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The global importance of grasslands underlined by the combination of multiple telemetry tracking techniques of a trans-equatorial loop migrant bird, the European roller (*Coracias garrulus*)

Orsolya Kiss^{1,2*}, Joanna B. Wong³, Béla Tokody², Szilárd J. Daróczy⁴, Lőrinc Bărbos⁴ and András Kelemen^{5,6}

Abstract

Migrant birds encounter different conditions and threats across seasons, so their population dynamics are affected by the events in both breeding and nonbreeding seasons. The decline of long-distance migrant, grassland specialist birds underlines the necessity of integrating the full annual cycle perspective in conservation research. The European roller (*Coracias garrulus*), as a long-distance migratory grassland bird, is an excellent model species for exploring the environmental parameters that may contribute to the vulnerability of birds with similar requirements through the full annual cycle. Here, we aim to identify the migration strategies and phenology to locate the stopover sites and wintering grounds and to describe the home-range size and habitat composition during the breeding season and the non-breeding season. We studied the breeding population of the Carpathian Basin between 2015 and 2021. We used GPS-UHF loggers to investigate movements during the breeding season and PTT tags and geolocators for tracking during the non-breeding season. For the habitat use analysis, we employed European and global land cover databases. We found that home-range size changed over the breeding season, the availability of grasslands affected the size of the home-range and the core area harboured the largest proportion of grasslands. During the non-breeding period, 108 stopover sites were identified. During autumn, rollers used more stopovers compared to the spring migration. Although rollers migrate on broad fronts during autumn migration, two main stopover regions were identified: a sub-Saharan and a subequatorial. Rollers spent significantly more time at the stopover sites in the sub-Saharan region than in the subequatorial region or during the spring migration. We found multiple migration pathways and a wide east-west spread over the wintering grounds in the southern savanna region. Rollers mainly used grassland habitats, especially on the wintering sites, where rollers spend the longest time during the non-breeding period. Here, we firstly provided a detailed overview of the spatial and temporal scale of rollers' habitat use through the full annual cycle, proving the global importance of grasslands in

*Correspondence:

Orsolya Kiss
kiss.orsolya@szte.hu

Full list of author information is available at the end of the article



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the conservation of long-distance migratory birds. In our view such detailed knowledge is crucial for developing conservation strategies applicable to the whole Afro-Palearctic flyway system.

Keywords Conservation, Grasslands, Migration, Sahel, Stopover, Geolocator, UHF logger, Satellite tracking

Introduction

Grasslands comprise one of Earth's dominant vegetation types, accounting for up to 40% of its terrestrial area [1] and 70% of the world's agricultural land area [2]. They provide a wide range of ecosystem services such as food production, carbon storage, soil erosion control, climate mitigation, and pollination, and play an important role in climate and water regulation and global biogeochemical cycles [3, 4]. They occur in almost all climatic zones, such as temperate grassland habitats like Eurasian steppes, North American prairies, or tropical and subtropical grasslands (savannas) mostly in Africa. Grasslands are vegetated habitats dominated by grasses or other graminoids, with a low abundance of trees or shrubs. Aside from constituting their biomes, can be found as components within other biomes (e.g. forest steppes, woody savannas) as well [5, 6]. Grassland habitats support exceptionally high small-scale species richness across a wide range of taxa and have some of the highest small-scale species richness on Earth in terms of numerous taxa ([1, 7] Chytrý et al. [8]), but their degradation is widespread and accelerating in many parts of the world [3]. Despite their ecological value, grasslands are among the most threatened ecosystems globally, with degradation intensifying in many regions [3]. This widespread habitat loss has contributed to significant declines in grassland bird populations [9], with a global review indicating that 58% of publications identified agriculture as a primary threat to this group [10]. Grassland specialist birds which are also long-distance Afro-Palearctic migrants have shown a pattern of sustained decline [11]. Long-distance migratory landbirds are declining faster than short-distance migrants or resident species [11, 12], and conservation actions often have failed to reverse these trends [13]. Throughout their annual cycle, migratory birds move between seasonal environments to find optimal environmental conditions and food availability [14, 15]. They encounter different conditions and threats across seasons [16], therefore, events in both breeding and nonbreeding seasons (i.e., wintering and migration) affect population dynamics (e.g., [17, 18]). The non-breeding period can buffer the further accumulation of carry-over effects from the previous breeding season and autumn migration [19], but adverse conditions on wintering grounds can also amplify the negative effects of unfavourable conditions during the previous breeding season on birds' survival [20]. Moreover, the daily mortality rate in raptors differs between the migration and stationary periods and is thought to be six times higher during migration

seasons (mean daily mortality rate = 0.00440) than in stationary periods (mean daily mortality rate 0.00075) [21]. Although long-distance migratory birds are exposed to different environmental conditions in widely separated geographical areas and exhibit large temporal and spatial variation in habitat use, research in animal ecology is severely biased towards the breeding period [16]. Thus, there is an urgent need to use a full annual cycle perspective to improve understanding of species biology, which can provide a robust scientific basis for the conservation of migratory birds [16].

The European roller (*Coracias garrulus*) (hereafter: roller) is a medium-sized insectivorous species whose population has significantly declined in Europe since the 1970s. It has become extinct in several countries such as Switzerland, Sweden, Finland, Denmark, and the Czech Republic, and elsewhere it is still decreasing, with the exception of a few countries with current positive trends (Carpathian Basin (Hungary, Serbia), Italy, France) [22]. The roller is a typical species of forest steppes or other grasslands with scattered woody vegetation. Grasslands provide the foraging site where rollers mostly prey on large *Orthoptera* and *Coleoptera* species, and cavities in the scattered large trees provide suitable nesting places [23]. Rollers are sit-and-wait predators; thus, small trees, bushes, or tall herbaceous plants serve as perches. Rollers also forage in other open habitats, such as agricultural fields or fallow lands, but avoid closed forests [23].

Recent publications on the European roller's migration show that this species uses various migration pathways across the European populations; however, these studies mostly focused on the Western European and Mediterranean populations [24, 25]. For migratory birds, conservation requires multilevel strategies, including information across the full annual cycle, distribution range and threats, and implementing conservation actions on a local scale [26, 27]. The need for conservation actions on non-breeding grounds was emphasized by the acceptance of the Flyway Action Plan for the European roller [28] through the Convention on Migratory Species (Bern Convention). However, this plan highlights the necessity for further research on migration patterns and species' habitat requirements during the non-breeding period. Although, research on non-breeding sites is highly important, but is often not feasible because of financial and safety issues in the target region. Remote sensing has become a useful tool for providing data on environmental drivers such as detecting land cover changes, the density of human-made structures, habitat

quality, etc. [29]. Tracking technologies like GPS or Platform Transmitting Terminal (PTT) tags offer highly accurate location data (ranging from less than 10 m to about 100 km) and enable researchers to study habitat use over the full annual cycle without conducting field studies on the non-breeding grounds.

Here, we aim to describe the spatial and temporal scale of the European roller habitat use through the full annual cycle. The novelty of this research lies in addressing a species that belongs to a highly endangered group – and is itself threatened – within a holistic framework covering the full annual cycle. Our approach provides a comprehensive picture of the birds' movements and land use throughout the year. In this way, the related nature conservation and ecological aspects can also be discussed together. Firstly, we aim to investigate the home-range size and home range habitat composition during the breeding season to identify the ratio and extent of grassland use during the reproductive period. Monti et al. [25] found that breeding phase (breeding and post-breeding period) can affect the space use in rollers, therefore here (H1) we also hypothesize that the home range size will change over the breeding season. Birds usually decrease their ranges during the incubation period and increase it during the chick-rearing period (e.g. Grzywaczewski [30]), therefore, we predict (P1) that the home range size will increase during the breeding season.

Habitat composition can influence the home range size. For instance, if suitable foraging sites are scarce or widely dispersed due to habitat fragmentation, birds must travel longer distances to reach them; consequently, birds can decrease the home range size with the increase of high-quality foraging area (e.g. [31]). Accordingly, we hypothesize (H2) that the habitat composition will affect the home range size. We further predict (P2) that home-range size will decrease with an increasing proportion of high-quality foraging habitats, such as grasslands.

Furthermore, we also hypothesize that (H3) habitat composition of core areas differs significantly from the other parts of the home range. We predict (P3) that core areas contain a higher amount good quality habitats like grasslands while other parts of the home range may contain a higher amount of lower quality habitats or temporarily available habitats.

Considering the non-breeding season, we aim to identify the migration strategies and phenology to locate the stopover sites and wintering grounds and to analyse the habitat composition, the home-range size, and the time spent on stopover sites and wintering grounds. Afro-Palaearctic landbird migrants using the Eastern flyway show high dispersion over Africa during the wintering period [32], travel with a broad front [32] and low migratory connectivity [33]. Loop migration was found in many roller populations in Europe. Rollers breeding

in Latvia and similar species like Red-backed shrike use counter-clockwise loop migration patterns [24, 34]. Therefore, we hypothesize (H4) that the population breeding in the Carpathian Basin follow similar migration patterns. We predict (P4) that the autumn migration is broad-fronted, the wintering region spreads over the South African savanna region, and in springtime, rollers migrate in a counter-clockwise loop through the Arabian Peninsula.

Generally, spring migration is faster than autumn migration [35]. Here we hypothesize (H5) that the length and duration of spring and autumn migrations differ. Specifically, we predict (P5) that during autumn migration, the total length of flight (the sum of flight segments between consecutive stopovers) is shorter, but utilize a greater number of stopover sites and spend longer periods at each. Consequently, although the total length of flight is shorter, the overall duration of the migration is expected to be longer.

Finally, we hypothesize (H6) that habitat use will differ between the stopover and wintering sites. We predict (P6) that rollers will use better quality habitats like grasslands during the longer stay on wintering sites, while on the stopovers, rollers might use more suboptimal habitats like agricultural fields or areas with high wood cover.

Materials and methods

Study species

The European roller is socially monogamous, usually having one brood per year. The first individuals arriving to the breeding grounds in the second half of April and the majority returning to the breeding sites in May. The incubation takes about 16–18 days; nestlings fledge after 26–28 days. Incubation starts before clutch completion; thus, nestlings hatch asynchronously at one-day intervals [23]. Both sexes take part in the incubation and the feeding.

Breeding season

To investigate the breeding home range, rollers were tagged in Hungary at two regions where the Roller Life (LIFE13/NAT/HU/000081) project action took place: the “Borsodi-Mezőség” in the north-eastern (approx. central coordinate: N 47.782500 N, 20.819722 E) Hungarian Great Plain, hereafter “North” and the “Alsó-Tisza völgy” (approx. central coordinate: 46.514400 N, 20.121700 E) in the southern part, hereafter “South”. The study areas are characterized mostly by grasslands and extensively managed croplands with conventional farmlands. Both sites are part of the Natura2000 network. To investigate the movements during the breeding period, we used high-precision Ecotone Pica GPS-UHF loggers (5.6 g). Rollers were captured at nest boxes and tagged after clutch completion, during incubation or the early nestling stage,

to minimize the risk of nest desertion [25, 36, 37]. We tagged the birds with GPS-UHF loggers by using a backpack harness with Teflon ribbon. The weight of the Teflon ribbon was about 0.8–0.9 g, so together with rings (0.5 g) the total mass of these tags was between 6.9 and 7.0 g. The total mass of the tag was smaller than 5% of the body mass of birds, therefore we did not tag birds with GPS-UHF loggers if their body mass was below 140 g.

Overall, 28 adult rollers, one per nest, were tagged during the incubation period between 2015 and 2020. 19 individuals were tagged at the “South” region and 9 were at “North” region. Birds were tracked for an average of 23.6 days (range: 10–43 days; individuals tracked for fewer than 10 days were excluded), yielding a mean of 1,088 locations per individual (range: 114–5,451). We analysed the home-range characteristics for 21 birds in total (see Table 1. in Supplementary information). All of them were followed during one breeding period. The loggers were programmed to collect fixes during the active periods of the rollers (from 6 am until 7 pm), collecting 2–10 fixes per hour. The duration of the daily duty cycle and the frequency of the data collection were modified according to the charge status of the tags’ battery to avoid the full depletion of the battery.

To investigate habitats used by the species, we used freely available land cover databases. CORINE Land Cover 2018 (<https://land.copernicus.eu/en/products/corine-land-cover/clc2018>) was used to calculate the land cover during the breeding season. This database provides European land cover information in a 100 m resolution raster with 44 thematic classes. Twelve land cover classes were found in the rollers’ home ranges that we reclassified into 7 categories, because they have the same ecological role as roller habitat: (i) arable fields – 211; (ii) complex agricultural areas – 242, 243 (two subcategories of heterogeneous agricultural areas); (iii) grasslands – 231 (pastures), 321 (natural grasslands). (iv) wetlands (inland marshes – 411 and water bodies – 512).

Non-breeding season

To investigate the movements and habitat use during the non-breeding period we tagged birds with PTTs and geolocators outside the above-mentioned breeding study sites in order to cover the species distribution range across Hungary. In Romania, rollers were tagged on the Western Plain, a region adjacent to the eastern border of Hungary. All sites situated in the Carpathian Basin (Supplementary information, Fig. 2).

Rollers are typically diurnal forager and migration occurs mainly during the night ([37]. In this study we aim to locate all the potential stopover sites where rollers land, therefore stopovers were defined as locations where rollers stayed for more than 24 h and showed non-directional movements. When rollers spend at least 24 h

in the same place, they likely use it for feeding or resting [37]. Rodríguez-Ruiz et al. [37] define the end of migration when rollers stop longer than 10 days once the bird had crossed the equator. However, in our study, two individuals stopped for a longer period in the subequatorial region (13 and 11 days), and both made a short stopover (of one and two days, respectively) after these longer ones and before reaching the wintering site. Therefore, the end of migration was defined as a stop longer than 15 days, after the bird had crossed the Equator. The movements within the stopover sites were excluded from the distance calculation of the autumn and spring migration routes. We defined the duration of autumn and spring migration as the number of days from the start of the migration to the arrival to the breeding or wintering sites.

To investigate the movements during the non-breeding period 5 g PTT tags (Microwave Telemetry Inc., Columbia, MD, USA) and 1 gr SOI-GDL 3 PAM geolocators (Swiss Ornithological Institute) were used in both Romania and Hungary. We trapped and tagged the birds using the same methods described in the previous section. Birds were tagged with PTTs using Teflon backpack harnesses, and geolocators were attached with Teflon leg-loop harnesses. In case of the PTTs, the total mass of the tag was smaller than 5% of the body mass of birds; it was smaller than 3% in case of the geolocators.

For PPT transmitter 8-h ON/ 15-h OFF and 10-h ON/ 24-h OFF duty cycle was employed. In Hungary, we tagged 9 birds with PTT and 2 with geolocators. In Romania, 2 rollers were tagged with PTTs and 3 geolocators. We analysed the data of PTT tagged birds which had stopovers in the sub-Saharan region (Hungary 8 PPTs, Romania 2 PTTs) (see Table 2. and Fig. 1. in Supplementary information).

To estimate stationary positions and migratory paths from the geolocators, we used the SGAT group model to analyse the collected light data [38]. We distinguished sunrise and sunset times using the R package TwGeos [39], and used the median reference solar zenith angles at the rollers’ breeding sites for calibration. Stark changes in sunrise, sunset, noon and midnight times were used to distinguish movement from stationary periods. Stationary periods were defined as stops $\geq$ two days. Using the twilight error distribution, flight speed distribution (gamma distributed; shape: 2.2, rate: 0.08) and a land mask (to give locations on land a higher prior), we ran the final model for 2000 iterations, resulting in the most likely median paths used by the rollers. Prior to the analysis, all locations from the PPT transmitters were filtered with the filter [40] in Movebank [41] to remove unrealistic Argos locations. Class Z Argos locations were also excluded. We used only PPT transmitter data for the analyses of stopovers, stationary sites indicated by

geolocators were excluded because of the high difference in the precision of the two tracking methods.

We recorded 16 autumn paths from 12 individuals (PTTs: 11, geolocators: 5) and 11 spring paths (PTTs: 8, geolocators: 3) from 7 individuals. One individual was tracked across multiple years (2016–2021 see Table 2. in Supplementary information). Based on the location of the autumn stopovers, two main regions were distinguished, and only 4.6% of the stopovers were located outside these regions during the autumn migration. The sub-Saharan autumn stopover region was located south of the Sahara Desert in the Sahelo-Sudanian belt, north of the Equator (between N 10–21° and E 15–31°), and the subequatorial region was south of the Equator and north of the wintering region (between S 2–18° and E 15–29°). During the spring migration, rollers used mainly East-Africa (Tanzania, Kenya, Somalia, South-Sudan) and the Mediterranean region (e.g. Turkey, Saudi-Arabia, Israel), but due to high spatial variability of the stopovers, and the low sample size per each type, contrary to autumn migration, we considered all spring stopovers as one group.

We retrieved the ring recovery data from Hungary between 1931 and 2024 from the database of the Hungarian Bird Ringing Centre. We got 18 recoveries for the autumn migration and 14 for the spring migration.

For analysing the habitat requirement of rollers during the non-breeding season, we used GlobCover Land Cover Maps (http://due.esrin.esa.int/page_globcover.php) which contains 22 classes corresponding to specific land cover types at a 300 m resolution raster. We identified 19 classes based on the most precise Argos fixes (2 or 3 class fixes) which were reclassified into five main habitat types: (i) croplands (11, 14, 20, 30); (ii) woody vegetation (40, 50, 60, 70, 100, 160, 180); (iii) grass-woody (110, 120, 130); (iv) grasslands (140); and (v) bare surfaces with sparse vegetation (<15%) vegetation or bare areas (150, 190, 200, 210) (see Table 3. Supplementary information for the details).

Analyses

For the home-range analysis, we used all fixes collected by the UHF logger. As classical home range estimation approaches may fail to deal with the complexities and biases of modern movement data [42], such as temporal autocorrelation, therefore we calculated Autocorrelated Kernel Density Estimation (AKDE) ('ctmm' R Package; [43]). We created 50% and 90% isopleths from the utilization distributions to define the core area (AKDE50) and full home range (AKDE90). To determine whether the core area (AKDE50) differed from the remaining part of the full home range, we compared the habitat composition of AKDE50 areas with the composition of the full home range (AKDE90) outside the AKDE50 area. Nest boxes were regularly monitored, and three breeding

stages were distinguished: incubation, early nestling, and active feeding. Weekly periods were defined from the day of tagging. If birds were tagged on full clutch with unhatched eggs, the first week was classified as incubation, the second as early nestling, and the following weeks as active feeding. In one case, two weeks were assigned to incubation based on the hatching date. When birds were tagged with one or two hatchlings, the first week was considered early nestling, followed by active feeding. As we aim to investigate the effect of breeding stage on the home range and the length of tracking period might affect the home range size; therefore, we counted the home range size for each weekly period. During the analyses, we used two categories: 'early nestling' (combining incubation and 'early nestling') and 'active feeding' period.

In the case of home ranges used during the breeding season, our aim was to reveal how the breeding stage (early nestling, active feeding) and habitat quality (within the full home range) affect home range size. We used two separate linear mixed-effect models (LMMs) for the areas of AKDE50 and AKDE90. In order to include the home range sizes in the LMM framework, we normalised their distributions using a log transformation. Furthermore, since land-cover proportions (grasslands, arable fields, complex agricultural areas, and wetlands) constitute compositional data (their sum being constrained to 100%), these predictor variables were transformed using an isometric log-ratio (ILR) transformation to avoid spurious correlations resulting from the constant-sum constraint [44]. The first ILR balance (ilr1) represents the ratio of grassland area relative to the other habitat types; thus, higher ilr1 values indicate greater dominance of grassland cover. The second ILR balance (ilr2) increases with the proportion of arable fields, whereas the third ILR balance (ilr3) increases with the proportion of complex agricultural habitats.

In the two separate LMMs the log-transformed home range sizes (areas of AKDE50 and AKDE90) set as the dependent variables. The fixed factors were the breeding stage (early nestling, active feeding) and the three ILR balances (ilr1, ilr2, ilr3). Bird ID and Year were included as random effects.

Subsequently, model selection was performed based on the Akaike Information Criterion corrected for small samples (AICc) [45], considering all possible combinations of fixed effects while keeping "breeding stage" mandatory in all models.

All analyses were performed in R using several packages. The compositions package was used to handle compositional habitat data and to apply the isometric log-ratio (ILR) transformation [46]. Linear Mixed-Effect Models were fitted using lme4, while the lmer package provided significance testing of fixed effects [47, 48]. Model

selection was conducted with MuMIn using the small-sample corrected Akaike Information Criterion (AICc) [49].

To study whether the relative proportions of different habitat types differed between the core area (AKDE50) and the remaining part of the full home range, we first transformed the land-cover data. The relative cover percentages of habitat types (grasslands, arable fields, complex agricultural habitats, and wetlands) were treated as compositional data, as the proportions within each observation sum to 100%. Such data require specific statistical handling because the components are not independent, an increase in one necessarily results in a decrease in another. To properly account for the compositional nature of the data, we applied the centered log-ratio (CLR) transformation, which expresses each component as the logarithm of its ratio to the geometric mean of all components within the same sample [50]. The CLR transformation projects the data into Aitchison geometry, where distances, variances, and correlations are mathematically valid and interpretable. Moreover, CLR-transformed variables can be used as dependent variables in LMMs and, as compositional data, can also be analysed using PERMANOVA, since the transformation removes the constant-sum constraint and projects the data into real Euclidean space [51]. For the CLR transformations, we used the *compositions* package [46]. Using these CLR-transformed datasets, we applied PERMANOVA to examine whether the habitat composition of the core area differs from that of the remaining part of the full home range. For this analysis, we used the “*compositions*” and “*vegan*” R packages [46, 52]. Moreover, we built four separate LMMs, each corresponding to one habitat type (arable fields, complex agricultural habitats, grasslands, wetlands). In each model, home range type (i.e., core area vs. remaining part of the full home range) was included as a fixed factor, while Bird ID and Year were included as random factors. The dependent variables were the CLR-transformed relative cover values of each habitat type. We also analysed the differences in the values of the dependent variables among the categories of the fixed factor using Tukey post-hoc tests.

To compare the length (km) of autumn and spring migration routes and the duration (days) of autumn and spring migration, and also the number of stopover sites during the autumn and spring migration we built Generalized Linear Mixed-Effect Models (GLMMs). Since the dependent variables (i.e., route length, route duration, and number of stopover sites) did not follow a normal distribution, we employed a negative binomial error distribution, which provided the best fit for our data. In all these three GLMMs, migration season was included as a fixed factor, whereas Bird ID and Year were treated as random factors. (Note: autumn migration and the

subsequent spring migration were assigned to the same year, corresponding to the start of that particular migration cycle.) For the analysis of time spent at individual stopover sites (dependent variable: days), we used a GLMM with an identical model structure, except that the fixed factor was stopover type (i.e., sub-Saharan, sub-equatorial, and spring stopovers). Following all of the above-mentioned GLMMs, we performed Tukey’s post hoc *s* to identify pairwise differences in the dependent variables among the categories of the fixed factor. All analyses were conducted in R using the packages “*glm-mTMB*”, “*car*”, and “*emmeans*” [53–55].

At the autumn stopovers and at the wintering sites, we determined the percentage of the most accurate Argos locations falling into different habitat types. To assess how the proportions of habitats used by birds differed among non-breeding locations (i.e. sub-Saharan, sub-equatorial, and wintering areas), we ran a PERMANOVA and built linear mixed models (LMMs). (During spring migration, the number of highly accurate locations was insufficient to reliably estimate habitat-use proportions.) These analyses were based on the CLR-transformed percentages of the habitat types (i.e. grasslands, grass-woody vegetation, woody vegetation, croplands, and bare surfaces). The PERMANOVA revealed overall differences in habitat composition among the non-breeding locations and also provided pairwise comparisons between the sub-Saharan vs. subequatorial, sub-Saharan vs. wintering, and subequatorial vs. wintering sites. We constructed five separate LMMs, where the dependent variables were the CLR-transformed percentages of the habitat types (i.e. grasslands, grass-woody vegetation, woody vegetation, croplands, and bare surfaces). In each model, location (i.e., sub-Saharan, subequatorial, and wintering area) was included as a fixed factor, while Bird ID and Year were treated as random factors. Differences in the values of the dependent variables among the categories of the fixed factor were analysed using Tukey’s post hoc *s*. All analyses were conducted in R using the packages “*compositions*”, “*emmeans*”, “*lme4*”, “*lmer*” and “*vegan*” [46–48, 52, 54].

Results

Habitat use on the breeding grounds

The core home-range size (AKDE50) was 15.1 ha in average (range: 2.35–80.5 ha), and the mean size of the full home range (AKDE90) was 85.6 ha (range: 17.4–337.4 ha).

The best-supported models for both the core area (AKDE50) and the full home range (AKDE90) included the breeding stage, *ilr1*, and *ilr2* as fixed effects. This indicates that both the breeding stage and habitat quality influence home range size. Home range size increased during the active feeding period compared with the early nestling stage (LMMs: AKDE50 – breeding stage:

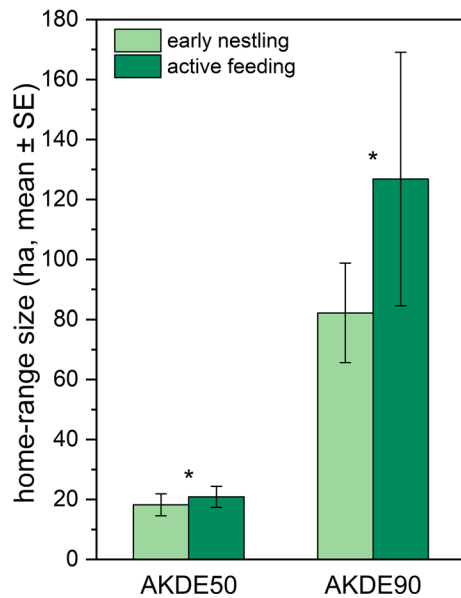


Fig. 1 Changes in home range size (core area – AKDE50; full home range – AKDE90) during the chick-rearing period. Asterisks indicate significant differences between the two chick-rearing stages (early nestling and active feeding)

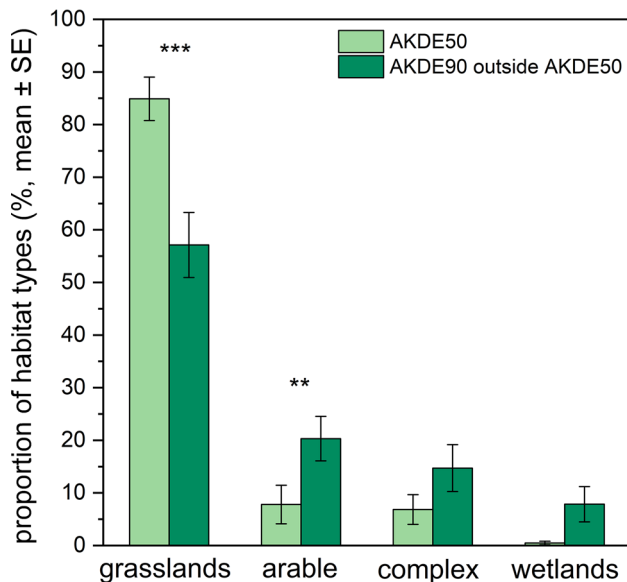


Fig. 2 Proportions of different habitat types (grasslands, arable fields, complex agricultural areas, and wetlands) within the core area (AKDE50) and in the remaining part of the full home range (AKDE90 outside AKDE50). Asterisks indicate significant differences: ** – $p < 0.01$; *** – $p < 0.001$

$F = 54.72$, $p < 0.05$; AKDE90 – breeding stage: $F = 54.53$, $p < 0.05$) (Fig. 1). The core home range increased on average from 18.24 ha to 20.85 ha, representing a 14.3% increase. The mean full home range increased from 82.23 ha to 126.8 ha, corresponding to a 54.2% increase. With an increasing proportion of grasslands, representing higher habitat quality, both core area and full home range size decreased (LMMs: AKDE50 – ilr1 : $F = 18.83$,

$p < 0.01$; AKDE90 – ilr1 : $F = 18.65$, $p < 0.01$). For the full home range (AKDE90), the proportion of arable fields had a significant effect: higher proportions of arable land were associated with larger home ranges (LMMs: AKDE90 – ilr2 : $F = 16.67$, $p < 0.05$). Among the random factors, Year was not significant, whereas Bird ID had a significant effect in all cases.

According to the results of the PERMANOVA, the habitat composition of the core area differed significantly from the remaining part of the full home range (PERMANOVA: $F = 2.38$, $p < 0.01$). The proportion of grasslands was higher within the core area than in the remaining part of the full home range (LMM: $F = 37.82$; $p < 0.001$; Tukey: $p < 0.001$) (Fig. 2). In contrast, the proportions of the other habitat types were lower within the core area compared to the remaining part of the full home range; however, this difference was statistically significant only for arable fields (LMM: $F = 9.71$; $p < 0.01$; Tukey: $p < 0.01$) (Fig. 2). Among the random factors, the effect of Bird ID was significant in all cases, whereas Year had no significant effect.

Phenology and full annual spatial distribution

The majority of rollers departed from the breeding grounds in the first two weeks of September (median date: September 6; IQR (interquartile range): September 3–12; range: August 15 – September 18). During the autumn, the rollers exhibited broad-fronted migration without using specific flight corridors. The sub-Saharan region was found to be an important autumn stopover region (35 stopover sites), where the rollers spent, on average, 43 days (27–58 days) on the stopovers. Rollers predominantly arrived at the sub-Saharan stopovers in September (median date: September 24; IQR: September 17 – October 9; range: September 5– November 3) and stayed there until mid-November. Rollers reached the subequatorial region mostly in November (median date: November 23; IQR: November 17 – December 2; November 1 – December 28), where 37 stopover sites were identified. Only 5 autumn stopover sites were located outside these two regions (north to the sub-Saharan region). Rollers arrived at the wintering grounds mainly in December (median date: December 5 IQR: November 26– December 6; range November 21 – January 7). Angola (\$15.13, E14.28), Namibia (\$17.68– 19.22; E17.51–20.56) and Botswana (\$18.52– 22.61; E24.02–25.72) were found to be the main wintering regions of the studied population; however, one individual tagged with a geolocator spent the winter farther north in Tanzania (\$7.1 E37.02). The largest distance between the two farthest wintering areas was 2636 km. One individual used three wintering sites, while another three birds used two distinct wintering sites, with an average distance of 221.2 km between the sites. Rollers stayed at the wintering grounds until March

(median date: March 14; IQR: March 2 – March 17; range: February 26 – April 1), and after short stops in East Africa (median date: April 10; IQR: March 29 – April 15; range: March 25 – April 21) and the Middle-East-Mediterranean region (median date: May 8; IQR: May 3 – May 10; range: April 25 – May 24), they arrived back to the breeding grounds mostly in May (median date: May 18; IQR: May 14– May 24; range: May 3 – June 4).

Counter-clockwise loop migration through the Middle East was found to be the main migration strategy for the roller population breeding in the Carpathian Basin. The majority of ring recovery data also showed the same pattern during the autumn migration, and showed a broad-fronted migration through the Mediterranean. 8 of the 14 spring ring recoveries were also located along the counter-clockwise loop migration pathway. However, four recoveries were not within the general migration path (counter-clockwise loop), they were in Italy instead of Turkey or Bulgaria, indicating that the Carpathian Basin's roller population may have another type of migration path (clockwise loop). One tagged individual (PTT ID:144365) started the spring migration with a short clockwise loop until the rainforest zone, then used the same migration route during the spring and autumn migration (Fig. 3).

The spring migration was significantly greater in distance (9549 ± 300 SE km) than the autumn migration (7884 ± 200 SE km) (GLMM: $F = 44.77$; $p < 0.001$; Tukey: $p < 0.001$). Despite this, the duration of the spring migration was shorter (mean 71.5 ± 4.15 SE days) than the autumn migration (mean 88.5 ± 3.98 SE days) (GLMM: $F = 13.10$; $p < 0.001$; Tukey: $p < 0.001$).

There was one individual whose migration we tracked for five consecutive years. Each year, this bird used the same counter-clockwise loop migration, the same breeding area in Hungary (Apaj region), and overwintered in Botswana (across various sites). The wintering sites across five years were located on average 217 km apart in the northern and central parts of Botswana. The bird usually used one wintering site, except in 2018, when it used two main Botswanan sites 391 km apart.

Stopovers

Altogether, 108 stopover sites were identified, 77 during the autumn and 31 during the spring migration. Rollers used more stopover sites during the autumn migration (4.4 ± 0.5 SE) than during the spring migration (3.6 ± 0.65 SE) (GLMM: $F = 4.81$; $p < 0.05$; Tukey: $p < 0.05$). The time birds spent at individual stopover sites depended significantly on the stopover type (GLMM: $F = 33.95$, $p < 0.001$).

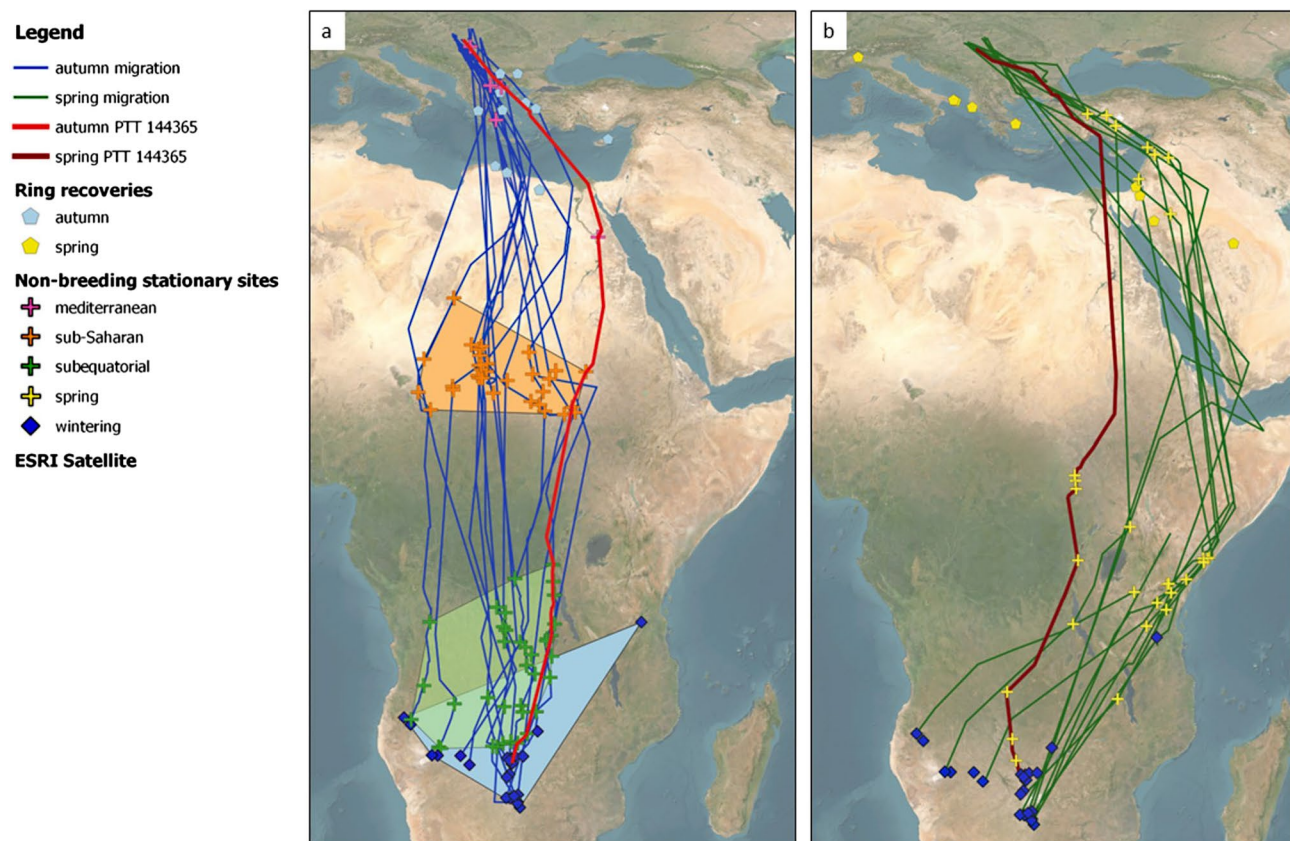


Fig. 3 Migratory pathways, stopover and wintering locations, and ring recovery locations: (a) autumn and winter; (b) spring

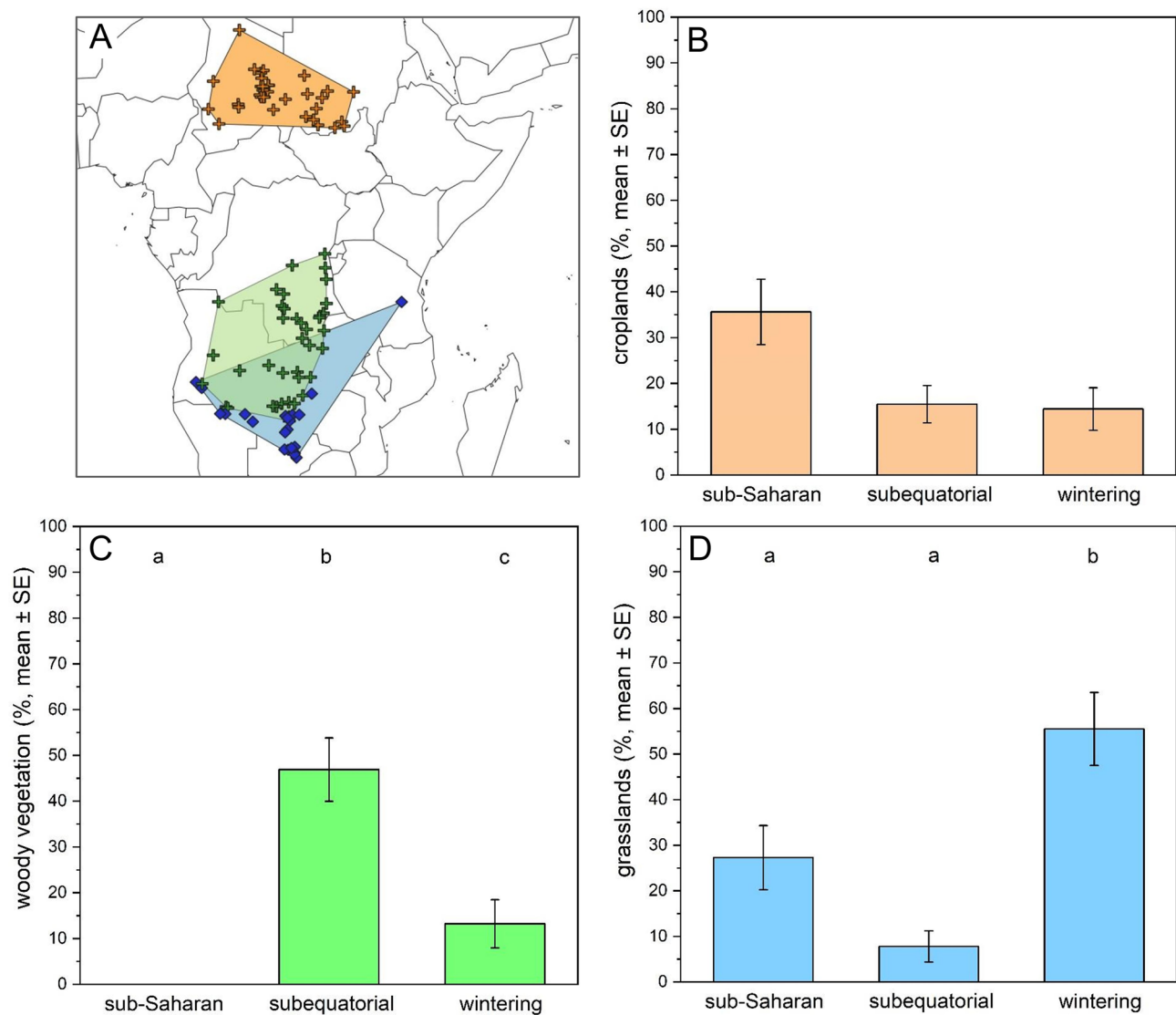


Fig. 4 (A) Location of sub-Saharan and subequatorial stopovers and the wintering sites (the convex hulls are presented for illustration only). The following panels show the proportions of the three most common habitat types, as indicated below: (B) croplands; (C) woody vegetation; (D) grasslands. The colour of the bars corresponds to the colour of the convex hull representing the location where the given habitat type was most dominant. Different letters indicate significant differences

Birds spent more time at sub-Saharan stopovers (16 ± 2.27 SE days) compared to both sub-equatorial (4.68 ± 0.73 SE days; Tukey: $p < 0.001$) and spring stopovers (4.07 ± 0.66 SE days; Tukey: $p < 0.001$). No significant difference was found between the latter two stopover types.

The PERMANOVA showed that the habitat compositions differed significantly among the non-breeding locations (PERMANOVA, overall model: $F = 13.49$, $p < 0.001$; sub-Saharan vs. subequatorial: $F = 16.19$, $p < 0.001$; sub-Saharan vs. wintering: $F = 11.80$, $p < 0.001$; subequatorial vs. wintering: $F = 10.97$, $p < 0.001$). According to our LMMs, the proportions of habitat types used by birds during the non-breeding period differed among locations only for grasslands and woody vegetation (grasslands:

LMM, $F = 12.08$, $p < 0.001$; woody vegetation: LMM, $F = 44.34$, $p < 0.001$). The proportion of grasslands was significantly higher at the wintering sites compared to the stopovers, while no significant difference was found between the two stopover types (Tukey tests: sub-Saharan vs. subequatorial, $p = 0.14$; sub-Saharan vs. wintering area, $p < 0.01$; subequatorial vs. wintering area, $p < 0.001$) (Fig. 4). The proportion of woody vegetation differed significantly among all three locations (Tukey tests: sub-Saharan vs. subequatorial, $p < 0.001$; sub-Saharan vs. wintering area, $p < 0.01$; subequatorial vs. wintering area, $p < 0.01$) (Fig. 4). For the remaining habitat types (grass-woody vegetation, croplands, and bare surfaces), no significant differences were detected. Among the random

factors, only Bird ID showed a significant effect, and this occurred only once, in the model for woody vegetation.

Discussion

Breeding home range size and seasonal patterns

Formerly, due to the lack of small, high-precision tracking devices, home range estimation largely relied on field observations. These observation-based studies found that rollers generally hunt in a 150 m [56] to 500 m [57] radius of the nest and can fly within 1–3 km from the nesting site during the breeding season [58]. This means rollers utilize a ca. 7–78 ha core area and ca. 300–2800 ha full home range size. By using high-precision tracking devices, we determined the home range size of the European roller during the breeding period and for the first time during consecutive stages of the chick-rearing period. In this study, we found the average core area size (AKDE50) to be 15.1 ha, and the average full home-range size (AKDE90) to be 85.6 ha. Our result showed the core area size similar to what was previously estimated as the full home range in Southern Hungary based on observation data (mean: 4.83 ha, range 2.25–24 ha) [59]. This highlights that the tagging methods are needed to get more precise information about the home range of the species, and it also assumes that the field observations tend to underestimate the full home range. From a conservation point of view, precise full home range data are essential for planning conservation management activities such as use of agricultural chemicals or grassland management practices.

Moreover, home range size might be affected by the geographical location, as well. Here we found similar home range size like Catry et al. [57] (70.9 ha, KDE95) in Portugal by using observation data. However, Monti et al. [36] used similar high precision devices in Croatia and Italy, and they found full home range size of 210 ha during the active breeding phase.

According to our prediction (P1), the results showed an increase in home range size over the chick-rearing period. This pattern could be explained by the changes in prey availability over the season. By intensively foraging around the nest-box during the early chick-rearing period, rollers may decrease the surrounding food abundance. At the same time, the growing nestlings require increased food intake, which could only be ensured by visiting new foraging sites at longer distances. On the other hand, roller chicks hatch asynchronously; therefore, parents are still incubating after the hatch of the first egg, which may also result in smaller home ranges. Lastly, parents may also stay close to the nest-box to defend the young hatchlings against predators, which probably limits the potential size of the home range. Changes in home range size over the breeding season have been found in other species using similar habitat like rollers

(e.g. Common kestrel: [60, 61] Little owl (*Athene noctua*): Grzywaczewski [30]).

Food availability is one of the most important factors affecting bird habitat use and home range size [62]. Habitat composition around the nesting site can affect the rollers breeding performance, though the food availability [63, 64]. Here, we were able to investigate the effect of habitat composition on the home range size during the breeding period. We confirmed that grasslands have fundamental importance in space use of rollers; and the high availability of good foraging sites like grasslands resulted in decreased home-range size. Although the quality of grasslands as foraging habitats for rollers may vary depending on management practices [65–67], our findings highlight the consistently high significance of this habitat type. Core areas were characterised by higher grassland quantity and increased grassland abundance may have decreased the energy expenditure of feeding rollers as they were able to collect enough food by using a smaller area. However, grassland management might also have contributed to the change of home range size over the breeding season. Mowing, which usually starts from the middle of June in Hungary and Romania, provides excellent foraging sites (low vegetation cover, injured insects or vertebrates), although only short-term, as the easily accessible food is also depleted by other predators. Thus, for rollers, visiting newly created foraging sites such as freshly mowed areas might be worth taking longer distances, which may increase the home range size. In Austria, Sackl et al. [68] found that rollers shifted the main foraging area from agricultural land to the freshly cut fallow and grasslands from June to mid-September. Besides grasslands, the use of extensive cropland by rollers has been reported several times [56, 57, 67]. In comparing the habitat composition between the core area and the full home range, we were able to confirm that agricultural habitats such as cropland could be used as foraging sites. We can assume that, as good quality feeding sites are depleted, suboptimal sites must also be used during the active feeding period.

Non-breeding residence and phenology

During the non-breeding period, rollers used various regions across Africa. We detected more stopover sites during the autumn migration and the birds spent longest time at the sub-Saharan stopovers compared to the spring migration or the subequatorial stopovers. For most Trans-Saharan migrant species, the sub-Saharan region serves as the wintering sites. Our results showed that the sub-Saharan region has high significance for rollers as a stopover, where roller spent on average 43 days (27–58 days) from September to mid-November, but none of the rollers used this region as a wintering site. This finding is in accordance with the results of Finch

et al. [24], who also found the Chad Basin as an important stopover site for rollers. Several species also use sub-Saharan stopovers; Eleonora's Falcons spent about 14 days in West Africa [69], while Red-backed Shrikes stayed for around 53 days [34], showing patterns similar to the studied roller population. Species using the Eastern Flyway of the African-Eurasian Flyway tend to spread over a large area in subequatorial Africa [32]. Our study showed that wintering regions of the studied roller population extended from Angola and Namibia to Botswana, Zimbabwe, and Tanzania. Similarly to the Red-backed shrikes, all roller population may benefit from the onset the wet season in the entire subequatorial savannah region [24, 34]. However, this high spread of population breeding in the Carpathian Basin over the wintering region hasn't been detected yet in other roller populations. According to the literature, there is a west-east distribution pattern in the location of wintering regions of the Roller. South-western roller populations (Spain, Portugal, France) tend to overwinter in the western part of the wintering range of the species (Angola, Namibia) ([70] Rodriguez-Ruiz et al. [37, 71]). Besides, ecological niche modelling (Rodriguez-Ruiz et al. [72]) also showed Botswana as a suitable area for the Spanish population, and predicted Zimbabwe and South Africa as important non-breeding residence sites for the overall population. Although Rollers from the Central Mediterranean region also used a wide area during the wintering season, if we look at the populations separately, rollers from Italy wintered in Angola, Namibia, Botswana and Zambia, and rollers from Croatia mainly in Botswana, Zambia, Zimbabwe and Mozambique [25]. Eastern European populations (Cyprus, Bulgaria) tend to winter in the Eastern savanna region like Tanzania and Kenya [24]. Considering the difference between high-latitude eastern breeders and the more southerly breeders, Finch et al. [24] suggested the existence of leapfrog migration; however, our results do not support this hypothesis, as Hungarian and Latvian rollers have an overlapping wintering range, and rollers from Latvia appear to winter more northward ([24]. The large winter distribution area of the studied population may be explained by the central location of the breeding areas in Europe, from where a wide range of wintering areas is accessible at the same energetic cost. The found variety of migratory pathways in the studied population may also support this hypothesis.

Differences in weather conditions and/or food supply in Africa may favour the development of different autumn and spring migration pathways [73]. Clockwise and counter(anti)-clockwise loop migration was found in several passerine species using the African-Eurasian Flyway [74]. We found that the most typical migration pathway was the counter-clockwise loop through the Arabian Peninsula for the studied rollers. This pathway

was also found in other insectivorous species breeding in Central or Eastern Europe, such as the Red-backed shrike [34]. Rollers breeding in Northern Europe used this pathway exceptionally [24]. However, not all studied rollers migrated in a loop pattern. One individual used almost the same route, starting the migration with a small western loop. This pattern was also found in a roller tagged in Cyprus [24]. Based on the ring recoveries, we also suspect a clockwise loop migration pathway in the spring migration through the Sahel and Italy. This pathway was also described in roller population breeding close to the Carpathian Basin, e.g. Austria [24] and it is a typical migration pathway of the rollers breeding in Croatia and Italy [25]. The roller population in southwestern Europe (Portugal, Spain, France) use similar migration pathways during the autumn and spring migration or follow clockwise loop migration strategy, just pathways located most westward compared to Central-Mediterranean populations [37, 70, 71]. The majority of the Hungarian population is located on the Hungarian Great Plain nowadays, but historical distribution of this population reached Austria [75], and genetic analysis showed a former connection between the Hungarian and the Austrian population in the past [76].

Migration routes can be related to the location of non-breeding areas [77], but according to our results the location of the wintering sites may not affect the migration strategy because rollers overwintering in Angola and Namibia followed the same loop migration pathways as the birds overwintering in Botswana. Individuals followed across multiple years were found to use similar areas and migratory pathways [24, 25]. In this study, we were able to follow one individual through consecutive years. This bird used the same strategy (counter-clockwise loop, wintering in Botswana) but did not use exactly the same wintering sites. Although, many migrant birds show site fidelity in the non-breeding season [78–81], in the case of on another *Coraciiform* species, the Hoopoe found that individual wintering sites often changed from year to year and distances between consecutive wintering sites can reach 1,000 km [82].

Birds using the western pathway in the African Eurasian Flyway generally depart earlier than birds following the eastern flyway [32]. In the case of the European rollers, both the year and location of the population influenced the timing of the migration [24, 37]. The initiation of the spring migration in our study was later than the median value for many populations in Europe (5 March, [24]). Former studies found a wide range for the spring departure date from the end of January until early April [24, 37, 70], our result also was in this range. We found the arrival to the breeding grounds between 3 May and 4 June, which is slightly later than recorded in most western European populations, which may be explained by the temperate continental climate of the Carpathian Basin (Spain: 14 April – 12 May, [37]

France: 8 May, [70] median arrival date to the breeding 4th May, [24]).

Conservation implications of grasslands and the European roller throughout the annual cycle

The composition and quality of habitats during the full annual cycle are important factors affecting population viability [83]. Habitat quality highly influences the reproductive output and survival of the individuals during the breeding season [84]. Stopovers are used shortly during the non-breeding season, but they are crucial spaces for refuelling, avoiding adverse environmental conditions, and ensuring the possibility of spatiotemporal adjustments [85].

During the last 200 years, at least 50% of all grassland areas have disappeared in the Eastern European region [86], and forest-steppe vegetation also suffered a large decline in Hungary [87]. Loss of their primary nesting and foraging sites is thought to be the main reason behind the large population decline of the European roller in Hungary [75]. While nest box programmes can partially compensate for nesting-site shortages [75, 88, 89], the preservation of grasslands is critical for sustaining food resources [90]. Long-term population trends of short- and long-distance migratory species in Europe are strongly related to climatic conditions on the breeding grounds and land cover change on the non-breeding grounds [91]. Our results indicate that land transformation and degradation in the Sahel can affect species even if they do not winter there, through extended stopover periods. Severe drought in this region was proven to be behind the decline of the breeding population of many species [92]. The area has experienced dry periods since the late 1960s, with a large-scale drought during 1982–1985 [93]. The drought affected Sahelian (Chad region) stopovers of the rollers, the wintering sites and the spring stopover regions in Somalia, as well.

Wintering habitats contribute to winter survival, influence the individual condition and phenology, e.g. using sub-optimal habitat at wintering grounds can result in delayed spring migration, negatively affecting breeding performance the following season [94, 95]. Here, we found the highest quantity of natural grasslands in the wintering region, where the rollers spend the longest time during the non-breeding period. Some areas in this region also suffer significant land use change e.g. 26% loss of natural land cover was recorded in Eastern Botswana due mainly to transition into croplands, built-up areas [96]. Long-distance migrant birds tend to show a high spread over the non-breeding range [33]. The same pattern was found in another European population of rollers [24], and our study also confirmed it. Weak migratory connectivity makes the population less threatened by local environmental conditions at one locality, but it raises the need for widespread international cooperation for the species' conservation. In the case of the rollers, migratory pathways may differ in mortality as illegal and legal hunting

pressure varies across regions [97] and this may have effect at population level [98]. To secure the conservation status of migratory lands on the African-Eurasian Flyway, the African-Eurasian Migratory Landbirds Action Plan (AEMLAP) [99] was accepted, and a roller-specific Flyway Action Plan (FAP) was also adopted [28]. Both plans emphasised habitat loss as one of the most important threats. The FAP emphasises the significance of promoting research programs to identify key habitats for European Rollers along the flyway and fill the knowledge gap on the migration pattern of species [28]. In accordance with that, our results highly contribute to knowledge about the roller migration and habitat use during the full annual cycle and help the fine tuning of listed actions in the FAP in time and space.

Conclusions

Preserving suitable habitats throughout the full annual cycle is one of the greatest challenges in the conservation of long-distance migrant species. Here, we investigated the habitat and space use of the European rollers breeding in the Carpathian Basin and confirmed the high importance of grasslands throughout the full annual cycle. Our results showed that the proportion of grasslands and the breeding phase have a significant effect on the home range size. We firstly described the migration routes, stopover regions and wintering areas of this population and confirmed multiple migration strategies and high spread over the wintering regions. Besides, we would like to highlight the significance of the subequatorial savannah region as a wintering region, which is also highly threatened by climate and land use changes in the future. We showed that a population with a relatively small spatial extent (the Carpathian Basin) relies on grassland habitats distributed over a large part of Africa, therefore, our results highlight the necessity of flyway-scale actions for more effective conservation, and the local field actions need to have the legal back-up of international conventions.

Abbreviations

AKDE Autocorrelated Kernel Density Estimation

Supplementary Information

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Supplementary Material 1

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Author contributions

OK, BT, SJD, LB, and AK conceived of the presented idea. OK, BT, SJD, and LD did the fieldwork. OK processed and analysed the PTT and UHF logger data. JBW processed and analysed the geolocator data. AK and OK did the statistical analysis. OK took the lead in writing the manuscript, and all authors discussed the results and commented on the manuscript.

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Data availability

PTT data can be found in [https://www.movebank.org/cms/movebank-main]: Rollerproject (Movebank ID:320565344) and Roller 2015 (Movebank ID: 93481044) and in [https://www.satellitettracking.eu/]. The European Roller (*Coracias garrulus*) is a strictly protected species, therefore fixes collected during the breeding period are not suggested to be shared publicly. These data will be made available on request. Geolocator data is available in the following data package: Wong, J., Hahn, S., Kiss, O., Dr. Tokody, B., Daróczi, S., & Stumberger, B. (2025). Geolocator Data Package: European Rollers (*Coracias garrulus*) in Hungary, Romania and Montenegro (1.1.1) [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.17882693>

Declarations

Ethics approval and consent to participate

The animal handling and tagging were carried out in accordance with national nature conservation laws as well as bird ringing and ethical regulations. Permit numbers in Romania are G118224, G118424 and OKTF-KP/58 – 16/2015 in Hungary.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Author details

¹Faculty of Agriculture, Institute of Animal Sciences and Wildlife Management, University of Szeged, Andrassy u. 15, Hódmezővásárhely HU-6800, Hungary

²BirdLife Hungary, Költő u. 21, Budapest HU-1121, Hungary

³Bird Migration Unit, Swiss Ornithological Institute, Seerose 1, Sempach CH-6204, Switzerland

⁴Milvus Group– Bird and Nature Protection Association, Crinului street 22, Târgu Mureş RO-540620, Romania

⁵Department of Ecology, University of Szeged, Közép Fásor 52, Szeged HU- 6726, Hungary

⁶‘Lendület’ Seed Ecology Research Group, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Alkotmány út 2–4, Vácrátót HU-2163, Hungary

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