# Breeding phase and outcome determine space use in European rollers *Coracias garrulus* prior to migration

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## Abstract

The breeding period is a demanding and time-constrained phase for migratory bird species. Breeding outcome and duration can interact with the extent and duration of post-breeding movements, resulting in individual differences in space use ultimately influencing later stages of the annual cycle. We present space-use and home range estimates during the breeding season for 21 European rollers *Coracias garrulus* tracked between 2018 and 2022, in Italy and Croatia. Using high-resolution spatial GPS data coupled with regular nest-box monitoring, we analyzed differences in space use during the incubation/nestling period versus post-breeding period prior to migration, accounting for the breeding outcome (successful vs. failure). We found that adult movements were strongly reduced during the first phase, whereas increased in the post-breeding phase, especially for failed breeders. Successful breeders remained in the surroundings of the nest site, whereas unsuccessful ones tended to abandon the nest and visit distant areas (up to 500 km) for long periods (60.5 ± 6.2 days). Breeding outcome did not influence the departure date of autumn migration, suggesting that failed breeders used this period for exploratory movements but not for advancing the onset of migration. Such exploratory movements may be functional to prospect and inform settlement decisions in failed breeders in search of new breeding opportunities and may be particularly important in migratory species, which generally have a limited period to gather information prior to autumn migration. The study demonstrates the need to investigate seasonal movements in different populations and the potential importance of prospecting post-breeding movements for long-distance migratory species.

**Key words:** animal movement, biologging, conservation, *Coraciidae*, Mediterranean, nest-box, population monitoring, prospecting movements, reproduction.

Migratory birds are subjected to large spatio-temporal variations in environmental conditions throughout their life cycle. Traveling through inter-continental flyways, migratory individuals experience multiple habitats within a landscape system (Newton 2010). The annual cycle of a migratory species is complicated by the fact that individuals deal with a wide range of factors encountered not only over long-distance journeys encompassing vast geographic areas (Knudsen et al. 2011; Studds and Marra 2011; Marra et al. 2014) but also during wintering and breeding periods. Varying ecological conditions during the year can drive movement strategies and generate alternative behaviors to meet the minimum requirements for survival (in the short term) and for maintaining fitness (in the medium to long term) (e.g., Newton 2010). Thus, investigating each phase of the life cycle is important for targeted conservation measures.

In particular, the breeding period is an important phase of the annual cycle (Berthold 2001), not only for reproduction but also because the duration and outcome of the reproduction itself can influence later stages of the annual cycle (e.g., Norris and Marra 2007; Bogdanova et al. 2011) or the

next season (Harrison et al. 2011). Breeding outcome (success vs. failure) and consequently the breeding duration can interact synergistically with the extent and duration of the post-breeding movements, and lead an individual to adopt different movement strategies prior to embarking on the long migratory journey (i.e., adjusting departure dates of autumn migration, selection of staging areas, etc.). After a successful breeding event, a period of post-fledging dependence period follows, with adults likely remaining in the surrounding of the nest site (e.g., Verhulst and Hut 1996; Sunde et al. 2003). In contrast, failed breeders can either choose to renest or abruptly abandon the breeding territory and start exploring distant areas, searching for foraging opportunities and/or prospecting for future breeding opportunities (e.g., Berger-Geiger et al. 2022). Long-distance migratory birds are extremely time-constrained as their stay at the breeding grounds is relatively short. In many species, only breeders that fail very early in the breeding season (laying period or soon after) can presumably afford to start a replacement clutch (Cramp and Simmons 1988; Newton 2010). Prospecting during the breeding season has been recorded predominantly in

non-breeding individuals or those whose nests failed before-hand (Cooper and Marra 2020; Ciaglo et al. 2021). Indeed, an individual may choose to reproduce on a site visited during the previous year and where it acquired information about habitat quality/suitability and resource availability (e.g., nest and trophic resources availability, reproductive performance of conspecifics; Avilés et al. 2000; Parejo et al. 2005; Patchett et al. 2022). Migratory species, constrained by strong selective pressures on migration phenology especially in spring for an early return to breeding grounds, may be expected to prospect for future nesting sites once the breeding season is over (Pärt et al. 2011). On the other hand, a failed breeder can also choose to advance the onset of migration reaching non-breeding destinations earlier to gain time against conspecifics, thus selecting better places for wintering (e.g., Bogdanova et al. 2011). Failed or sabbatical breeders, often molt earlier because they are freed from their breeding duties, thus being less constrained by molting schedules to reach wintering grounds (e.g., Catry et al. 2013). In addition, site fidelity and breeding success can differ between age classes, being also directly dependent on the age of the bird and survival prospects. For example, in the European roller *Coracias garrulus* (hereafter "Roller"), juveniles' apparent survival was found to be significantly lower than that of adults, although highly overlapping between sexes, whereas the effect of age or sex on nest site fidelity was not apparent (Rodríguez-Ruiz et al. 2020). However, Roller males raising more fledglings in one year were more likely to return to the same site the following year (Rodríguez-Ruiz et al. 2020). In addition, other factors such as habitat composition and diversity, as well as resource availability have been found to influence space use and breeding performances (e.g., Avilés et al. 2000). How birds behave and which factors shape their movement decisions can hence differ among habitats, years, populations, and/or individuals (e.g., Clobert et al. 2009).

Here, we focus on the breeding biology of the Roller, a long-distance migrant and an insectivorous, obligate secondary cavity-nesting species typical of agricultural landscapes, and of conservation concern (Cramp and Simmons 1988; Finch et al. 2017). The species has suffered greatly from habitat loss at breeding sites, caused by changing agricultural practices that extensively occurred across Europe in the last decades (Franco and Sutherland 2004; Giralt et al. 2008; Butler et al. 2010). Modernization and intensification of agricultural production had a presumably 2-fold effect on the Roller: a decrease in prey availability (brought by the conversion of pastures to arable lands, traditional arable land into monoculture, as well as intensified use of pesticides) and a decrease in the availability of natural nesting cavities (brought by removal of hedges and trees). These limiting factors differently affected different populations (Finch et al. 2019). As a result, roller populations suffered a significant decline, and local extinctions of breeding populations were recorded in several countries (Cramp and Simmons 1988; Kovács et al. 2008; BirdLife International 2017). To reverse this trend, direct management measures, such as nest-box provisioning, were implemented which contributed to national recoveries (e.g., Avilés and Parejo 2004, Ružić et al. 2014; Kiss and Tokody 2017; Barišić et al. 2018; Monti et al. 2019). However, the species cannot yet be considered in a favorable conservation status as it has been decreasing in the last 30 years across its European breeding range (Keller et al. 2020). The roller has been listed as the EU priority species and thus deserves protection along the entire flyway (BirdLife International 2017; Tokody et al. 2017). Since local populations might be limited by different factors, context-dependent conservation interventions may be necessary and might vary across the species' European breeding range (Kovács et al. 2008, Finch et al. 2019). This highlights the importance of conducting comparative ecological studies of different populations (Kiss et al. 2014; Finch 2016; Saunders 2016).

Innovations in tracking technologies have favored advances in the fundamental understanding of ecology and animal behavior, providing an enormous volume of data (e.g., the era of big data; López-López 2016) and research possibilities. Thanks to that, an increasing number of studies have investigated the migration ecology and wintering range of the Roller (Catry et al. 2014; Emmenegger et al. 2014; Rodríguez-Ruiz et al. 2014; Finch et al. 2015).

Yet, although several studies have investigated Rollers' breeding ecology in Spain (e.g., Avilés et al. 2000; Avilés and Parejo 2004), France (e.g., Bouvier et al. 2014; Schwartz et al. 2020), Austria (e.g., Tiefenbach 2009) and other countries (Kovács et al. 2008; Kiss et al. 2014; Saunders 2016; Finch et al. 2019), substantial gaps still exist, both geographically and thematically, especially concerning specific phases of the annual cycle. Little attention has so far been given to Roller's movement ecology during the breeding period (e.g., Saunders 2016) and in particular the post-breeding movements prior to autumn migration. For example, it is unclear how and where Rollers spend time before and after nesting, before starting the migration, and which factors drive these movements. Moreover, studies comparing movement parameters between different breeding populations have not yet been carried out in detail.

The aim of this study was to investigate Roller's spatio-temporal variation in movement components at breeding grounds, using high temporal and spatial resolution global positioning system (GPS) data coupled with regular population monitoring. We aimed at (1) quantifying Roller home range size and other key movement components (e.g., mean daily distance and mean distance to nest site) at breeding grounds, looking for differences in space use between phases (e.g., incubation/chick rearing phase versus post-breeding phase); (2) investigating the spatio-temporal variation of movement components in relation to reproductive outcome (success vs. failure). We specifically tested whether adult birds behaved/moved accordingly and quantified it. Finally, (3) we investigated prospecting movements, their extent and duration, both during the breeding and post-breeding phase.

## Materials and Methods

### Study areas and populations

The study was performed in 2 different areas of the Mediterranean region hosting Roller breeding populations: one in Central Italy (Monti et al. 2019) and another in coastal Croatia (Barišić et al. 2018). In Italy, to improve nest site availability for the species, nest-boxes on metal pylons of high-voltage power lines have been installed since 2010, across the provinces of Rome and Viterbo (42°12′ N 11°53′E) in the Lazio region (Monti et al. 2019). This area, of about 700 km², is characterized by intensive arable farmland and organic cereal crops, fragmented by grasslands with bushes and trees: urban artefacts are present but in low density.

Other habitats include fallow fields mainly used for livestock rearing and olive groves (Monti et al. 2019).

Similarly, birds breeding in nest-boxes in Ravni Kotari region (44°05′N 15°30′E, northern Dalmatia) represented the study population in Croatia. The Ravni Kotari area, of about 651 km², has been designated as a NATURE 2000 site (https://eunis.eea.europa.eu/sites/HR1000024). As reported by Barišić et al. (2018), most of the localities where Rollers are currently breeding are remains of former marshlands that have been drained and transformed into fertile agricultural fields and grasslands. Poplar trees have been planted in hedgerows along excavated drainage channels as windbreaks, forming a grid of trees. Transformation of marshes into pastures provided suitable forging grounds, whereas poplars provided nesting cavities. As poplars have not been renewed over the years, to improve nest site availability, nest-boxes have been provided since 2013 in Ravni Kotari.

## Population monitoring

Roller population monitoring involved repeated surveys of population metrics, to be implemented for ecological purposes (sensu: Sutherland et al. 2004). In both countries, Roller breeding populations have been monitored every year since 2010 (Italy) and 2011 (Croatia). Rollers usually arrive at the breeding grounds over a period of several weeks between late April and early May. The onset of egg-laying is normally between late May and mid-June. The initiation of a replacement clutch after the failure of the first clutch is possible, though rare in the Roller (Cramp and Simmons 1988; Parejo et al. 2011). Nest-boxes were checked weekly during the breeding season (between the end of April and the end of July) to assess occupancy and main breeding parameters (e.g., clutch size, number of hatched eggs, and fledged chicks). A nest-box was considered occupied if at least one egg was laid (e.g., Finch 2016). The hatching date was determined in the field for each nest-box by visual inspection of the chicks' age (Birdlife Hungary 2013). A breeding attempt was considered "successful" if at least one chick fledged.

## Capture and tracking techniques

Between 2018 and 2021, 21 adult rollers (Italy: 3 females and 7 males, 17 breeding events; Croatia: 5 females and 6 males, 14 breeding events), were trapped in their nest-box during incubation after clutch completion or during the nestling period. Since both sexes participate in the incubation and rearing phase (Cramp and Simmons 1988), both females and males were opportunistically trapped. These birds were tagged with 3.5g GPS loggers with automatic wireless radio download: Gipsy-Remote XS (Technosmart Europe srl, Rome, Italy) in Italy, and NanoRadio Tag-3 (Milsar Technologies, Cluj, Romania) in Croatia. Captured birds were measured and ringed with a metal ring in Italy and with metal and plastic (black with yellow 3-letter inscription) rings in Croatia. Sex was assessed by visual inspection of morphological characters and, for Italian birds, confirmed by molecular methods (e.g., Griffiths et al. 1998). Loggers were mounted as a backpack 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; $n = 20$). Devices were initially programmed to collect daytime GPS position every 30 min and, when necessary, remotely reprogrammed via a stand-alone unit (base station). Those that were showing

signs of battery depletion were reprogrammed to collect position in wider time intervals than 30 min, depending on the battery status. For Croatian birds, as most of the loggers consistently manifested unfavorable battery conditions and to avoid battery failure, the loggers were reprogrammed to collect a position every 4 h outside the nesting area, i.e., when out of reach for reprogramming. Thus, the frequency of acquisition of the positions was adjusted according to the state of the battery, sometimes resulting in non-uniform daily relocations, depending on individual birds and periods. Data were gathered using a base station that allows automatic wireless radio downloading links of all remote devices in its working range (up to 500 m in line of sight). GPS data were systematically downloaded during each field visit provided that the bird stayed in the vicinity of the nesting area and/or the following year, on the return of the tagged individual to the nesting area. Although quantitative data on Roller natal and breeding philopatry is limited (Parejo et al. 2005), breeding dispersal is believed to be low, with Rollers often nesting in the same cavity in subsequent years (Cramp and Simmons 1988; Finch 2016), thus permitting high chances of remote data downloading. Details on the number of transmitters deployed, year of deployment, bird's ID, and monitoring periods are reported in Table I.

## 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. Since we were interested in evaluating differences in movement tactics during different phases of the breeding season, the tracking data were distinguished into the following phases: (1) A "pre-breeding phase" (PRBP) including movements between the arrival to breeding areas after spring migration and the start of egg laying (date assessed per field visits). (2) An "active breeding phase" (ABP), when a bird behaves as a central place forager (Bell 1990) tightly linked to the nest site. We set this phase to start with the laying of the first egg and to include incubation and/or nestling-rearing stages. Nestlings hatch asynchronously and stay in the nest for 25–30 days (Cramp and Simmons 1988), and as long as there is at least one nestling in the nest, the parent continues to behave as a central place forager. Thus, we set the ABP to end after 30 days from the day when the first egg hatched. (3) A "post-breeding phase" (POBP), when a bird is no longer tied to its nesting place, between the end of the ABP and the onset of autumn migration. Notably, as it was not possible to clearly distinguish from GPS and field data the threshold between post-breeding (last phase of young provisioning) and pre-migratory movements (preparation for autumn migration) in the case of successful breeders, we referred only to post-breeding movements in a broader sense (phase in which the bird is no longer closely linked to the nest), thus including also movements in the context of migration preparation within the POBP.

The start of autumn migration was defined as a southward movement of >100 km/day without a return flight towards the north, following Berger-Geiger et al. (2022).

The ABP and POBP can vary considerably according to the breeding outcome. Thus, we further distinguished if the breeding attempt was: (1) "successful", if at least one chick fledged or (2) "failed", if the eggs did not hatch, were predated/stolen, and/or no chicks fledged (thus, in these cases the ABP was truncated). This further classification helped in

defining the final and initial date for both the ABP and POBP, respectively.

## Home ranges and movement components

To describe the breeding areas, we estimated the individuals' home ranges (HR, 95% kernel) and core areas (CA, 50% kernel) based on all GPS positions through fixed kernel density contours (sensu Worton 1989), with the R "adehabitatHR" package (Calenge 2006). As an alternative metric, we also computed the Minimum Convex Polygon (MCP) encompassing all GPS locations obtained for each bird (Worton 1989). We summarized and contextualized movement statistics by linear and cumulative distances. Linear distances were those traveled between consecutive GPS locations. By summing the distances between all consecutive GPS locations recorded daily, we got an estimate of the distance traveled per day (dependent on the number of fixes). From that, we computed the mean daily distance for both ABP and POBP. Similarly, the mean distance to the nest was calculated as the average among all the distances of each fix from the nest, during each referring phase. For each phase, minimum and maximum distances to the nest site were also computed. All these metrics should be considered as a lower estimate since additional flight segments most likely occurred between 2 recorded fixes. In addition, the number of fixes per day (and thus metrics' accuracy) was associated with the battery status of GPS loggers.

## Statistical analysis

Due to the limited sample size during the PRBP ($N = 11$), possible differences in movement components between populations (Croatia vs. Italy) and sex were tested through the non-parametric independent 2-group Mann–Whitney $U$ test. During the ABP and the POBP, movement components and space use by rollers were analyzed using generalized linear mixed models (GLMMs; Zuur et al. 2009). We modeled 4 spatio-temporal response variables separately: (1—3) HRs, CAs, and MCP size estimates; and (4) mean distance to nest. Due to a skewed distribution of residuals for the presence of extreme values in the dataset, these variables were log-transformed. To specifically address our working hypotheses, analyses were carried out at 2 levels (Appendix S1). In the first model selection, we included the following predictors: Country (categorical; reference level: Italy vs. Croatia) to account for inter-population variability; sex (categorical; reference level: males vs. female) to account for gender variability in movement strategies; and phase of the breeding season (categorical; reference level: ABP vs. POBP) to account for differences in space use between phases. In the second model selection, we replaced one of the predictors (i.e., the sex, as non-significant in the first model selection) with the breeding outcome (categorical; reference level: successful vs. failure). In all models, the "individual's ID" and "year" were used as random effects, to take into account repeated observations in the case of individuals monitored for several years. For each response variable, we calculated and compared a set of biologically plausible models, including different combinations of predictors, according to the information-theoretic approach (Burnham and Anderson 2002). Accordingly, each model evaluation, including a different combination of predictors, could represent a different

a priori hypothesis. The null model was also evaluated to allow for an assessment of model performance relative to a fixed baseline (Mac Nally et al. 2018). Following a conservative approach (Burnham and Anderson 2002; Richards 2008; Richards et al. 2011), we did not select models with $\Delta$AICc $\geq 2$ in respect to the best model (the model with the lowest AICc value), as well as models with an AICc value greater than that of any simpler alternative, thus achieving either a set of top-ranked models or a single best model for each response variable while accounting for nesting (Tables 3 and 5). According to Richards et al. (2011), we based inference on selected models. For each response variable and from each selected model, we estimated coefficients of predictors and 95% confidence intervals. Estimates for the best models are reported in Tables 4 and 6. The effects of predictors were assessed by checking whether 95% confidence intervals of coefficients overlapped 0. Models were validated through visual inspection of residual patterns (Zuur et al. 2009). All the analyses were performed in R version 4.0.3 (R Core Team 2020), through the packages MuMIn (for model selection; Bartoń 2013) and lme4 (for GLMMs; Bates et al. 2015). Plots for the top-ranked models were obtained using package "effects" version 4.2-0 (Fox 2003, 2019) and readapted using "ggplot2" version 3.2.1 (Wickham 2016). The independent 2-group Mann–Whitney $U$ test was used to search for differences in departure dates between successful versus failed breeders ($N = 13$). Descriptive statistics are reported as mean ± $SD$.

## Results

Twenty-one rollers were tracked over 5 years (2018–2022). Overall, the dataset included 31 breeding events since 6 birds from Italy and 3 from Croatia were monitored for 2 consecutive breeding seasons (Table 1). In addition, 1 bird did 2 breeding attempts in the same year with different partners and at different nests, which were considered as distinct breeding events. In one case, a bird settled in a natural cavity during its second breeding season. Out of 31 breeding events, 74.2% were successful ($N = 23$) and 25.8% unsuccessful ($N = 8$). The majority of failures were recorded in Italy (all but one). We retained a total number of 31,224 valid GPS locations, evenly distributed between the 2 main periods (15,891 during the ABP and 13,228 during the POBP) and considerably less for the PRBP (2,105). The mean number of GPS positions per bird was 512 ± 423 during the ABP and 778 ± 602 during the POBP. According to the available data per individual and season, the sample size may vary between different analyses. Only individuals with complete POBP data were used for running the generalized linear mixed models. For PRBP phase (from arrival to nest site occupancy), data were obtained for 11 events from 10 individuals (5 from Croatia and 5 from Italy; 3 females and 7 males), with a mean number of GPS locations per bird of 191 ± 287.

### Movement components across periods

PRBP lasted on average 19.2 ± 11.1 days. Movements were restricted in the surrounding of the successively occupied nest site (Appendix S2). HR was 34.3 ± 109.1 km$^2$ and CA 7.5 ± 24.2 km$^2$. MCP was 26.8 ± 67.1 km$^2$, whereas the mean daily distance and mean distance to nest were

**Table 1.** Information for 21 adult Rollers (31 breeding events) tracked between 2018 and 2022 in Central Italy and Croatia

| Breeding event | Country | Year | Ring code | Sex | Start ABP | End ABP | N. of fix ABP | Breeding Outcome | Start POBP | End POBP | N of fix POBP |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Croatia | 2018 | KA2388 | M | 07/06/2018 | 27/06/2018 | 852 | Successful | 28/06/2018 | 21/07/2018$ | 1037 |
| 2 | Croatia | 2018 | KA2389 | F | 10/06/2018 | 05/07/2018 | 451 | Successful | 06/07/2018 | 03/09/2018° | 481 |
| 3 | | 2019 | KA2389 | | 29/05/2019 | 19/06/2019 | 28 | Successful | NA | NA | NA |
| 4 | Croatia | 2018 | KA2390 | M | 11/06/2018 | 05/07/2018 | 1194 | Successful | 06/07/2018 | 03/09/2018° | 1211 |
| 5 | | 2019 | KA2390 | | 08/06/2019 | 31/07/2019 | 498 | Successful | 01/08/2019 | 09/09/2019° | 385 |
| 6 | Croatia | 2018 | KA2392 | M | 19/06/2018 | 11/07/2018 | 872 | Successful | NA | NA | NA |
| 7 | Croatia | 2019 | KA2449 | F | 04/07/2019 | 07/08/2019 | 708 | Successful | 08/08/2019 | 10/09/2019° | 535 |
| 8 | Croatia | 2019 | KA2450 | M | 05/07/2019 | 01/08/2019 | 1020 | Successful | NA | NA | NA |
| 9 | Croatia | 2019 | KA2452 | M | 06/07/2019 | 14/07/2019 | 111 | Failure | NA | NA | NA |
| 10 | Croatia | 2020 | KA2738 | F | 08/06/2020 | 05/07/2020 | 836 | Successful | 06/07/2020 | 09/09/2020° | 1686 |
| 11 | Croatia | 2020 | KA2739 | F | 10/06/2020 | 09/07/2020 | 73 | Successful | 10/07/2020 | 15/07/2020$ | 17 |
| 12 | Croatia | 2020 | KA2377 | M | 15/06/2020 | 08/07/2020 | 140 | Successful | 09/07/2020 | 17/09/2020° | 276 |
| 13 | | 2021 | KA2377 | | 01/06/2021 | 28/07/2021 | 125 | Successful | NA | NA | NA |
| 14 | Croatia | 2020 | KA2675 | F | 25/06/2020 | 14/07/2020 | 356 | Successful | NA | NA | NA |
| 15 | Italy | 2019 | H214101 | M | 24/06/2019 | 09/07/2019 | 419 | Successful | NA | NA | NA |
| 16 | Italy | 2019 | H214125 | M | 27/06/2019 | 03/07/2019 | 168 | Failure | 04/07/2019 | 09/09/2019° | 935 |
| 17 | | 2020 | H214125 | | 04/06/2020 | 18/06/2020 | 88 | Successful | NA | NA | NA |
| 18 | Italy | 2018 | H207548 | M | 20/06/2018 | 04/07/2018 | 1126 | Failure | 05/07/2018 | 05/09/2018° | 2191 |
| 19 | | 2019 | H207548 | | 08/06/2019 | 03/08/2019 | 1393 | Successful | 04/08/2019 | 27/08/2019$ | 993 |
| 20 | Italy | 2020 | H218344 | M | 27/06/2020 | 22/07/2020 | 668 | Successful | 23/07/2020 | 01/09/2020° | 432 |
| 21 | | 2021 | H218344 | | 11/06/2021 | 05/07/2021 | 189 | Successful | NA | NA | NA |
| 22 | Italy | 2019 | H212221 | F | 14/06/2019 | 01/07/2019 | 313 | Failure | NA | NA | NA |
| 23 | Italy | 2019 | H212223 | M | 20/06/2019 | 29/07/2019 | 1432 | Successful | 30/07/2019 | 03/09/2019° | 404 |
| 24 | | 2021 | H212223 | | 24/06/2021 | 21/07/2021 | 982 | Successful | NA | NA | NA |
| 25 | Italy | 2019 | H212220 | F | 23/06/2019 | 07/07/2019 | 593 | Failure | NA | NA | NA |
| 26 | Italy | 2020 | H218306 | F | 28/05/2020 | 04/06/2020 | 136 | Failure | 05/06/2020 | 27/07/2020$ | 1376 |
| 27 | Italy | 2020 | H218338 | M | 19/06/2020 | 22/07/2020 | 442 | Successful | 23/07/2020 | 12/09/2020° | 116 |
| 28 | | 2021 | H218338 | | 01/06/2021 | 28/07/2021 | 153 | Successful | 29/07/2021 | 20/09/2021° | 135 |
| 29 | Italy | 2020 | H218335 | M | 12/06/2020 | 24/06/2020 | 327 | Failure | NA | NA | NA |
| 30* | | 2020* | H218335 | | 30/06/2020 | 08/07/2020 | 129 | Failure | 09/07/2020 | 08/09/2020° | 1018 |
| 31 | | 2021 | H218335 | | 31/05/2021 | 20/06/2021 | 69 | Successful | NA | NA | NA |

*Indicates a second breeding attempt with another female at another nest in the same year.
$Indicates interrupted monitoring during POBP prior to autumn migration (POBP data associated with these birds were not included in the model selection).
°Indicates the onset of migration.
Abbreviation: N. of fix: number of GPS-positions (fixes) recorded.

2.8 ± 4.3 km/day and 1.1 ± 1.4 km, respectively (*N* = 11). However, when excluding bird #KA2390 as the only one which repeatedly moved between 2 areas ca 24 km apart, home range metrics were limited to nests' surroundings for all other birds (HR: 1.4 ± 1.6 km², CA: 0.2 ± 0.3 km²). Accordingly, the mean distance to nest drastically dropped (0.3 ± 0.2 km; *N* = 10). Bird #H207548 reached a maximum distance to the nest of 23.3 km, but positions this far from the nest were seen only once. During this phase, movement components did not differ between populations and sexes (Table 2).

During the ABP, home ranges and core areas were restricted. On average, HR was 2.1 ± 2.7 km², CA 0.3 ± 0.6 km² and MCP 4.1 ± 5.1 km² (*N* = 31). The mean daily distance was 7.4 ± 7.1 km/day, whereas the mean distance to nest was 0.4 ± 0.4 km. The maximum distance to nest recorded during this period was 12.4 km (bird #H214125). When considering ABP data only, a significant "Country" effect emerged with the Italian Rollers showing larger movement components than the Croatian Rollers, as retained by model selections (Appendix S3).

During the POBP, all Rollers increased their home ranges and core areas, as retained by the first model selection (Table 3–4; Figure 1A,B). In particular, mean HR was 7,945.6 ± 30,747.4 km² and CA 570.3 ± 2,140.3 km² (*N* = 17). MCP was 8,444.9 ± 31,622.8 km². However, two individuals (#H214125 and #H218335), which performed very large excursions, mainly contributed to these high values, whereas for all the others the increase was less marked but still significant (HR = 33.3 ± 33.4 km²; CA = 6.0 ± 7.1 km; Independent 2-group Mann–Whitney *U* test: = U = 13; *P* = 0.001; *N* = 15). The mean distance to nest site was about ca 60.1 fold higher during the POBP (24.1 ± 76.1 km) than during the ABP. Model selection retained an additive effect

between phase and country (Tables 3–4; Figure 1C,D; Appendix S4), indicating higher distances to nests for Italian Rollers during the POBP, and thus suggesting a more focused

**Table 2.** Differences in Roller's movement components ($N$ = 11) between populations (Croatia vs. Italy) and sexes during the pre-breeding phase (PRBP), tested through the non-parametric independent 2-group Mann–Whitney $U$ test

| Movement components | Population | | Sex | |
|---|---|---|---|---|
| | $U$ | $P$ | $U$ | $P$ |
| HR | 11 | 0.5 | 7 | 0.3 |
| CA | 14 | 0.8 | 10 | 0.7 |
| MCP | 8 | 0.2 | 6 | 0.2 |
| Mean daily distance | 12 | 0.6 | 9 | 0.5 |
| Mean distance to nest | 13 | 0.7 | 11 | 0.8 |

HR: home range (km²), CA: core area (km²), MCP: minimum convex polygon (km²), mean daily distance (km/day), mean distance to nest (km).

analysis (see second model selection). The predictor "sex" was never retained.

In the second model selection, all movement components were influenced by a significant effect between the phase and the breeding outcome (Table 5–6; Figure 2). Specifically, HR, CA, MCP and mean distances to nest were significantly larger during POBP, and in particular for failed breeders (Table 5–6; Figure 2A–D; Appendix S4).

Mean dates of departure for autumn migration did not differ between successful and failed breeders (Independent 2-group Mann–Whitney $U$ test: $U$ = 13, $P$ = 0.7; $N$ = 13). For 10 out of 13 birds (77%), autumn migration started within the first decade of September (range of departure date: 01/09-20/09; $N$ = 13).

## Large prospecting movements

We recorded peculiar long-distance prospective movements by 2 failed breeders (Figure 3). In particular, the maximum distance to the nest recorded during the POBP was 515.2 km (bird #H214125). This bird abandoned the nest on 03/07/2019 (a few days after the abandonment of the

**Table 3.** Result of the first model selection on the effects of country (Italy vs. Croatia), sex (male vs. female) and phase (active breeding phase vs. post-breeding phase) on movement components of breeding Rollers: selected models with ΔAICc < 2 and with an AICc value smaller than that of any simpler alternative, while accounting for nesting. Summaries of selected models are shown. Sample size is reported in brackets.

| Response variable (sample size) | Model_id | Models retained | K | AICc | ΔAICc | Weight | Cum. Weight | logLik |
|---|---|---|---|---|---|---|---|---|
| Home range—HR 95% (45) | 1 | ~Phase + Country | 6 | 202.82 | 0.00 | 0.33 | 0.33 | –94.30 |
| | 2 | ~Phase | 5 | 202.94 | 0.12 | 0.31 | 0.64 | –95.70 |
| Core area—CA 50% (45) | 1 | ~Phase | 5 | 223.13 | 0.00 | 0.32 | 0.32 | –105.80 |
| Minimum convex polygon (45) | 1 | ~ Phase + Country | 6 | 187.37 | 0.00 | 0.41 | 0.41 | –86.58 |
| | 2 | ~Phase | 5 | 188.66 | 1.29 | 0.21 | 0.62 | –88.56 |
| Mean distance to nest—km (45) | 1 | ~ Phase + Country | 6 | 142.12 | 0.00 | 0.43 | 0.43 | –63.96 |

**Table 4.** First model selection: best models of country (Italy vs. Croatia), sex (male vs. female) and phase (ABP—active breeding phase *vs.* POBP—post-breeding phase) on movement components of breeding Rollers, assessed through GLMMs. Coefficients (β), *SE* and 95% confidence intervals (95% CIs) are shown. In bold are marked the 95% confidence intervals which do not include 0

| Response variable | To-ranked model | Predictor | β | SE | 95% CI | |
|---|---|---|---|---|---|---|
| Home range—HR 95% | 1 | (Intercept) | –0.4195 | 0.4820 | –1.3641096 | 0.5251202 |
| | | Phase (POBP) | 4.1525 | 0.6309 | **2.9160230** | **5.3890737** |
| | | Country (Italy) | 1.0197 | 0.5969 | –0.1502242 | 2.1895437 |
| | 2 | (Intercept) | 0.1353 | 0.3697 | –0.589256 | 0.8598231 |
| | | Phase (POBP) | 4.1955 | 0.6447 | **2.931923** | **5.4591252** |
| Core area—CA 50% | 1 | (Intercept) | –1.9895 | 0.4698 | –2.910229 | –1.068747 |
| | | Phase (POBP) | 4.6747 | 0.7954 | **3.115681** | **6.233774** |
| Minimum convex polygon | 1 | (Intercept) | 0.1645 | 0.4036 | –0.62666492 | 0.9556001 |
| | | Phase (POBP) | 3.3076 | 0.5337 | **2.26159885** | **4.3536929** |
| | | Country (Italy) | 1.0114 | 0.4972 | **0.03687891** | **1.9860101** |
| | 2 | (Intercept) | 0.7191 | 0.3110 | 0.1095798 | 1.328682 |
| | | Phase (POBP) | 3.3310 | 0.5576 | **2.2381220** | **4.423780** |
| Mean distance to nest—km | 1 | (Intercept) | -1.6303 | 0.2490 | –2.1183655 | –1.142136 |
| | | Phase (POBP) | 2.8812 | 0.3179 | **2.2581774** | **3.504130** |
| | | Country (Italy) | 0.7693 | 0.3123 | **0.1571366** | **1.381496** |
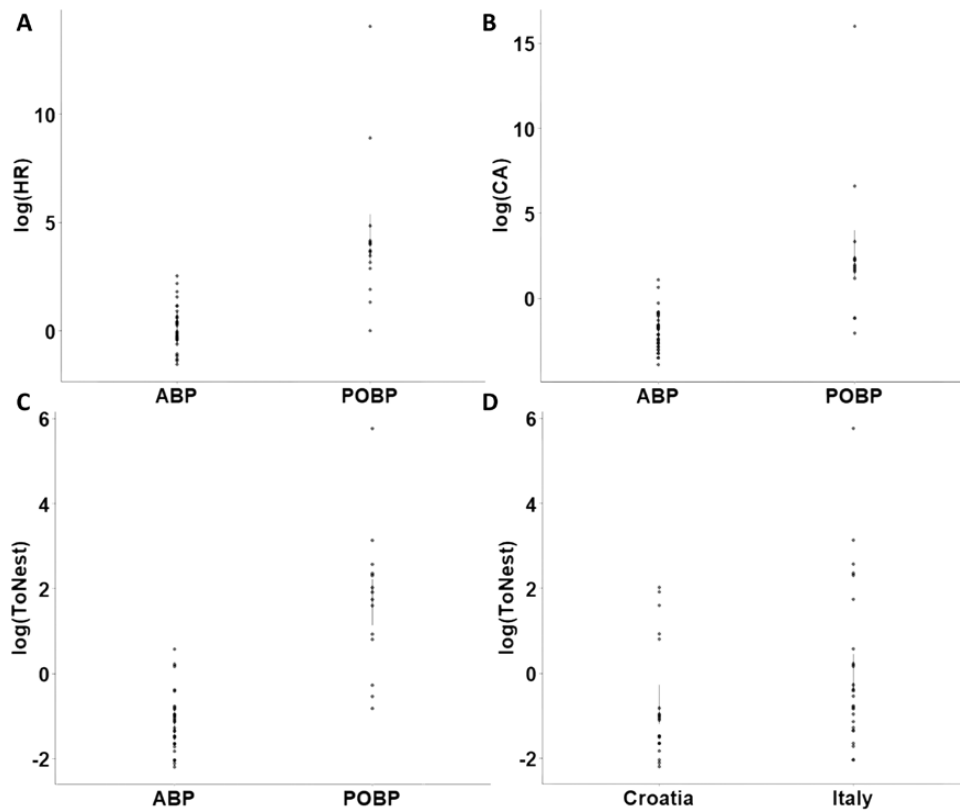
**Figure 1.** First model selection. Plots for the top-ranked models on movement components of breeding Rollers in relation to fixed predictors. Only significant predictor effects are shown (Ref. Table 3 and 4). Movement components by phase (ABP—active breeding phase vs. POBP—post-breeding phase) and country (Italy vs. Croatia); (A) log transformed home range (log(HR)) by phase; (B) log transformed core area (log(CA)) by phase; (C) log transformed mean distance to nest (log(ToNest)) by phase and (d) log transformed mean distance to nest by country. Plots have been obtained using package "effects" version 4.2-0 (Fox, 2003; Fox and Weisberg, 2019) and readapted using "ggplot2" version 3.2.1 (Wickham, 2016).

**Table 5.** Result of second model selection on the effects of country (Italy vs. Croatia), phase (active breeding phase vs. post-breeding phase) and breeding outcome (successful vs. failure) on movement components of breeding Rollers: selected models with ΔAICc < 2 and with an AICc value smaller than that of any simpler alternative, while accounting for nesting. Summaries of selected models are shown. Sample size is reported in brackets.

| Response variable (sample size) | Model_id | Models retained | K | AICc | ΔAICc | Weight | Cum. Weight | logLik |
|---|---|---|---|---|---|---|---|---|
| Home range—HR 95% (45) | 1 | ~Phase*Breeding outcome | 7 | 188.82 | 0.00 | 0.77 | 0.77 | –85.90 |
| Core area—CA 50% (45) | 1 | ~Phase*Breeding outcome | 7 | 213.20 | 0.00 | 0.71 | 0.71 | –98.09 |
| Minimum convex polygon (45) | 1 | ~Phase*Breeding outcome | 7 | 168.87 | 0.00 | 0.76 | 0.76 | –75.92 |
| Mean distance to nest—km (45) | 1 | ~Phase + Breeding outcome | 6 | 142.11 | 0.00 | 0.20 | 0.20 | -63.95 |

partner) and started exploring distant areas in northern and central/southern Italy, as well as in coastal areas of Croatia overlapping the Croatian Roller population breeding range (Figure 3a). The bird crossed the Adriatic Sea five times until departing for the autumn migration on 09/09/2019. Such sea-crossings were always carried out at night (range departure-arrival time: 18:44-02:12), with a mean instantaneous speed of 44.5 ± 6.9 km/h km/h and at an average altitude of 204.6 ± 273.8 m a.s.l.

In another case, the bird #H218335 made 2 reproductive attempts in 2020, but both failed (Table 1). After the abandonment of the nest (on 08/07/2020 during the second attempt), it started moving further and on 10/08/2020 started ranging across the region of Lazio, Abruzzo, Molise, Campania, and returning to its territory on the 16/08/2020 (maximum

distance to nest 208.9 km; Figure 3B). This bird departed for autumn migration on the 08/09/2020.

## Discussion

We found changes in home range sizes and variation in distances traveled during the breeding season by adult Rollers, providing evidence of individual differences in space use according to breeding phase and breeding outcome. As expected, we found that home ranges and core areas as well as distances to nest increased in the post-breeding phase, though such an increase was less marked in successful than in failed breeders. After a successful breeding event, adults significantly increased their home ranges and core areas but mostly remained in the surroundings of the nesting area until

**Table 6.** Second model selection: best models of country (Italy vs. Croatia), phase (ABP—active breeding phase vs. POBP—post-breeding phase) and breeding outcome (successful vs. failure) on movement components of breeding Rollers, assessed through GLMMs. Coefficients (β) and 95% confidence intervals (95% CIs) are shown. In bold are marked the 95% confidence intervals which do not include 0

| Response variable | To-ranked model | Predictor | β | SE | 95% CI | |
|---|---|---|---|---|---|---|
| Home range—HR 95% | 1 | (Intercept) | 0.7243 | 0.5842 | –0.4207908 | 1.8693988 |
| | | Phase (POBP) | 7.6940 | 1.0678 | **5.6011251** | **9.7869424** |
| | | Breeding outcome (successful) | –0.7762 | 0.6718 | –2.0928657 | 0.5405148 |
| | | Phase (POBP) * Breeding outcome (successful) | –4.4055 | 1.2141 | **–6.7851115** | **–2.0258675** |
| Core area—CA 50% | 1 | (Intercept) | –1.2125 | 0.7661 | –2.713976 | 0.2889354 |
| | | Phase (POBP) | 8.4452 | 1.3996 | **5.702099** | **11.1882858** |
| | | Breeding outcome (successful) | –1.0243 | 0.8808 | –2.750623 | 0.7019828 |
| | | Phase (POBP) * breeding outcome (successful) | –4.7784 | 1.5913 | **–7.897256** | **–1.6595189** |
| Minimum convex polygon | 1 | (Intercept) | 1.2675 | 0.4640 | 0.3580687 | 2.1768529 |
| | | Phase (POBP) | 6.5910 | 0.8769 | **4.8723225** | **8.3097624** |
| | | Breeding outcome (successful) | –0.7320 | 0.5372 | –1.7849211 | 0.3209261 |
| | | Phase (POBP) * breeding outcome (successful) | –4.1125 | 0.9972 | **–6.0669520** | **–2.1579931** |
| Mean distance to nest—km | 1 | (Intercept) | –0.5675 | 0.3281 | –1.210646 | 0.07567483 |
| | | Phase (POBP) | 2.9318 | 0.3081 | **2.327898** | **3.53576644** |
| | | Breeding outcome (successful) | –0.8740 | 0.3597 | **–1.578944** | **–0.16913492** |
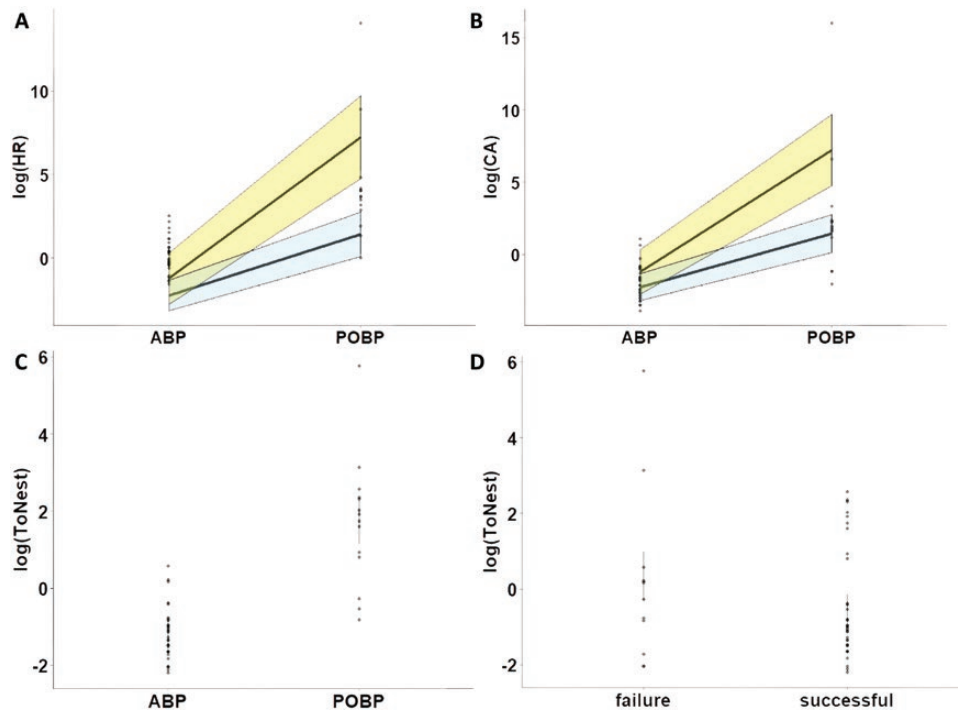


**Figure 2.** Second model selection. Plots for the top-ranked models on movement components of breeding Rollers in relation to fixed predictors. Only significant predictor effects are shown (ref. Table 5 and 6). Movement components by phase (ABP—active breeding phase vs. POBP—post-breeding phase) and breeding outcome (successful = light blue vs. failure = yellow); (A) log transformed home range (log(HR)) by phase * breeding outcome; (B) log transformed core area (log(CA)) by phase * breeding outcome; and (C) log transformed mean distance to nest (log(ToNest)) by phase and (D) log(ToNest) by breeding outcome. Plots have been obtained using package "effects" version 4.2-0 (Fox, 2003; 2019) and readapted using "ggplot2" version 3.2.1 (Wickham, 2016).

the onset of migration, suggesting a period of post-fledging dependence. These birds did not explore distant areas because they were probably busy providing parental care to the young. In contrast, failed breeders tended to move away from the nesting sites towards secondary sites. These movements were generally different in timing and distance compared with migratory movements. Similar post-breeding movements have been described also for other bird species (e.g., western marsh harrier *Circus aeruginosus*; Strandberg et al. 2008; osprey *Pandion haliaetus* Monti et al. 2018;
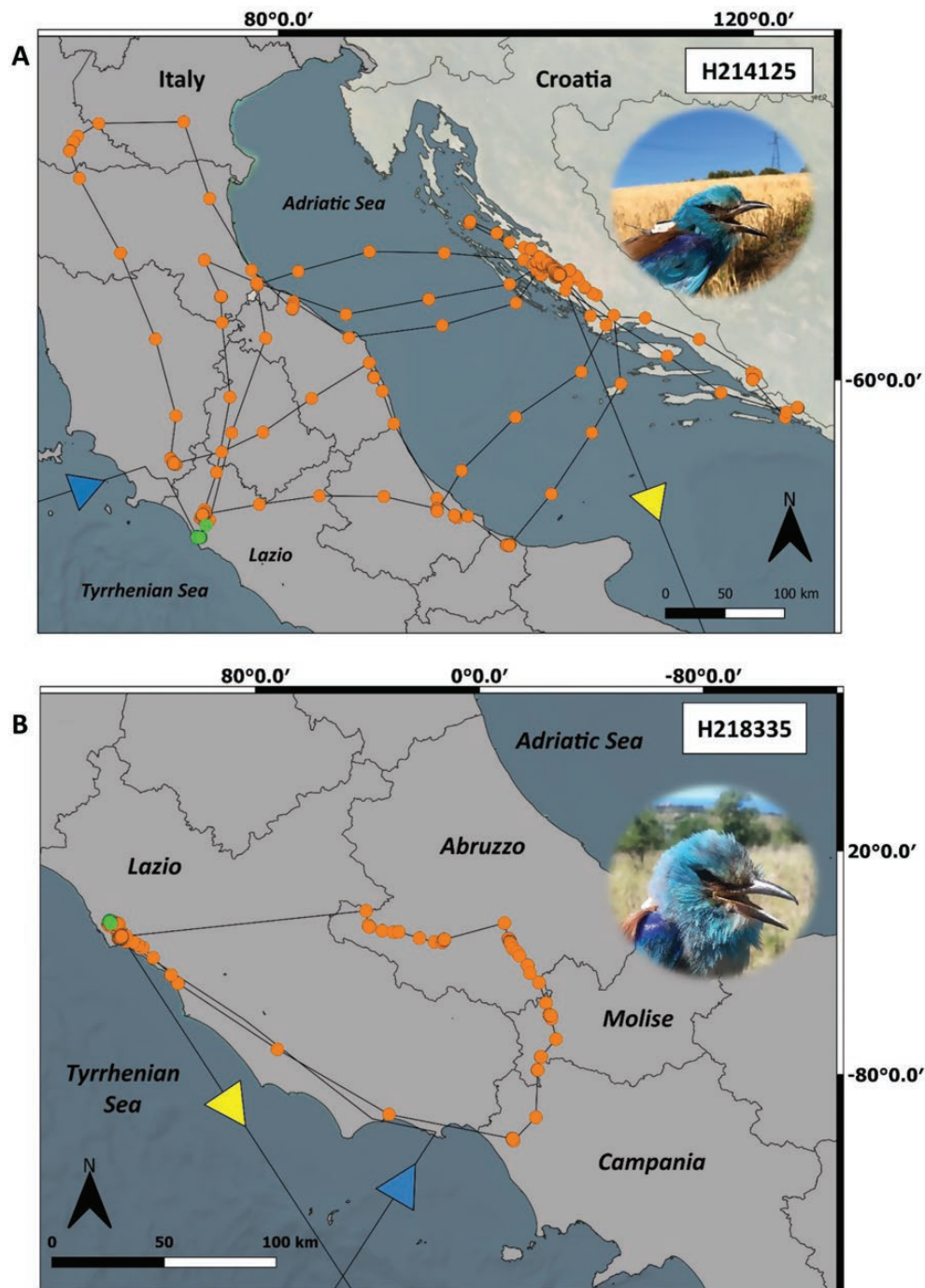
**Figure 3.** Examples of long distances movements carried out by Rollers who failed reproduction, during ABP—active breeding phase (green) and POBP—post-breeding phase (orange). Triangles represent the main direction of spring migration (blue) and autumn migration (yellow) at the time of arrival and departure, respectively. (A) bird #H214125 who abandoned the nest on 03/07/2019 (a few days after the abandonment of the partner) and started exploring distant areas in northern and central/southern Italy as well as in coastal areas of Croatia (max distance to nest 515.2 km). The bird crossed the Adriatic Sea 5 times until departing for the autumn migration on 09/09/2019; (B) bird #H218335 who made 2 reproductive attempts in 2020, but both failed. After the abandonment of the nest on 08/07/2020 during the second attempt, it started moving further on 10/08/2020 ranging across the regions of Lazio, Abruzzo, Molise, Campania and returning on 16/08/2020 (max distance to nest 208.9 km). This bird departed for autumn migration on 08/09/2020. Photos of Rollers are by Flavio Monti.

Montagu's harrier *Circus pygargus*; Berger-Geiger et al. 2022; flammulated owls *Psiloscops flammeolus*; Ciaglo et al. 2021). It has been argued that autumn prospecting movements could inform individuals about alternative areas to be used in the following breeding seasons to increase breeding opportunities and fitness. For example, Arlt and Pärt (2008) showed how

male northern wheatears *Oenanthe oenanthe* that prospected prior to autumn migration were more likely to change breeding territories in the subsequent year. Similar findings have been reported in young white-crowned sparrows *Zonotrichia leucophrys*: Morton et al. (1991) showed how juvenile males that spent more time in an area after fledging were more likely

to return there to breed in subsequent years. Patchett et al. (2022) demonstrated the function of post-fledging dispersal in first breeding territory selection for males of Cyprus wheatear *Oenanthe cypriaca*.

Interestingly, failed breeders did not advance the onset of autumn migration, although they could potentially have done so, being no longer tied to the nest site and not having dependant young to care for. This could be explained by 2 not-mutually exclusive reasons: (a) major "primary" migratory traits, such as timing (i.e., departures and arrivals) and routes (i.e., the direction of main migration axes, distances covered, and destinations), are thought to be mostly controlled genetically and driven primarily by an endogenous clock-and-compass system (Berthold 1996; Thorup and Rabøl 2001). This means that despite more time available, failed breeders did not migrate in advance because of stringent genetic traits related to departure dates. (b) The time available after failure was used to carry out explorative movements potentially useful for acquiring information on other suitable breeding areas for successive years, or even for acquiring resources to increase body condition in preparation for migration. While successful breeders rely on the fact that a successful reproductive season is informative enough for guiding nest selection the following year (if all the other variables remain stable between years: habitat suitability, resources availability, presence of a mate), failed breeders should search for an alternative "solution" to minimize the risk of failing in a nesting attempt again. For example, it has been documented that breeding failures lead to a higher percentage of divorce in raptors and seabirds (Martin et al. 2014; Mercier et al. 2021), with the breeding outcome as the most important predictor of mate retention (e.g., Wagner et al. 2022). Breeding dispersal likely increases between years in case of unsuccessful reproductive outcome (Forero et al. 1999; Öst et al. 2011).

In our case, various causes may underlie the differences found in breeding success. On the one hand, almost all failed breeders belonged to the Italian population which was affected by poachers, who removed chicks illegally from nestboxes (Garofalo et al. 2022). On the other hand, differences during ABP between the 2 countries (Appendix 3) may be a consequence of differences in habitat quality between the 2 areas: a presumably higher habitat quality in Croatia due to a high proportion of fallow land caused by agricultural abandonment, compared with a lower habitat quality in Italy due to intensive arable farmland and cereal crops (Monti et al. 2019). Consequently, greater trophic availability in an area would reduce the need to move from the nest (e.g., smaller movement components) to find food and vice versa, possibly affecting breeding success. However, "Country" was not retained in the model selection incorporating breeding outcome, suggesting that the Roller space use during POBP was not influenced by the difference between the countries, although this cannot be completely excluded due to the small sample size. To decisively answer this question, a more in-depth study should be conducted, with a specific focus on the quality of the habitat patches (taking into account the crop rotation of the patches during the same season) and on the food availability (by sampling invertebrate communities).

Exploring distant areas for collecting information on suitable breeding areas is costly as it imposes different trade-offs. For example, a bird crossing a large body of water is at higher risk of perishing if confronted with poor weather conditions (e.g., Newton 2010). Furthermore, the risk of predation increases as the bird's ability to quickly find cover is decreased in unfamiliar areas, or as it may encounter novel predators (e.g., Yoder et al. 2004). In long-distance migrants, the post-breeding phase could represent the only time available during the year for collecting information on breeding grounds (Patchett et al. 2022). In the pre-breeding phase, birds cannot afford to prospect as they must quickly establish a breeding territory and engage in other essential breeding activities such as mate searching, courtship, nest building, and copulation (Newton 2010). Indeed, the Rollers, after arriving to the breeding grounds, mostly did not search around, but rather showed restricted movement components while settling in an area which was subsequently used for breeding. This is in line with recent findings in other migratory bird species, using the post-breeding season as the optimal time to prospect and inform settlement decisions for future breeding seasons (Ciaglo et al. 2021; Patchett et al. 2022). By territory prospecting during the post-breeding phase, the bird can gain knowledge of potential breeding sites prior to autumn migration and increase its chances of selecting high-quality sites for subsequent years, eventually augmenting fitness in the future. While this cannot be statistically validated with our dataset, we found that 5 Rollers which were successful in the first year kept their nesting site the following year and successfully bred again. In contrast, three Rollers which failed in the first year changed nesting sites (but not area) in the following year, then resulting in successful breeding. However, why does an unsuccessful breeder moves hundreds of km and then return to the same site or population to breed the following year? A possible explanation consistent with the species ecology could be that, although extensive explorations may inform the individual about potential breeding or foraging areas, costs imposed by moving to a new area may for some individuals prove to be too high. The Roller is believed to be a highly philopatric species based on numerous anecdotal data of the same individuals breeding in the same nest sites for successive years. Although, such data can be highly biased because the probability of observing a bird which moved to a distant nesting area is low. Furthermore, agricultural habitats are prone to swift transformation and Rollers are probably not able to predict changes in habitat quality throughout the season. For example, good habitat quality on arrival could quickly deteriorate (e.g., due to intensive land management), eventually resulting in lower levels of breeding success. A great percentage of breeding Rollers choose to breed in the same nesting area, moving on average less than 1 km between breeding attempts (e.g.; Rodríguez-Ruiz et al. 2020). Thus, it could be implied that in most cases the cost-benefit ratio for breeding Rollers is perhaps more favorable in familiar surroundings than in unfamiliar ones, despite the difference in habitat quality. In the case of failed breeders in Italy, it seems unlikely that habitat quality had an effect on the breeding success given that habitat composition was similar between successful and failed breeders (*unpublished data*) and considering that failures were mostly due to poachers' activity. This was corroborated by the fact that the birds returned to the same area, even though not to the same nest-box probably influenced by the previous breeding outcome at a specific nest-box. A larger dataset of multi-individual repeated tracks over several years would be needed to quantify breeding dispersion in the Roller and to fully understand the cost and benefits of switching to a new nesting area.

Prospecting movements of Rollers in this study were large, both in terms of distances covered and time spent traveling around. Initially, we thought that failed breeders would visit neighboring sites to acquire detailed "public information" on the fate of the closest nest-boxes/sites. Indeed, some of the failed breeders and especially successful breeders stayed in the general breeding area. However, 2 failed breeders were recorded making large prospecting movements, even to very distant areas (Figure 3). In particular, the bird #H214125 moved between central Italy and Croatia several times, curiously linking our 2 study populations. Other resightings offer insight into potential connectivity between the 2 populations: a Roller (bird code: #H205899) born and ringed as a *pullus* by our team in the Pianaccio di Montebello locality (Lazio) on 05/07/2016, then resighted after 684 days on the 20/05/2018 in Ravni Kotari, Croatia at Roller's breeding locality (distance in line of sight: ca 350 km), accompanied by a mate (thus suggesting it finally bred in Croatia); and a more recent observation of the individual (bird code: #KA3016—plastic ring: CMP) ringed on the 09/07/2021 as *pullus* in Ravni Kotari, Croatia and observed after 303 days on 08/05/2022 in the Italian study site near Monte Romano (Lazio) (distance in line of sight: ca 350 km). These findings likely suggest gene flow among two breeding nuclei and the existence of a metapopulation. However, as stated above, it is also possible that other factors such as discrepancies in habitat quality and food availability between the 2 populations lead to different space use patterns and roaming behavior, thus not necessarily supporting a metapopulation hypothesis.

Future work should investigate individuals' breeding success and fitness in the long term, particularly in relation to different phases of the annual cycle, especially how the outcome of each phase might prompt individual responses. In this sense, further studies focusing on exploratory movements and how these affect breeding site selection in the following years are of critical importance. In addition, it would be worth evaluating the role of age classes in the relationship between exploratory movements and subsequent breeding success, as well as site fidelity between juvenile and adult birds and between males and females. Familiarity with potential breeding sites acquired by first-calendar-year individuals during the post-fledging dispersal period may be important to support first settlement decisions (e.g., Patchett et al. 2022) and could potentially improve with the age and experience of the bird.

In conclusion, the breeding phase and outcome determine space use and particularly influence post-breeding prospecting movements prior to migration in this long-distance migrant species. On arrival at the breeding grounds, Rollers mostly showed restricted movements in the vicinity of the future nest. Home ranges and core areas as well as distances to nest increased in the post-breeding phase compared with the active breeding phase, though such an increase was less marked in successful than in failed breeders. Failed breeders did not advance the migration start but rather engaged in far-reaching and long-lasting prospecting movements. In this sense, the most extreme was an individual that crossed the Adriatic Sea five times before embarking on autumn migration. Studying how individuals' life-history factors relate to post-breeding dispersal and nest site selection across years could help in depicting potential carry-over effects at the population level, particularly in an era of rapid climate and environmental changes.

Investigating the drivers affecting each phase of the complex life cycle of migrating birds is the key to assessing factors of vulnerability and predicting biological responses for conservation purposes.

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## Conflict of Interest statement

The authors declare no conflict of interest.

## Author Contributions

F.M. and S.B. originally formulated the idea. S.C., F.M., S.B., D.C., V.T., J.K, and C.C. conducted fieldwork. F.M. and S.B. collaborated in imaging and performing analysis and wrote the original draft of the manuscript. All authors contributed critically to the manuscript and gave final approval for publication.

## Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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