should be noted that the majority of studied Rollers in the past were tracked via light-level geolocators, hence the possibility of greater uncertainty in location and date estimates compared to satellite-tracking data (e.g., Rodríguez-Ruiz et al. 2014). However, it seems that differences in departure dates are associated with sampled populations and, more importantly, with the migratory route followed. This latter point is central, as long-distance migratory bouts require long refuelling stages or frequent short stays to feed *en route* to compensate for energy expenditure associated with migration (e.g., Alerstam 1993). In the case of Central Mediterranean Rollers that, after departure, have to cope with the crossing of two consecutive large ecological barriers such as the Mediterranean Sea and the Sahara desert, the feeding *en route* option is not possible. Western Rollers crossing Gibraltar and following a coastal route may adopt this strategy, thus departing earlier in July and August, as already suggested by Rodríguez-Ruiz et al. (2014). Central Mediterranean Rollers instead have to

delay the onset of autumn migration, probably to increase fuel stores in preparation for such demanding crossings.

Regarding the use of stopovers in autumn, our results are in line with previous studies and further confirm the importance of tropical and subtropical grassland habitats of Central Africa (Emmenegger et al. 2014; Catry et al. 2014; Rodríguez-Ruiz et al. 2014; Finch et al. 2015). The Italian-Croatian Rollers did not target Lake Chad but rather stopped in open areas of savannah habitats located about 500–1000 km east of the lake, between Chad and Sudan (Fig. 1).

During the spring migration, once Rollers crossed over the central African rainforest belt, they stopped for a long period in the subtropical grassland habitats (mostly in Cameroon and the Central African Republic) for ~ 25 days between March and April. There, seasonal rainfalls in this period of the year promote arthropod abundance to reach its peak (Zwarts et al. 2009; Nwaogu 2023). Afterwards, Rollers resumed their migration north by following a more eastern route compared to autumn, crossing the Libyan and Algerian Sahara desert until the North African coasts facing the Mediterranean Sea. Compared to previous studies, our Rollers used a new spring route-specific stopover site in northern Tunisia, where they probably waited for optimal weather conditions before initiating the sea-crossing. This would be in line with other studies reporting that in the channel of Sicily, between Cap Bon and southeastern Sicily, adverse north-westerly winds often blow in spring (e.g., Agostini et al. 2022).

Central Mediterranean Rollers mostly migrated during the night, aligning with the findings of Rodríguez-Ruiz et al. (2014) regarding Iberian Rollers. They travelled at different speeds depending on the habitat they traversed. As expected, the highest speeds were recorded while crossing two major ecological barriers: the sea and the desert. Since this species cannot stop over open water, they must cross it with a protracted non-stop powered flight. Similarly, the desert represents an ecologically inhospitable area for most of the migratory landbirds (e.g., Biebach et al. 2000; Jiguet et al. 2019a, b). However, while crossing the desert, Rollers interrupted their flight during the day, thus not making a single non-stop flight. Additionally, we recorded two individuals stopping for several days in the desert, suggesting that these birds were able to exploit trophic resources even in this seemingly barren habitat. Alternatively, unfavourable flying conditions could have prevented them from taking off. Rollers slowed down and stopped for longer periods in savannah areas, as this habitat provides good foraging opportunities (e.g., orthoptera, Rodríguez-Ruiz et al. 2014). These areas were utilized for extended stopovers in both seasons.

Regarding repeatability, we found that individuals tracked in successive years showed high consistency of certain migratory parameters. However, we caution about

the uncertainty of these results due to a low sample size in terms of tracks and individuals. We also found partial overlap between years in individual winter home ranges, suggesting a high fidelity to winter quarters. As far as we know, this is the first time that repeatability between successive years in migration patterns is reported for the Roller. At the same time, we found a large population variability in migratory parameters, as individuals varied in migration routes, timing of migration, and wintering areas between them. A pattern that was already recorded in other long-distance trans-Saharan migrants (e.g., osprey *Pandion haliaetus*: Vardanis et al. 2016, hoopoe *Upupa epops*: van Wijk et al. 2016, common swift *Apus apus*: Wellbrock et al. 2017, Cyprus wheatears *Oenanthe cypriaca*: Patchett et al. 2022).

Conclusions: Implications for conservation

Our study describes new migratory routes for Central Mediterranean Rollers and contributes to completing the puzzle of the pan-European migratory and wintering patterns for the species (Finch et al. 2015). It also provides further support to previous findings gathered with less precise devices, such as light-level geolocators (e.g., Rodríguez-Ruiz et al. 2014). For Central-Mediterranean Rollers, we could outline macro-areas important for the survival of this population outside the breeding period: the northern savannah zones used for long stopovers and mostly located between Chad and Sudan in autumn and in Central African Republic/Cameroon in spring. We also reveal new route-specific stopover sites on the Mediterranean shores during spring, in northern Tunisia, where Rollers stopped for the last stay before returning to Europe. In line with previous studies (e.g., Finch et al. 2015; Rodríguez-Ruiz et al. 2019), wintering grounds were located in southern Africa and used areas partially overlapped between individuals of the two populations, although Italian Rollers tended to winter more on the west than Croatian Rollers, resulting in a large wintering-belt spanning from Namibia till Mozambique.

One-third of European breeding bird species are migrant birds that occur across the continent and winter in Africa, with many of these species experiencing serious declines from multiple causes in multiple areas of the flyway. Effective conservation strategies at the flyway level require scientific networks, cooperation, and coordination of existing local research efforts. Rodríguez-Ruiz et al. (2019) emphasized that different breeding populations may face different conservation threats in their respective non-breeding range and highlighted the importance of analysing multiple populations to develop an integrated and effective conservation plan for the species as a whole. Our study contributes to this objective by providing new ecological information for target Roller populations at the scale of the species' flyway. Such information is essential to support conservation efforts and facilitate the implementation and regular updating of the Roller's action plan. These findings are aligned with international initiatives aimed at integrating research, policy and actions to produce a comprehensive Species Action Plan portfolio (Marcacci et al. 2023). These efforts are crucial for the conservation of Afro-Palearctic migratory landbirds at the flyway scale.

Declarations

Ethics approval All applicable international, national, and/or institutional guidelines for the use of animals were followed. In Italy, captures, handling and tagging procedures were conducted by the Italian Institute for Environmental Protection and Research (ISPRA), under the authorization of Law 157/1992 [Art.4(1) and Art 7(5)], which regulates research on wild bird species and under authorization no. G12783 of 19/10/2021 issued by Regione Lazio. Capture and tagging of birds in Croatia were conducted under the required licence from the Ministry of Enviroenmental protection and Energy.

References

Agostini N, Panuccio M, von Hardenberg J, Monti F (2022) Potential importance of wind patterns and conspecific guidance opportunities for the conservation of the Egyptian Vulture *Neophron percnopterus* in Italy. Bird Conserv Int 33:e13. https://doi.org/10.1017/S0959270922000089

Alerstam T (1993) Bird migration. Cambridge University Press, Cambridge

Barišić S, Tutiš V, Ćiković D, Kralj J (2018) European roller *Coracias garrulus* in Croatia: Historical review, current status and future perspective. Larus 53:19–31

Bartoń K (2020) MuMIn: Multi-model Inference. R package version 1.43.17. https://cran.r-project.org/web/packages/MuMIn. Accessed 1 July 2022

Berger-Geiger B, Heine G, Kumaraswamy A, Galizia CG (2022) Changing places: Spatial ecology and social interactions of female and male Montagu's harrier *Circus pygargus* in the Spanish Extremadura. J Ornithol 163:165–179. https://doi.org/10.1007/s10336-021-01914-9

Biebach H, Biebach I, Friedrich W, Heine G, Partecke J, Schmidl D (2000) Strategies of passerine migration across the Mediterranean Sea and the Sahara Desert: a radar study. Ibis 142:623–634. https://doi.org/10.1111/j.1474-919X.2000.tb04462.x

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HG, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Brown DJ (2015) International Single Species Action Plan for the Conservation of the Eurasian Curlew *Numenius arquata arquata*. AEWA Technical Series No. 58, Bonn, Germany

Calenge C (2006) The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Catry I, Catry T, Granadeiro JP, Franco AM, Moreira F (2014) Unravelling migration routes and wintering grounds of European rollers using light-level geolocators. J Ornithol 155:1071–1075. https://doi.org/10.1007/s10336-014-1097-x

Cox DT, Brandt MJ, Mcgregor R, Ottosson U, Stevens MC, Cresswell W (2011) Patterns of seasonal and yearly mass variation in West African tropical savannah birds. Ibis 153:672–683. https://doi.org/10.1111/j.1474-919X.2011.01150.x

EBCC (2022) European Breeding Bird Atlas 2 website. European Bird Census Council, http://ebba2.info (04/04/2024)

Emmenegger T, Mayet P, Duriez O, Hahn S (2014) Directional shifts in migration pattern of rollers (*Coracias garrulus*) from a western European population. J Ornithol 155:427–433. https://doi.org/10.1007/s10336-013-1023-7

Finch T, Saunders P, Avilés JM et al (2015) A pan-European, multi-population assessment of migratory connectivity in a near-threatened migrant bird. Divers Distrib 21:1051–1062. https://doi.org/10.1111/ddi.12345

Finch T, Dunning J, Kiss O, Račinskis E, Schwartz T, Sniauksta L, Szekeres O, Tokody B, Franco A, Butler SJ (2017) Insights into the migration of the European roller from ring recoveries. J Ornithol 158:83–90. https://doi.org/10.1007/s10336-016-1374-y

Fisher I, Ashpole J, Scallan D, Proud T, Carboneras C (2018) International Single Species Action Plan for the conservation of the European Turtle-dove *Streptopelia turtur* (2018 to 2028). European Commission Technical Report. https://data.europa.eu/doi/10.2779/743376. Accessed 19 Apr 2024

Fox J (2003) Effect displays in R for generalised linear models. J Stat Softw 8:1–27. https://doi.org/10.18637/jss.v008.i15

Fox J, Weisberg S (2019) An R Companion to Applied Regression, 3rd edn. Sage, Thousand Oaks, CA

Griffiths R, Double MC, Orr K, Dawson RJ (1998) A DNA test to sex most birds. Mol Ecol 7:1071–1075. https://doi.org/10.1046/j.1365-294x.1998.00389.x

Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CE, Robinson BS, Hodgson DJ, Inger R (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6:e4794. https://doi.org/10.7717/peerj.4794

Hartig F (2022) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html. Accessed 19 Apr 2024

Jiguet F, Burgess M, Thorup K et al (2019a) Desert crossing strategies of migrant songbirds vary between and within species. Sci Rep 9:20248. https://doi.org/10.1038/s41598-019-56677-4

Jiguet F, Robert A, Lorrillière R et al (2019) Unravelling migration connectivity reveals unsustainable hunting of the declining ortolan bunting. Sci Adv 5:eaau2642. https://doi.org/10.1126/sciadv.aau2642

Kiss O, Catry I, Avilés JM et al (2020) Past and future climate-driven shifts in the distribution of a warm-adapted bird species, the European Roller *Coracias garrulus*. Bird Study 67:143–159. https://doi.org/10.1080/00063657.2020.1784842

Kovács A, Barov B, Urhun C, Gallo-Orsi U (2008) International Species Action Plan for the European Roller *Coracias garrulus garrulus*. Besenyotelek, Hungary, pp 1–52

Limiñana R, Soutullo A, López-López P, Urios V (2008) Pre-migratory movements of adult Montagu's harriers *Circus pygargus*. Ardea 96:81–96. https://doi.org/10.5253/078.096.0109

Marcacci G, Briedis M, Diop N, Diallo AY, Kebede F, Jacot A (2023) A roadmap integrating research, policy, and actions to conserve Afro-Palearctic migratory landbirds at a flyway scale. Conserv Lett 16:e12933. https://doi.org/10.1111/conl.12933

Monti F, Nelli L, Catoni C, Dell'Omo G (2019) Nest box selection and reproduction of European Rollers in Central Italy: A 7-year study. Avian Res 10:13. https://doi.org/10.1186/s40657-019-0150-0

Monti F, Barišić S, Cannarella S, Ćiković D, Tutiš V, Kralj J, Catoni C (2023) Breeding phase and outcome determine space use in European rollers *Coracias garrulus* prior to migration. Curr Zool 70:137–149. https://doi.org/10.1093/cz/zoad006

Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev 85:935–956. https://doi.org/10.1111/j.1469-185X.2010.00141.x

Nebel C, Kadletz K, Gamauf A, Haring E, Sackl P, Tiefenbach M, Winkler H, Zachos FE (2018) Witnessing extinction: population genetics of the last European Rollers (*Coracias garrulus*) in Austria and a first phylogeographic analysis of the species across its

distribution range. J Zool Syst Evol Res 57:461–475. https://doi.org/10.1111/jzs.12256

Newton I (2004) Population limitation in migrants. Ibis 146:197–226. https://doi.org/10.1111/j.1474-919X.2004.00293.x

Nwaogu CJ, Tieleman BI, Cresswell W (2019) Weak breeding seasonality of a songbird in a seasonally arid tropical environment arises from individual flexibility and strongly seasonal moult. Ibis 161:533–545. https://doi.org/10.1111/ibi.12661

Nwaogu CJ (2023) Fitting birds' annual cycle events to seasonal fluctuations in the Afro-tropics. Symposium: "Dealing with though seasons: a comparison of annual cycle strategies in African residents and Afro-palearctic migrants". 14th European Ornithologists' Union Congress, University of Lund, Sweden

Patchett R, Kirschel AN, Robins King J, Styles P, Cresswell W (2022) Age-related changes in migratory behaviour within the first annual cycle of a passerine bird. PLoS ONE 17:e0273686. https://doi.org/10.1371/journal.pone.0273686

Rodríguez-Ruiz J, de la Puente J, Parejo D, Valera F, Calero-Torralbo MA, Reyes-González JM, Zajková Z, Bermejo A, Avilés JM (2014) Disentangling migratory routes and wintering grounds of Iberian near-threatened European rollers Coracias garrulus. PLoS ONE 9:e115615. https://doi.org/10.1371/journal.pone.0115615

Rodriguez-Ruiz J, Mougeot F, Parejo D, De La Puente J, Bermejo A, Avilés JM (2019) Important areas for the conservation of the European Roller Coracias garrulus during the non-breeding season in southern Africa. Bird Conserv Int 29:159–175. https://doi.org/10.1017/S095927091800014X

Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, van Bommel FPJ (2006) Long-term population declines in Afro-Palearctic migrant birds. Biol Conserv 131:93–105. https://doi.org/10.1016/j.biocon.2006.02.008

Strandberg R, Klaassen RH, Hake M, Olofsson P, Thorup K, Alerstam T (2008) Complex timing of Marsh harrier Circus aeruginosus migration due to pre- and postmigratory movements. Ardea 96:159–171. https://doi.org/10.5253/078.096.0202

Trierweiler C, Klaassen RH, Drent RH, Exo KM, Komdeur J, Bairlein F, Koks BJ (2014) Migratory connectivity and population-specific migration routes in a long-distance migratory bird. Proc R Soc B 281:20132897. https://doi.org/10.1098/rspb.2013.2897

van Wijk RE, Bauer S, Schaub M (2016) Repeatability of individual migration routes, wintering sites, and timing in a long-distance migrant bird. Ecol Evol 6:8679–8685. https://doi.org/10.1002/ece3.2578

Vardanis Y, Nilsson JÅ, Klaassen RH, Strandberg R, Alerstam T (2016) Consistency in long-distance bird migration: contrasting patterns in time and space for two raptors. Anim Behav 113:177–187. https://doi.org/10.1016/j.anbehav.2015.12.014

Vickery JA, Ewing SR, Smith KW, Pain DJ, Bairlein F, Škorpilová J, Gregory RD (2014) The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156:1–22. https://doi.org/10.1111/ibi.12118

Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: unraveling migratory connectivity. Trends Ecol Evol 17:76–83. https://doi.org/10.1016/S0169-5347(01)02380-1

Wellbrock AHJ, Bauch C, Rozman J, Witte K (2017) "Same procedure as last year?" Repeatedly tracked swifts show individual consistency in migration pattern in successive years. J Avian Biol 48:897–903. https://doi.org/10.1111/jav.01251

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168. https://doi.org/10.2307/1938423

Zuur AF, Ieno EN (2016) A protocol for conducting and presenting results of regression-type analyses. Methods Ecol Evol 7:636–645. https://doi.org/10.1111/2041-210X.12577

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York

Zwarts L, Bijlsma RG, van der Kamp J, Wymenga E (2009) Living on the edge: wetlands and birds in a changing Sahel. KNNV Publishing, Zeist, The Netherlands

Zwarts L, Bijlsma RG, van der Kamp J (2023) Effects on birds of the conversion of savannah to farmland in the Sahel: habitats are lost, but not everywhere and not for all species. Ardea 111:251–268. https://doi.org/10.5253/arde.2022.a24

Authors and Affiliations

Flavio Monti[1] [ORCID] · **Sebastian Cannarella[2]** · **Davor Ćiković[3]** · **Vesna Tutiš[3]** · **Jelena Kralj[3]** · **Carlo Catoni[2]** · **Sanja Barišić[3]** [ORCID]

✉ Flavio Monti
flaviomonti00@gmail.com

[1] Institute of Research on Terrestrial Ecosystems (IRET), National Research Council (CNR), Campus Ecotekne, 73100 Lecce, Italy

[2] Ornis Italica, Piazza Crati 15, 00199 Rome, Italy

[3] Institute of Ornithology, Croatian Academy of Sciences and Arts, Gundulićeva 24, 1000 Zagreb, Croatia