

JOURNAL OF AVIAN BIOLOGY

Research Article

Reproductive flexibility in a single-brooded migrant: can the European roller *Coracias garrulus* adapt to extreme weather events?

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Journal of Avian Biology

2026: e03502

doi: [10.1002/jav.03502](https://doi.org/10.1002/jav.03502)

Subject Editor: Suvi Ruuskanen

Editor-in-Chief: Staffan Bensch

Accepted 25 November 2025



Global climate change has intensified extreme weather events, including short-duration but intense rainfall, which can significantly impact avian reproduction. This study examines the effects of extreme rainfall on the reproductive phenology and performance of the European roller *Coracias garrulus*, a single-brooded migratory bird, in a semiarid ecosystem. We analysed breeding parameters during 2023, characterised by exceptionally intense and concentrated rainfall, and compared them with long-term data (2006–2024). Our results indicate that breeding phenology in 2023 exhibited significant shifts. Rollers initiated egg-laying approximately five days earlier than the long-term average in the early breeding season, while late-season laying was delayed by approximately 11 days. The prolonged breeding season was marked by a high incidence of breeding failures, particularly during incubation. Moreover, we observed an unprecedented surge in apparent replacement breeding attempts, a rare phenomenon in this single-brooded species. Despite these challenges, overall population productivity remained consistent with long-term averages because successful breeding was heavily concentrated in resilient nest substrates, nest boxes and sandstone burrows, which buffered the weather's impact and compensated for catastrophic failures in stone cavities. Our findings underscore the European roller's capacity for reproductive flexibility, but also suggest the significant fitness costs and constraints associated with these adaptive responses. These results highlight the need for conservation strategies that consider climate-induced phenological shifts and the importance of nest box designs optimised to mitigate the interacting adverse effects of extreme rainfall and subsequent heatwaves.

Keywords: behavioural response, climate change, extreme weather events, long-term data, reproductive flexibility



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Introduction

Global warming has intensified extreme climatic events such as heatwaves, droughts, and floods (Trenberth 2008, Westra et al. 2013, Fischer and Knutti 2016, Fowler et al. 2021, IPCC 2021). A growing scientific consensus suggests that many species may lack the adaptive capacity to keep up with climate change (Radchuk et al. 2019). Phenotypic plasticity, the ability to adjust traits in response to environmental changes, could help species cope with rapid shifts (Chevin et al. 2013). Assessing this plasticity, particularly in traits vital for fitness, is crucial for conservation efforts and identifying vulnerable populations (Donelson et al. 2023). However, measuring plasticity in natural populations remains challenging (Arnold et al. 2019) and often requires extensive longitudinal data to accurately correlate environmental changes with phenotypic responses (Nussey et al. 2007).

In birds, reproductive timing and success are strongly influenced by environmental factors, including rainfall patterns (Kostrzewa and Kostrzewa 1990, Potapov 1997, Skinner et al. 1998, Jovani and Tella 2004, Carrillo and González-Dávila 2010, Bionda and Brambilla 2012). While the relationship between breeding success and general rainfall trends is well documented, the impact of short-duration but intense rainfall periods has received less attention (but see Anctil et al. 2014, Fisher et al. 2015, Schöll and Hille 2020). Such extreme weather events, which are projected to increase in both frequency and intensity (Westra et al. 2014), can negatively affect bird populations by disrupting thermoregulation, reducing food availability, raising predation risks, or causing nest flooding, all contributing to nest failure (Anctil et al. 2014, Schöll and Hille 2020).

In single-brooded bird species, nest failure caused by extreme weather events can have particularly significant consequences, as opportunities for replacement broods are often constrained by temporal and physiological trade-offs between breeding and migration (Arroyo et al. 2002). This study investigates the response of the European roller *Coracias garrulus*, a single-brooded migratory bird, to extreme rainfall episodes. The European roller is a suitable model for this study because it exhibits some degree of reproductive flexibility. While delayed reproduction can disrupt the annual cycle of long-distance, trans-Saharan migrants, potentially jeopardising their survival (Hedenström et al. 2007), the roller's breeding season (ca from the end of April until mid-July) may allow for some compensatory adjustments. Additionally, as a secondary cavity-nesting species, the European roller uses various cavity types, each associated with distinct reproductive patterns (Valera et al. 2022), which may influence its adaptability to environmental challenges.

Our research was conducted in a semiarid ecosystem, where precipitation patterns are critically important but highly variable (Lioubimtseva 2004). These ecosystems are projected to experience substantial changes under future climatic scenarios (Melillo et al. 1993, Bazzaz et al. 1996, Whitford 2002). Due to their sensitivity to global climatic

fluctuations and interannual rainfall variability, these regions offer valuable insights into how species respond to extreme weather events. By comparing reproductive parameters from a year with unusually intense rainfall to long-term breeding data, our study aims to 1) evaluate the impacts of extreme weather conditions on European roller reproductive performance, and 2) assess the species' capacity for reproductive flexibility in the face of environmental challenges.

Material and methods

Study area and study species

The study area (~ 50 km²) lies in Campo de Tabernas (Almería, SE Spain, 37°05'N, 2°21'W). It comprises badlands interspersed with olive and almond groves, dry streambeds (*ramblas*), and steppe habitats. The region has a semi-arid Mediterranean climate with a substantial summer water deficit. Mean annual rainfall is approximately 230 mm (range: 124.4–466.6 mm), with significant inter- and intra-annual variability (Lázaro et al. 2001). Mean annual temperature is 18°C, with minor inter-annual variations but considerable intra-annual fluctuations (Lázaro et al. 2004).

The European roller experienced significant population declines across its European breeding range during the 20th century and was classified as 'Near Threatened' in the early 2000s (BirdLife International 2019). Although the species is currently listed as 'Least Concern', populations continue to decline in some strongholds (Gameiro et al. 2020), and its Spanish population is considered 'Endangered' (Cardalliaquet and Avilés 2021). The roller is a secondary cavity-nesting species, breeding naturally in tree cavities, sandstone burrows, and human structures (Cramp 1998, Valera et al. 2022). Its nesting behaviour is limited to selecting a cavity, as it does not engage in activities such as lining the nest. The species readily accepts nest boxes, and conservation actions involving nest-box installation led to local population recoveries (Rodríguez et al. 2011, Václav et al. 2011, Kiss et al. 2017, Monti et al. 2019), though this dependency on artificial cavities renders the roller a conservation-reliant species (Gameiro et al. 2020). In our study area, rollers laid their first eggs between 23 April and 17 June from 2006 to 2024, typically producing clutches of 4 to 5 eggs (range: 1–7). They rear a single brood per year (Cramp 1998, Fry et al. 2020). Egg hatching is distinctly asynchronous (Václav et al. 2008). Nestlings are altricial, hatching naked and developing closed feather sheaths by approximately 13 days of age. In this population, incubation lasts around 21 days, with fledging occurring 22–24 days after hatching (Václav et al. 2008). Rollers undergo a complete post-breeding moult, which begins in the breeding areas around June, is suspended before migration, and resumes at the wintering grounds (Cramp 1998). As trans-Saharan migrants, rollers leave the study area between the third week of July and the third week of August and begin their spring migration around mid-February (Rodríguez-Ruiz et al. 2014).

Nest box scheme and study period

Nest-site availability for European rollers in the study area was progressively enhanced through the installation of nest boxes at two-year intervals from 2005 to 2009 (2005 and 2006: 13 nest boxes; 2007 and 2008: 23 nest boxes; 2009: 54 nest boxes; Václav et al. 2011). Between 2010 and 2024, the number of available roller nest boxes fluctuated slightly, ranging from 54 to 71 (Valera and Václav 2021). Additionally, in 2023, 20 nest boxes suitable for rollers were installed by other parties as part of a mitigation measure for renewable energy projects in the study area. This study focuses on the period from 2006 to 2024, during which comparable data on breeding parameters for the study population were systematically collected.

Fieldwork

Sandstone burrows, stone cavities in bridges, and nest boxes, which are primarily used for nesting by rollers in our study area, were inspected periodically (approximately every 2 to 6 days) each year for roller nest occupancy. Cavities were considered occupied by rollers if at least one egg was recorded in them during regular inspections. Once roller occupancy was detected, nests were inspected more frequently (approximately every 2–4 days). During regular nest inspections, we monitored and recorded egg-laying date, clutch size, number of hatchlings, fledgling numbers, and breeding failure. In some cases (less than 10% per year), the start of laying was back-calculated considering the 1.5-day interval between the laying of two successive eggs. Nest inspections after fledging helped to detect some late nestling losses and to correct the number of fledged young. This post-fledging check also allowed for the definitive determination of initial clutch size, as our long-term observations confirm that unhatched eggs are not removed by the parents and remain in the nest cavity. A breeding attempt was considered to be successful if at least one juvenile fledged.

Although rollers rear a single brood per year, they may lay a replacement clutch following breeding failure under certain circumstances (Fry et al. 2020). Identifying replacement clutches unequivocally requires knowledge of the nest occupants' identity, which was unavailable in this study since the birds were not uniquely colour-banded. While colour-banding was attempted in the initial years of this long-term project, it proved impractical for comprehensive monitoring due to the difficulty of reading bands on this species and a deliberate decision to minimise handling stress on a conservation-reliant population. Therefore, we have adopted the term 'apparent replacement clutch' throughout the manuscript to reflect this uncertainty. Our classification was based on a single, conservative criterion: an apparent replacement clutch was defined as a new clutch that appeared in the same cavity where a previous breeding attempt had been confirmed to have failed earlier in the same season.

Due to difficulties in monitoring less accessible nest cavities, particularly natural ones, specific breeding parameters, such as clutch size and hatchling numbers, could not be determined for some roller nests. As a result, sample sizes, which represent the number of active breeding attempts where data could be collected, vary across breeding parameters. For the entire dataset (2006–2024, excluding 2023) and for the year 2023, the sample sizes were: laying dates ($n = 884/73$ breeding attempts), clutch size ($n = 839/63$ breeding attempts), hatchling number ($n = 841/73$ breeding attempts), fledgling number ($n = 851/74$ breeding attempts), and breeding success ($n = 990/75$ breeding attempts). A detailed breakdown of the number of breeding attempts by nest type and year is provided in Table 1.

Meteorological data

Precipitation data for the study area from May to mid-July (the main breeding period) were obtained from the meteorological station in Tabernas ($37^{\circ}05'N$, $2^{\circ}18'W$; Red de

Table 1. Proportions of failed breeding attempts out of all breeding attempts for the three main nest types.

Year	Nest boxes	Sandstone burrows	Stone cavities	Total
2006	0/7 (0.0)	4/23 (17.4)	3/20 (15.0)	7/50 (14.0)
2007	1/12 (8.3)	4/19 (21.0)	5/19 (26.3)	10/50 (20.0)
2008	4/17 (23.5)	3/15 (20.0)	1/14 (7.1)	8/46 (17.4)
2009	5/28 (17.8)	2/14 (14.3)	5/15 (33.3)	12/57 (21.0)
2010	4/34 (11.8)	0/11 (0.0)	2/11 (18.2)	6/56 (10.7)
2011	5/38 (13.2)	1/9 (11.1)	2/16 (12.5)	8/63 (12.7)
2012	8/33 (24.2)	2/6 (33.3)	6/14 (42.8)	16/53 (30.2)
2013	18/41 (46.3)	7/9 (77.8)	3/11 (27.3)	28/61 (45.9)
2014	9/29 (31.0)	2/4 (50.0)	2/6 (33.3)	13/39 (33.3)
2015	3/37 (8.1)	0/7 (0.0)	1/8 (12.5)	4/52 (7.7)
2016	7/37 (18.9)	1/3 (33.3)	2/10 (20.0)	10/50 (20.0)
2017	1/39 (2.6)	0/6 (0.0)	1/10 (10.0)	2/55 (3.6)
2018	2/38 (5.3)	0/5 (0.0)	0/8 (0.0)	2/51 (3.9)
2019	8/41 (19.5)	0/6 (0.0)	0/9 (0.0)	8/56 (14.3)
2020	2/48 (4.2)	1/6 (16.7)	1/8 (12.5)	4/62 (6.5)
2021	6/49 (12.2)	0/5 (0.0)	1/8 (12.5)	7/62 (11.3)
2022	3/56 (5.4)	0/2 (0.0)	1/8 (12.5)	4/66 (6.1)
2023	12/62 (19.3)	1/4 (25.0)	6/9 (66.7)	19/75 (25.3)
2024	18/60 (30.0)	4/5 (80.0)	2/6 (33.3)	24/71 (33.8)

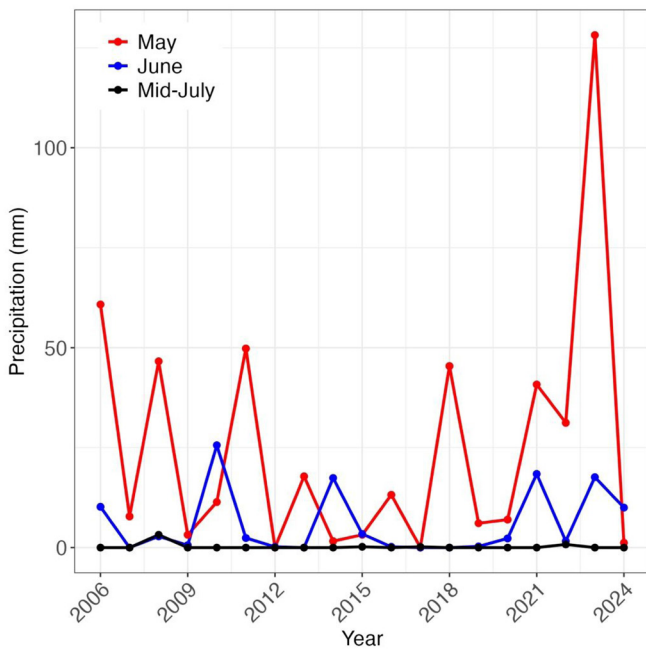


Figure 1. Accumulated precipitation during May, June and the first half of July in Tabernas from 2006 to 2024.

Información Agroclimática de Andalucía 2024) and are presented in the Results section (Fig. 1). Because torrential rains often occur in localised areas, we also gathered data on unusually heavy rainfall in 2023 from the north-eastern part of the study area, specifically from the Benizalón meteorological station ($37^{\circ}16'N$, $2^{\circ}23'W$), managed by the Asociación Meteorológica del Sureste (AMETSE) (ca 25 km from the meteorological station in Tabernas).

Data analysis

We analysed whether breeding phenology and performance in the extreme rainfall year 2023 deviated from long-term averages recorded between 2006 and 2024. Specifically, we examined egg-laying date, clutch size, number of fledglings, and breeding success. Egg-laying dates for all years were analysed for three phases of the breeding season. This approach accounts for the distribution of laying dates, which does not conform to a unimodal normal distribution but may exhibit multiple peaks (Fig. 2). To reflect a natural variation in the European roller's breeding phenology, we calculated mean laying dates for three season phases: 1) early (first quartile of laying dates), 2) mid (middle two quartiles), and 3) late (last quartile; Fig. 2). Breeding success was examined as a binary, nest-level outcome, indicating whether a nest produced at least one fledgling or none, for all nests where egg-laying was recorded.

Differences between breeding data from 2023 and reference years (2006–2022, 2024) were analysed using mixed models within a Bayesian framework. The analysis followed a two-step process. In the first step, we obtained long-term averages across the three season phases for each response variable, using the season phase as a fixed predictor. Default

(flat) priors were applied to regression coefficients. In the second step, the long-term averages were used as informative priors for 2023 data to incorporate prior knowledge about fixed predictors. To avoid over-constraining the model while accounting for uncertainty, prior standard deviations were conservatively increased by a factor of two, ensuring broader prior distributions. Leave-one-out (LOO) cross-validation was used to evaluate model fit across different prior specifications. The expected log predictive density (ELPD) differences confirmed that models with informative priors with wider standard deviations (SD) performed comparably to models with weakly informative priors (ELPD differences < 2) and considerably better than models with narrow (original) informative priors (ELPD differences > 20).

Laying dates, clutch size, and fledgling numbers were modelled using Gaussian mixed models, assuming normally distributed errors. While count data are often analysed using models with a Poisson or negative binomial error structure, we selected a Gaussian framework after careful consideration of our data's specific properties and our analytical goals. Our raw count data are characterised by significant underdispersion. Given our large sample sizes, the central limit theorem ensures that parameter estimates from Gaussian models are robust and reliable, even when the underlying data are not perfectly normal. Furthermore, this choice was methodologically advantageous within our Bayesian framework. The use of a Gaussian likelihood with a Gaussian informative prior (a conjugate pair) provides a computationally stable model where the posterior mean is a transparent, precision-weighted average of our long-term data (the prior) and the 2023 data (the likelihood), enhancing both methodological coherence and interpretive clarity. Finally, diagnostic checks of our fitted models confirmed that residuals were approximately normally distributed and that all predictions were biologically realistic, satisfying the core assumptions for valid statistical inference.

Breeding success was analysed using a logistic (Bernoulli) model. All models included nest type as a random effect to account for differences among birds breeding in sandstone burrows, stone cavities, and nest boxes (Valera et al. 2022). In long-term data models, year was included as an additional random effect to address variation across years. Nest identity was not included as a random effect in long-term models because individual nest cavities were not consistently monitored across years. For Gaussian models, the effects of fixed and random factors were modelled for both location (mean) and scale (variance) parameters to account for heterogeneity in variances across season phases, nest types, and years.

Posterior hypothesis testing assessed whether breeding parameters in the extreme rainfall year 2023 differed from those in the reference years. We tested point hypotheses comparing the posterior means of breeding parameters obtained in the two-step process. A difference was considered significant if its 95% credible interval (CrI) did not include zero.

Bayesian models were fitted with the 'brms' ver. 2.22.0 package (Bürkner 2017) in R ver. 4.4.2 (www.r-project.org). Model parameters were estimated using Markov chain Monte

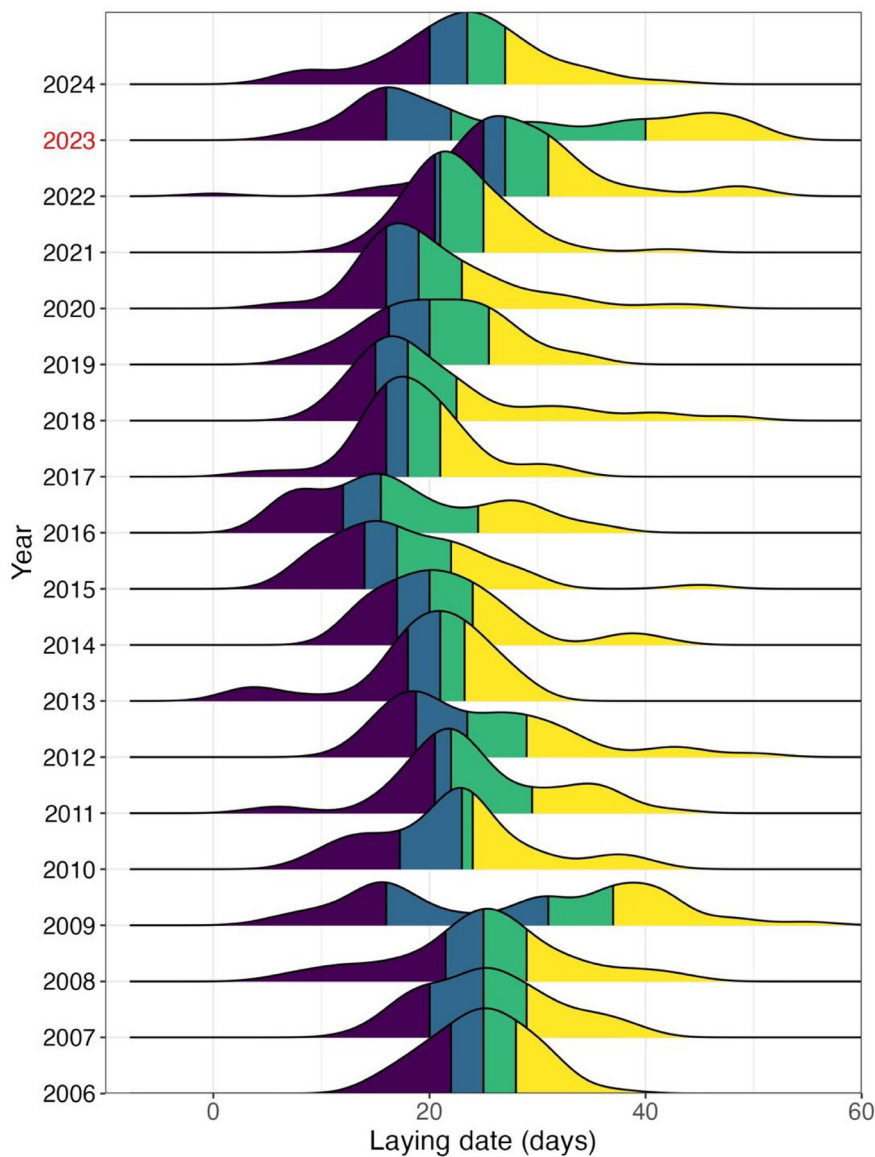


Figure 2. Density distribution of egg-laying dates for European rollers in SE Spain, 2006–2024 (Day 0 = April 23). The year with extreme rainfall is marked in red. Colour fills indicate quartiles.

Carlo (MCMC) methods with the static Hamiltonian Monte Carlo and No-U-Turn sampler (NUTS) algorithm, implemented in Stan (Bürkner 2017). Each model was run with four chains of 20 000 iterations. Convergence was assessed using: 1) trace plots and R-hat statistics, and 2) effective sample size (ESS) statistics to ensure reliable posterior mean and variance estimates (Kruschke 2021).

Model accuracy was evaluated using posterior predictive checks to confirm that the models adequately represented the data. Furthermore, we assessed model reliability using Pareto k diagnostics obtained from LOO cross-validation (Vehtari et al. 2017). The ELDP and its standard error from LOO analysis were used to compare models with different prior specifications (Vehtari et al. 2017). All Bayesian model estimates are reported as posterior means with 95% CrI.

Results

Interannual rainfall pattern

Precipitation during the main breeding period (1 May to 15 July) is typically infrequent and limited. May is the rainiest month, with precipitation ranging from 0 to 128.2 mm over the study period, while July is the driest, with a range of 0.0 to 3.2 mm (Fig. 1). In 2023, May recorded the highest rainfall, with 15 rainy days and 128.2 mm in Tabernas. In the north-eastern part of the study area, precipitation was even heavier, with 10 rainy days totalling 191.5 mm. Rainfall in both areas was concentrated within a few days in 2023. That year, nearly half of Tabernas' May precipitation (62.8 mm) fell in a single day (22 May), while 101.3 mm fell in just two days (21 and 22 May) in the north-eastern area.

All other rainy Mays during the study period – 2006, 2008, 2011, 2018, and 2021 (Fig. 1) – had more evenly distributed precipitation. During these years, rainy days and single-day maximum rainfall were: 2006 – 9 days, 26.8 mm; 2008 – 10 days, 30.6 mm; 2011 – 13 days, 34 mm; 2018 – 8 days, 28.4 mm; and 2021 – 6 days, 33.8 mm.

Breeding phenology

An assessment of laying dates for the period 2006–2024 shows that the timing of breeding was typically unimodal in most years (Fig. 2). However, some years (2009, 2016, 2023) exhibited multiple peaks. The 2023 breeding season was particularly notable for its pronounced non-unimodality, with the late-season peak accounting for 19 of 73 breeding attempts. Consequently, the 2023 breeding period was exceptionally prolonged, with many nests remaining active into the second half of July. The latest nest contained 21-day-old nestlings as of 27 July.

In 2023, roller breeding phenology exhibited significant shifts compared to the average of the reference years (2006–2024, excluding 2023; Fig. 2, 3; Supporting information). Rollers laid eggs approximately 5 days earlier than

usual during the early breeding season (earliest 25% of laying dates) in 2023 (Fig. 3A; Supporting information). The mean laying date during this early period was estimated at day 9.44 in 2023 (2/3 May; Supporting information). A significant shift towards earlier laying was observed, with a posterior probability of 5% for the two-sided hypothesis that the mean laying date in 2023 equalled 14.53 (7/8 May; Supporting information). In contrast, rollers laid eggs approximately 11 days later than usual during the late breeding season (latest 25% of laying dates) in 2023, representing a significant delay in late-season laying (Fig. 3C; Supporting information). The mean laying date during the mid-breeding season (two inner quartiles of laying dates) in 2023 did not deviate from the long-term average (Fig. 3B; Supporting information).

Laying dates in 2023 varied significantly among the three nest types (SD = 6.72 days, 95% CrI: 0.49 to 18.91). Throughout the 2023 season, rollers breeding in the three nest types laid eggs about 4 to 5 days later than the long-term average (Supporting information), with rollers nesting in nest boxes laying eggs about one day earlier than those nesting in sandstone burrows (Supporting information).

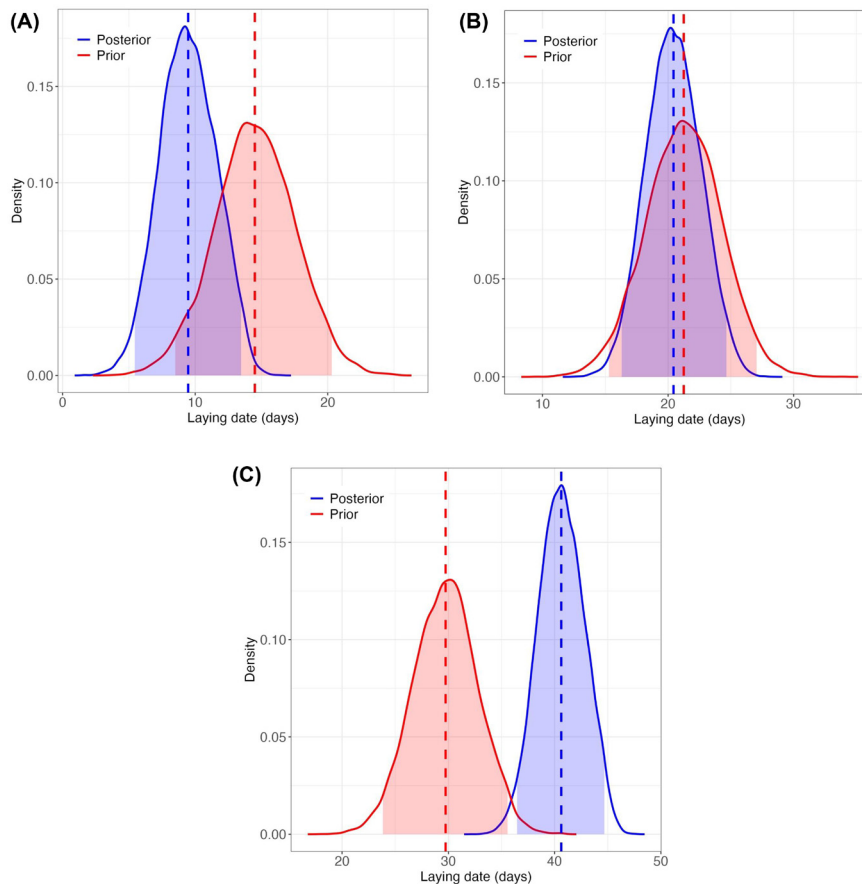


Figure 3. Prior and posterior density distribution of egg-laying dates for European rollers in SE Spain (2006–2024) during (A) early, (B) mid, and (C) late breeding phases (Day 0 = 23 April). Estimates of laying dates from 2006 to 2024 (excluding 2023) were used as priors for the 2023 model. The posterior distribution represents model-based estimates for 2023. Shaded areas denote 95% credible intervals, and dashed lines indicate mean laying dates.

Breeding performance

In 2023, clutch size, number of fledglings, and breeding success did not significantly deviate from long-term averages (Supporting information). Clutch size in 2023 was generally smaller, although the differences were not statistically significant for any season phase (Supporting information). The effect of nest type on clutch size was significant ($SD=0.85$ eggs, 95% CrI: 0.07 to 2.76). While not statistically significant, rollers in nest boxes tended to lay smaller clutches, averaging approximately half an egg less than the long-term average (Supporting information). Based on the long-term average clutch sizes for this population (4.3 to 5.2 eggs; Supporting information), this represents a substantial reduction in potential reproductive output of approximately 11–13%. In contrast, deviations from the overall average for stone cavities and sandstone burrows were less distinct (Supporting information).

While the number of fledglings in the early season of 2023 tended to be lower than the long-term average, the differences were not significant for any phase of the season (Supporting information). The random effect of nest type was significant ($SD=1.82$ fledglings, 95% CrI: 0.49 to 4.44). Rollers nesting in stone cavities had the poorest fledgling numbers, achieving about one fledgling fewer than the average (Supporting information). Negative deviations for nest boxes and sandstone burrows were less pronounced (Supporting information).

Breeding success (probability of fledging at least one young) in 2023 tended to be lower during the early and mid-season phases and higher in the late season than long-term averages (Supporting information). The effect of nest type on breeding success was significant (back-transformed logits: $SD=89.6\%$, 95% CrI: 58.7 to 99.7). Rollers nesting in stone cavities exhibited the lowest breeding success (back-transformed logits: 11.3%, 95% CrI: 1.7 to 46.9), significantly lower than the overall average (Supporting information). Breeding success in nest boxes achieved intermediate levels (44.3%, 95% CrI: 18.5 to 71.6), though not deviating significantly from the average (Supporting information). Rollers in sandstone burrows performed relatively best (78.1%, 95% CrI: 18 to 99.9) but showed the most considerable variation (Supporting information).

Breeding failure and multiple breeding attempts

Breeding failure rates varied over the study period, ranging from 3.6 to 45.9% across all nest types (Table 1). While generally low, they were highest in 2012, 2013, 2014, 2023, and 2024. Of these years, failures were most frequent during the nestling phase in 2013, 2014, and 2024 (Table 2), whereas in 2023, nearly 80% occurred during incubation.

From 2006 to 2024, 20 apparent replacement breeding attempts were recorded. These were infrequent (0–2 instances per year) from 2006 to 2024, except in 2023, when they surged to seven. All apparent replacement breeding attempts were successful, producing 33 fledglings from 2006 to 2022 and 2024, and 20 in 2023.

Table 2. Proportion of failures during the incubation and nestling phase for those attempts where the moment of failure could be determined (all three nest types pooled).

Year	Incubation phase	Nestling phase
2006	4/7 (57.1)	3/7 (42.8)
2007	8/10 (80.0)	2/10 (0.0)
2008	0/5 (0.0)	5/5 (100.0)
2009	10/12 (83.3)	2/12 (16.7)
2010	5/5 (100.0)	0/0 (0.0)
2011	7/8 (87.5)	1/8 (12.5)
2012	8/16 (50.0)	8/16 (50.0)
2013	11/28 (39.3)	17/28 (60.7)
2014	4/13 (30.8)	9/13 (69.2)
2015	1/3 (33.3)	2/3 (66.7)
2016	3/10 (30.0)	7/10 (70.0)
2017	1/2 (50.0)	1/2 (50.0)
2018	2/2 (100.0)	0/0 (0.0)
2019	5/8 (62.5)	3/8 (37.5)
2020	1/3 (33.3)	2/3 (66.7)
2021	4/7 (57.1)	3/7 (42.8)
2022	1/4 (25.0)	3/4 (75.0)
2023	15/19 (79.0)	4/19 (21.0)
2024	6/23 (26.1)	17/23 (73.9)

Discussion

This study highlights the European roller's capacity for reproductive flexibility in response to extreme weather events, offering valuable insights into avian responses to climate change. The 2023 breeding season, acting as a natural experiment, revealed significant alterations to breeding phenology, a high rate of failed breeding attempts during the incubation phase, and an unprecedented increase in compensatory breeding attempts. The re-use of numerous nest sites for a second attempt within a single season – an event that is otherwise exceptionally rare in our study system – represents a remarkable response to the widespread, weather-induced breeding failures. Despite the environmental challenges in 2023, clutch size, fledgling numbers, and breeding success remained consistent with long-term averages, though significant variation occurred across different nest substrates.

Mechanisms and consequences of heavy rainfall on breeding

Heavy rainfall disrupts breeding attempts through several mechanisms, including increased predation, temporary difficulty in finding prey, or nest flooding (Schöll and Hille 2020). The impact of this event was not uniform across the population, providing clear evidence of an ecological interaction between the extreme weather and nest-site quality. This is best illustrated by the dramatically divergent failure rates in 2023, which ranged from a catastrophic 67% in stone cavities to 19% in nest boxes. Overall, approximately a quarter of breeding attempts in the study area failed due to intense and concentrated precipitation. While substantial, this failure rate was lower than nearly half or one-third of failed attempts recorded during the drought-affected seasons of 2012, 2013, 2014, and 2024.

Failed nests frequently exhibited wet interiors, likely compromising thermoregulation and reducing egg viability. Stone cavities proved particularly vulnerable, as they faced additional challenges, including increased rodent activity, with mice scavenging live or dead nestlings or seeking shelter within these cavities. This aligns with earlier findings that stone cavities are associated with relatively cold and humid microclimates (Amat-Valero et al. 2014), poor breeding performance (Valera et al. 2022), and a declining occupancy trend (Valera et al. 2019). Conversely, rollers nesting in sandstone burrows and nest boxes achieved higher fledgling production, offsetting the poor reproductive performance observed in stone cavities. This strong mediating effect of nest type also explains the variation in the number of young fledged. A key finding of our study is that the average number of fledglings produced per *successful* nest in 2023 was statistically indistinguishable from the long-term average. This overall stability, however, masks the strong underlying influence of nest-site quality. Our models show that the few pairs that managed to hatch young in the highly vulnerable stone cavities produced significantly fewer fledglings than the mean. Therefore, the population's overall productivity was maintained because pairs nesting in more resilient sites – namely, nest boxes and sandstone burrows – were able to fledge a normal number of young, effectively compensating for the poor output from suboptimal nests. Also, while nest boxes exhibited the lowest raw failure rate (19.3%), our models estimated the highest probability of breeding success for rollers in sandstone burrows (78.1%). Although the latter estimate is associated with considerable uncertainty due to the small sample size for this nest type, our results suggest that natural burrows were highly resilient to the extreme rainfall, dramatically outperforming the highly vulnerable stone cavities.

Tree cavities, predominantly used in the northern parts of the roller's breeding range, merit further investigation for their ability to resist water intrusion. Nesting birds routinely occupy tree cavities even in tropical forests with annual precipitation exceeding 4000 mm, suggesting their effectiveness in managing high rainfall (Boyle et al. 2008). Indeed, rollers in the study area have increasingly occupied natural cavities in eucalyptus trees excavated by the Iberian green woodpecker *Picus sharpei*, stressing the importance of preserving diverse nesting options (Valera et al. 2019, 2022).

Artificial nest boxes, widely used as a conservation tool across the roller's breeding range, provide critical nesting opportunities for roller populations. However, our findings suggest that while rollers in nest boxes outperformed those using stone cavities, they performed similarly or slightly worse than rollers in sandstone burrows. This suggests that current nest box designs only partially address the challenges posed by extreme rainfall. Enhancing insulation, reducing rain exposure (e.g. Fig. 4), improving drainage, and ensuring structural resilience are crucial steps to optimise artificial nests for species like the European roller to mitigate the impacts of heavy rain events (Valera et al. 2024).

Beyond the direct effects on nest microclimate, the intense rainfall likely triggered broader ecological consequences by



Figure 4. Nest boxes mounted on poles offer an opportunity to reduce exposure to both sun and rain with the addition of an installed roof.

severely reducing the availability of key insect prey. Heavy rain is known to suppress the activity of large flying insects (Chen et al. 2019), which would have created an acute energetic trade-off for breeding adults, particularly for incubating females. This could lead to clutch neglect, chilling, and ultimately, the high rates of incubation failure we observed in 2023.

Adaptive responses to extreme weather

The timing of extreme weather events plays a critical role in shaping avian responses. The 2023 breeding season may represent a unique case, as heavy rainfall coincided with the peak breeding season (mid-May) when most pairs were laying or incubating eggs. Intense rainfall may directly disrupt embryo development or indirectly hinder parental care by increasing

thermoregulatory demands (Radford and Du Plessis 2003, Fisher et al. 2015, Öberg et al. 2015). The unprecedented rates of nest failure during the incubation phase in 2023, coupled with an unusually high number of apparent replacement breeding attempts, suggest an adaptive behavioural response to extreme weather conditions (c.f. Bolger et al. 2005). Other years in our long-term study also exhibited atypical breeding patterns, such as the bimodal laying distribution observed in 2009. However, the 2023 season was defined by a unique syndrome of events: a highly concentrated rainfall event, a high proportion of failures occurring specifically during incubation, and a sharp increase in apparent replacement breeding. While it is not possible to unequivocally identify these breeding attempts as true replacement clutches by the original pair without marked individuals, several lines of evidence from our long-term monitoring support this as the most biologically plausible explanation. Based on over two decades of observation in this population, nest cavities are consistently abandoned for the remainder of the season following failures due to intraspecific conflict or predation; rapid take-over and re-laying have not been recorded under such circumstances. Furthermore, our previous research has demonstrated that rollers exhibit an aversion to unsuccessful sites, preferring to nest further from cavities that failed in the preceding year (Václav et al. 2011). This established behavioural pattern makes it highly unlikely that the surge in 2023 was driven by new pairs actively choosing to occupy recently failed nests. From an ecological perspective, the key finding is the population-level phenomenon of nest cavity reuse for a second breeding attempt within a single season.

Nest abandonment, while atypical for the European roller, may represent a trade-off between investing in offspring with low survival prospects and conserving resources for adult survival (Winkler 1987). Such threshold-based behavioural response of adult rollers indicates the high survival costs associated with intense rainfall and carries important evolutionary implications. Selective pressures favouring reproductive deferral under adverse environmental conditions might drive greater phenotypic plasticity or shifts in parental strategies over time (Radford and Du Plessis 2003, Hidalgo Aranzamendi et al. 2019).

The 11-day delay in late-season laying is of profound biological importance, as successful reproduction in this semi-arid system is a race against the predictable onset of harsh summer conditions. The arrival of intense summer heatwaves typically brings a sharp decline in the availability of insect prey (Carter et al. 2025) and creates thermally stressful microclimates in nest cavities (Corregidor-Castro et al. 2023). This timing creates a potential 'double jeopardy' scenario, exposing nestlings to developmental risks from heat stress while forcing parents into a trade-off between provisioning and their own thermoregulation. Usually, breeding this late would be a high-risk strategy. However, we propose that the same intense rainfall that caused the initial failures also prolonged the ecological opportunity for late breeding by increasing productivity and temporarily moderating temperatures. While

this allowed for an adaptive response, the delay still imposes significant costs by reducing the time available for essential post-breeding moult and pre-migratory fattening, potentially compromising future survival and reproductive success for both adults and their late-fledged offspring (Arroyo et al. 2002, Webster et al. 2002, Hedenström et al. 2007).

Our findings suggest that the European roller can buffer the events of heavy rainfall through behavioural responses like replacement breeding. However, this capacity may be severely limited if such events occur later in the breeding cycle. Furthermore, the feasibility of replacement breeding in 2023 was likely facilitated by an earlier breeding onset compared to the long-term average, a shift likely triggered by an unusually warm and dry April 2023 with temperatures well above the seasonal average. This highlights climate change's complex and context-dependent consequences on avian reproductive strategies (Bowers et al. 2016).

Conservation implications and future directions

Our findings stress the need for appropriately designed nest boxes to mitigate the challenges of ongoing climatic changes. While significant attention has focused on reducing heat stress in artificial nests (Cstry et al. 2011, Corregidor-Castro et al. 2023), less emphasis has been given to mitigating the effects of heavy rainfall (but see Leroux et al. 2018). Management strategies should prioritise nest designs incorporating protective features against extreme rain, as these events can have immediate and severe consequences for reproductive success and population stability (Valera et al. 2024). Nest boxes not only serve as a valuable conservation tool but also provide insights into similar ecological effects in natural nesting cavities. Since all nest types are essential to European roller conservation, future research should explore how climatic variability shapes breeding performance across different nesting environments.

Additionally, our findings reveal the potential impact of changing climatic conditions on reproductive success in a long-distance migratory bird. Long-term studies are crucial to evaluate the fitness trade-offs between nest abandonment and continued parental care during extreme weather events, as even short-term impacts can have significant consequences for the demography of threatened populations (Pérez-Granados et al. 2023). Investigations into the genetic basis of behavioural flexibility, the population-level consequences of such strategies, and the impact of other stressors (e.g. food scarcity) and moderators (e.g. nest type) could provide deeper insights into the adaptive potential of bird populations (c.f. Yannic et al. 2014). Expanding research to include multiple populations across the species' range could help identify broader patterns of the species' resilience and vulnerability to environmental variability. Specifically, future research should aim to model the interactive effect of multiple climatic variables, including both precipitation and temperature extremes, to better predict population responses. These efforts will be essential for informing conservation strategies under future climate scenarios.

Acknowledgements – We thank E. Moreno, T. Martínez, L. Bolonio, J. Benzal, and J. Pérez Cabeza for their help during fieldwork. We are grateful to Asociación Meteorológica del Sureste (AMETSE) for sharing their meteorological data. The Consejería de Sostenibilidad y Medio Ambiente (Junta de Andalucía) facilitated this study.

Funding – RV was supported by a VEGA grant from the Ministry of Education of the Slovak Republic (no. 2/0111/24). FC-V was supported by the postdoctoral contract "Margarita Salas" (CT18/22) funded by MICIU/AEI/10.13039/501100011033 and the European Union "NextGenerationEU"/PRTR. FV received financial support from the projects CGL2008-00562, CGL2014-55969, PGC2018-097426-B-C22, and TED2021-130035B-100 (funded by MCIN/AEI/ 10.13039/501100011033/FEDER, "ERDF A way of making Europe", and the European Union "NextGenerationEU"/PRTR). JV received financial support from the Juan de la Cierva program (FJC2021-048057-I) funded by MICIU/AEI/10.13039/501100011033 and the European Union "NextGenerationEU"/PRTR.

Conflict of interest – The authors declare no conflict of interest.

Author contributions

Radovan Václav: Formal analysis (lead); Writing – original draft (lead); Writing – review and editing (equal). **Francisco Castaño-Vázquez:** Conceptualization (supporting); Investigation (equal); Writing – review and editing (equal). **Jesús Veiga:** Investigation (equal); Writing – review and editing (equal). **Francisco Valera:** Conceptualization (lead); Funding acquisition (lead); Investigation (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the CSIC Institutional Repository: <https://doi.org/10.20350/digitalCSIC/17837> (Václav et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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