

Mountain grasslands as a stopover habitat for Red-backed Shrikes *Lanius collurio* in the Pyrenees

Juan Arizaga^{1,*}, Jordi Castelló² & Pere Josa³

Arizaga J., Castelló J. & Josa P. 2025. Mountain grasslands as a stopover habitat for Red-backed Shrikes *Lanius collurio* in the Pyrenees. *Ardea* 113: 185–194. doi:10.5253/arde.2025.a18

Understanding how birds use stopover areas is essential for the effective conservation of migratory bird populations. Here, we evaluate the role of high-altitude grasslands in the Central-Eastern Pyrenees as autumn stopover habitat for the Iberian population of the Red-backed Shrike *Lanius collurio*. Using data from a standardized mist-netting program (2010–2024), we analysed age-related patterns in abundance, fuel load, fuel deposition rate and stopover duration. First-year birds were captured much more often (91.5%) and they did not have a longer stopover duration than adults. However, both age classes had a low mean fuel load (0.0338 ± 0.0536 SD, i.e. 3.4%) and a minimal fuel deposition rate, suggesting that the Pyrenees might not serve as a main refuelling site. Instead, the region may function as a transient area for the shrikes, particularly for first-year birds at the onset of their first migration. Despite the low fat accumulation, the high number of individuals using this area highlights its potential relevance. The mosaic of pastures and open habitats aligns with the shrikes' foraging preferences and may support a migration strategy based on short-distance flights with low energy reserves. Given the ongoing population decline and habitat loss, preserving these herbaceous areas is critical to ensure safe passage for species like the Red-backed Shrike. Our findings underscore the need to protect not only key fuelling sites but also early-phase resting habitats along migratory flyways.

Key words: fuel load, conservation, migration, mountain pastures, ringing, stopover duration

¹Department of Ornithology, Aranzadi Sciences Society, Donostia, Spain;

²Estació Biològica Pallars Jussà (EBPJ); Lleida, Spain;

³BIOSCICAT - Societat Catalana de Ciències per la Conservació de la Biodiversitat; Tarragona, Spain.

*corresponding author (jarizaga@aranzadi.eus)



Most long-distance migratory bird populations rely on stopover sites, where they reload energy reserves before resuming their journeys to their destination areas (Chernetsov 2012, Newton 2023). Fuel load (amount of energy reserves), fuel deposition rate (rate at which birds accumulate fuel) and stopover duration (time spent at given stopover sites) are key factors influencing migration strategies (Alerstam & Lindström 1990).

The Red-backed Shrike *Lanius collurio* (hereafter 'shrike') is a long-distance migratory passerine breeding across much of the Euro-Siberian region that overwinters through eastern and southern Africa (Moreau 1972, Tøttrup *et al.* 2012, Harris & Franklin 2000,

Pedersen *et al.* 2020, Franks *et al.* 2022, Bryson & Pajmans 2023). Its European population is experiencing dramatic declines in several regions (BirdLife International 2021), due to various factors, such as habitat changes, new models of agricultural management and practices and other types of environmental stressors and climate change (Olsson 1995, Bani *et al.* 2009, Tellería 2018b, Knozowski *et al.* 2024). Several of such threats occur outside the breeding quarters, e.g. during the migration period (Brochet *et al.* 2016). Conservation strategies should prioritize, in part, a better understanding of the use of potential stopovers along migratory routes (Fransson *et al.* 2005, Warnock 2010, Schmaljohann *et al.* 2022), in order to identify

key fuelling and/or resting areas, which would deserve priority habitat preservation and restoration.

Iberian Red-backed Shrikes presumably leave their breeding quarters from late-July to August (Tøttrup *et al.* 2017), to pass through the Pyrenees, following a west-east to southwest-northeast migratory axis, on their route to the Balkans across southern France and the northern part of Italy (Pedersen *et al.* 2020). Studies based on light-level geo-locators show that all European shrikes use the same route and share the same main stopover places, with the main stopover region in Europe in autumn being the Balkan peninsula, where these birds stay an average of 15 days before crossing the Mediterranean and the Sahara desert until they reach their next important stopover area in the sub-Saharan region in East Africa (Tøttrup *et al.* 2012, Pedersen *et al.* 2020). These previous studies considered, however, a limited number of shrikes marked in Iberia, which means that for this population, which shows a very long-distance migratory flyway, the existence of other potential important stopover areas might simply pass unnoticed due to lack of data.

Shrikes prey upon insects, including beetles, wasps, bees, ants, crickets, grasshoppers, lizards, rodents and small passerine birds (Tryjanowski *et al.* 2003a,b, Lefranc & Worfolk 2022), that they find in open landscapes (Panov 2011), with a preference for pastures and grasslands with cattle (Brandl *et al.* 1986, Lizarraga 2004, Morelli *et al.* 2012, Molina *et al.* 2022, Arizaga *et al.* 2023). The Pyrenees, therefore, may play a role as a potential stopover region for the Iberian

shrike population, as they are an obligate region of passage but, also, as they offer plenty of opportunities to refuel due to the extensive availability of presumably optimal habitat. A previous study on birds marked in the León province (northwest Spain) did not show a notable use of the Pyrenees, but this conclusion was based on six adult birds (Tøttrup *et al.* 2017). Therefore, the strategy of first-year birds is still unknown and it is possible that strategies may differ between age classes (Tryjanowski & Yosef 2002).

This study is based on data collected over more than a ten-year period in a standardized mist-netting monitoring program on migrant bird populations at a potential stopover area, mostly comprising of pastures at high altitude in the Eastern part of the Pyrenees. It aims at quantifying use of this habitat by shrikes as a stopover during the autumn migration period and determine the ecological importance of this mountain chain for the conservation of the south-western (Iberian) Palaearctic population.

METHODS

Sampling area and data collection

The study was carried out in montane grasslands of the Pyrenees, where shrikes were captured using mist nets as part of a long-term standardized (constant effort-based) ringing program at the MigraVallFosca project (Josa & Castelló 2020). The monitoring station was located at Aguiró, municipality of Torre de Capdella

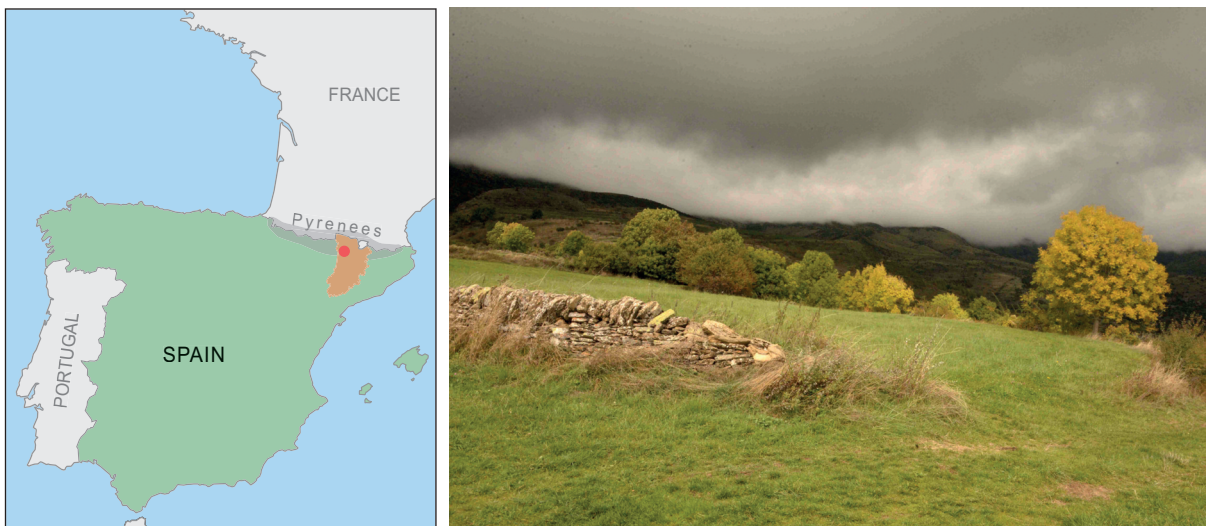


Figure 1. Sampling site, province of Lleida (light brown area), Spain, in the Central-Eastern part of the Pyrenees. Photo: typical habitat, dominated by managed meadows.

(Lleida, Catalonia, Central-Eastern Pyrenees; Figure 1). Situated at an altitude of 1470 m, the bird ringing site features a heterogeneous habitat mosaic, mostly comprised of open landscapes of managed alpine meadows, with some scattered hedgerows (Dog Rose *Rosa canina*, Blackthorn *Prunus spinosa*, Alpine Buckthorn *Rhamnus alpina*) and a few tree stands of Wild Cherry *Prunus avium* and Ash *Fraxinus excelsior*. This landscape is shaped by grazing with traditional extensive livestock, with no agro-chemical treatments applied to meadows.

Between 2010 and 2012, the number and position of the mist nets was modified until a final, definitive setup was achieved which reached an optimal threshold between the number of birds caught and sampling effort. Due to this lack of standardization in 2010–2012, the data collected in this period were only used for the analyses that did not demand sampling uniformity (for details see ‘statistical analysis’). Since 2013, we used 300 linear meters of mist nets disposed in nine lines at fixed sites. Nets were open c. 1 h before dawn till 5 h after dawn during 2010–2022, and 4 h after dawn in 2023 and 2024, due to the increasing number of days that were too hot, risking bird safety. In this period (2013–2024), the station was active from 22 July (mean: 4 August) to 29 September (mean: 18 September), with an annual mean of 33 sampling days (for details see Table S1).

Captured shrikes were ringed, aged as first-years or adults (corresponding to the age EURING codes 3 and 4, respectively, based on plumage characters; Jenni & Winkler 1994). Next, their wing length (± 0.5 mm accuracy), body mass (± 1 g, weighed with a digital balance) and fat scores (Kaiser 1993) were measured.

Statistical analysis

We used all the data for all analyses, except for our analyses to determine the phenological patterns of the abundance and to estimate stopover duration. In these cases, we only used the data collected from 2013 onwards. In all analyses, except of stopover probability, we evaluated one biologically relevant model. Variable significance (as presented in Table 1–3) was determined based on an ANOVA.

Statistical analysis: population structure and phenology

To test for the existence of variation in the proportion of age classes between temporal intervals (10-day periods) throughout the migration season, we used a χ^2 -test. All recaptures were relative to birds ringed before at the station and in the same year (Table S1), so only first captures were considered for the analysis,

given that recaptured shrikes were already present in the site when they were ringed.

To analyse phenological patterns of abundance between age classes, we conducted a Generalized Linear Mixed Model (GLMM) on the number of captures with 10-day time intervals (as a continuous variable), age (as a factor) and sampling effort (as a factor: 2013–2022 vs. 2023–2024) as predictor variables, and year as a random factor, with a log-linear link function with negative binomial error distribution. We included sampling effort as a factor because we reduced the sampling effort from 5 to 4 h after dawn in 2023–2024, as compared to 2013–2022. The negative binomial distribution was selected in spite of an alternative model approach using the Poisson distribution, due to overdispersion ($\chi^2 = 6.72$, $P < 0.001$). We did not consider a finer phenological scale, e.g. on a daily basis (Cattry *et al.* 2018, Maggini *et al.* 2020, Arizaga *et al.* 2022), because the data set had many gaps: the mean percentage of sampling days per year over the total was 56.6% and only in 2015, 2018, 2023 and 2024 this value reached c. 70%; for details see Table S1).

Statistical analyses: fuel load and fuel deposition rate

Fuel in birds is mostly accumulated as subcutaneous fat (Butler 2016) and, therefore, body mass gain of migrants that stop over is highly correlated with fuel loading (Salewski *et al.* 2002). To determine the influence of possible environmental and morphological factors on fuel levels, we conducted a GLMM on body mass, with the following independent variables: wing length, date, recapture (first capture event vs. last recapture for those birds which were recaptured at our station and in the same year) and age (first-years vs. adults). Moreover, we included year as a random factor, given that local or even wide-scale conditions could vary among years and this may have an impact on fuelling (Schaub *et al.* 2008).

Thereafter, we also expressed mean body mass as a fuel load estimate (f) relative to lean body mass (m_0). Predicted lean body mass can be calculated with a regression line of body mass (m) on wing length for those birds for which their fat level has been scored as zero following the Kaiser classification (Kaiser 1993). However, we only found four birds with no fat, with most shrikes exhibiting relatively low fat levels, mostly scored from 1 to 3 on a 0–8 scaled classification (though the highest value found in our sample was 6; Figure 2). Therefore, we conducted an ANOVA on body mass with wing length and fat, and from here we obtained a

predicted lean body mass for each bird. From here, fuel load was calculated as $f = (m - m_0)/m_0$. Negative predicted f values were assigned a zero ($f = 0$).

Following the rationale explained for body mass, we considered mass deposition rate as a proxy for fuel deposition rate. We calculated mass deposition rate as the difference of body mass between the last and first capture event for those birds that were recaptured once or on more occasions within the season, divided by the number of days elapsed between the two captures (observed stopover duration). To determine the influence of driving factors on mass deposition rate, we conducted a General Additive Mixed Model (GAMM) on mass deposition rate, with the following independent variables: a linear effect of wing length, month, initial body mass and age, a random effect of year, and a non-linear effect of observed stopover duration, because mass deposition rate could vary with stopover duration (Arizaga *et al.* 2010). Apart from this, we also conducted a GLMM on the observed stopover duration with age and initial fuel load (fuel load at first capture event) as predictors and year as a random factor.

Statistical analyses: stopover probability

Detection probability rarely equals 1, so the real stopover duration is likely to be longer than the observed stopover duration (Schaub *et al.* 2001). Cormack-Jolly-Seber (CJS) survival models on captures and recaptures for open populations have proved to be very adequate to estimate stopover duration in birds, given that real survival from one day to the next is close to 1, so apparent survival in these migratory birds (φ) equates to their probability of staying one more day in the stopover site (Schaub *et al.* 2001). Similar formulas can be used to estimate the probability of a bird being present at a site the day before its first capture event (γ), and the combination of both estimates can be used to estimate stopover duration. Normally, φ and γ tend to be symmetric, so estimating φ is sufficient to explore factors shaping stopover duration. In this work, we only calculated φ .

We considered the data set for the period 2013–2024, consisting of 710 rows (individuals) by 61 columns (from 22 July to 20 September). Years were lumped into a single ‘fictitious’ year, because we had no sample size to estimate mean φ values across all the study years. As we had a relatively high proportion of missed sampling days (Table S1), it was not realistic, due to sampling size constraints, to estimate year- and time-dependence on φ , and the effect of potential factors driving variation on daily rates of φ (Bolshakov

et al. 2003, Bulyuk & Tsvey 2006, Andueza *et al.* 2013). Therefore, here we aim to just estimate a mean φ .

Before starting to test the above described CJS models, we used a goodness-of-fit (GOF) test using U-CARE (Choquet *et al.* 2009) to see whether the data fitted well to CJS assumptions. The global GOF test was not significant ($\chi^2 = 107.44$, $P = 1.000$), nor the specific test to detect transients – birds staying for just one day – ($Z = 1.28$, $P = 0.202$) or trap-dependence ($Z = 1.12$, $P = 0.264$). CJS models estimate φ and p (probability of recapturing a bird that is already present). Apart from a basic starting model with constant φ and p , we also tested for models with an effect of the age (first-years vs. adults) on φ , p or φ and p . Moreover, even though the specific test to detect transients was not significant, we forced alternative models considering time-dependence on φ (with just two age

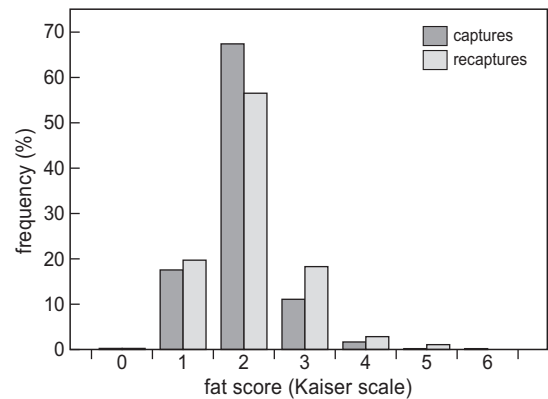


Figure 2. Frequency distribution of the fat deposits (Kaiser 1993) measured on Red-backed Shrikes stopping over in grasslands at high altitude in the Pyrenees, during their autumn migration.

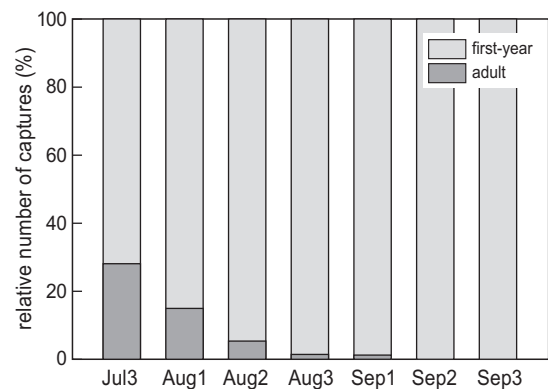


Figure 3. Percentage of captures in relation to their age class, segregated by 10-day periods (Jul3 stands for 21–31 July; Aug1 for 1–10 August, etc.). Total sample size: 820 individuals.

cohorts) on either first-years (φ_{FY1} , φ_{FY2}), adults (φ_{AD1} , φ_{AD2}) or both age categories (Pradel *et al.* 1997). From here, the proportion of transients, T , is calculated as $T = 1 - (\varphi_1/\varphi_2)$. From a biological standpoint, transients would be birds that stop over for just one day, as compared to birds that stop for longer (Schaub & Jenni 2001). Models were ranked in relation to their small sample size-corrected Akaike values (AICc), where models with the lowest values had a better fit to the data and models differing in less than 2 AICc units were considered to have similar support (Burnham & Anderson 1998). We also tested for a possible effect of initial fuel load on φ by considering a subset of the data previously used (not all birds had their initial body mass measured) and comparing a basic model with constant φ and p (one of the models that best fitted data; see Results for details) with another one with an effect of fuel on φ with constant p .

All statistics except the CJS models were done using the software R v. 4.3.1 (R Core Team 2023), with the packages ‘dplyr’ (Wickham *et al.* 2023), ‘lmerTest’ (Kuznetsova *et al.* 2017) and ‘mgcv’ (Wood 2017). The CJS models were conducted in MARK (White & Burnham 1999).

RESULTS

Population structure and phenology

Overall, first year birds were much more abundant than adults (91.5%, $n = 750$ vs. 70 individuals). This proportion was not constant within season ($\chi^2_6 = 73.95$, $P < 0.001$), with the presence of adults decreasing progressively from 28% by the end of July to 0% during the last two 10-day intervals of September (Figure 3).

Abundance varied between 10-day time intervals, age classes and depending on the sampling effort, with an interaction between age and 10-day intervals (Table 1). The mean number of captures per day tended to decrease across the season, but this decline was steeper in adults (Figure 4). The amount of variance associated with the mean was highest in July.

Fuel load and fuel deposition rate

Body mass was not affected by any of the included variables (Table 2). First captures of shrikes weighed on average 26.0 ± 7.0 g (\pm SD, $n = 820$) and they had a mean fuel load of 0.034 over lean body mass (i.e. $3.4 \pm 0.054\%$).

The mean mass deposition rate tended to increase linearly with the date and decrease with increasing body mass in the first capture event (Table 3, Figure 5).

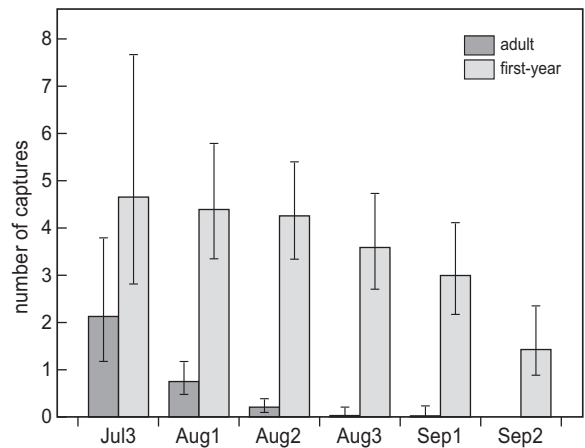


Figure 4. Predicted number of captures per day (\pm 95% confidence interval) of first-year and adult birds, according to the model shown in Table 1.

Table 1. Results from a Generalized Linear Mixed Model relating the number of captures to 10-day time intervals, age and sampling effort (2013–2022 vs. 2023–2024) as predictor variables (10-day interval is a continuous variable and the rest are factors), and year as a random factor (r^2 conditional = 0.960, r^2 marginal = 0.958), with log-linear link function with negative binomial errors distribution.

Predictor variables	$\beta \pm$ SE	P
Intercept	1.94 \pm 0.18	<0.001
10-day interval	-0.18 \pm 0.05	<0.001
Age (Adults)	0.08 \pm 0.40	0.852
Age \times 10-Day	-0.98 \pm 0.16	<0.001
Effort (Period 2023–2024)	-0.49 \pm 0.17	0.004

Reference values β parameter estimates ($\beta = 0$): Age: first-year, Effort: 2013–2022 period

Table 2. Results from a Linear Mixed Model relating body mass to wing length, age, date and recapture (Rec: first capture event vs. last recapture for those birds recaptured within the area and in the same year) as predictor variables, including year as a random factor (r^2 conditional = 0.80, r^2 marginal <0.01).

Predictor variables	$\beta \pm$ SE	P
Intercept	19.58 \pm 3.38	<0.001
Wing length	0.02 \pm 0.01	0.090
Age (Adults)	0.82 \pm 0.46	0.078
Date	0.02 \pm 0.01	0.140
Rec: last recapture	1.09 \pm 0.93	0.240

Reference values β parameter estimates ($\beta = 0$): Age: first-year, Rec: first capture event

We observed a significant, non-linear positive effect of the observed stopover duration on mass deposition rate ($F_1 = 9.54, P < 0.001$; Figure 5). The linear relationship of the observed stopover duration on body mass change was not significant for adults ($r^2 = 0.001, P = 0.894$), but was significant for first-year birds ($r^2 = 0.045, P = 0.005$; Figure 6).

Stopover probability

The mean (\pm SD) observed stopover duration for the shrikes that were recaptured within the same year was 5.4 ± 4.6 d for first-year birds and 6.5 ± 6.0 d for adults. This difference between age classes was not significant ($F_1 = 2.38, P = 0.125$). Initial fuel load did not have any significant effect on observed stopover duration ($F_1 = 0.028, P = 0.868$). The percentage of birds recaptured was 21.4% for adults and 25.2% for first-year birds.

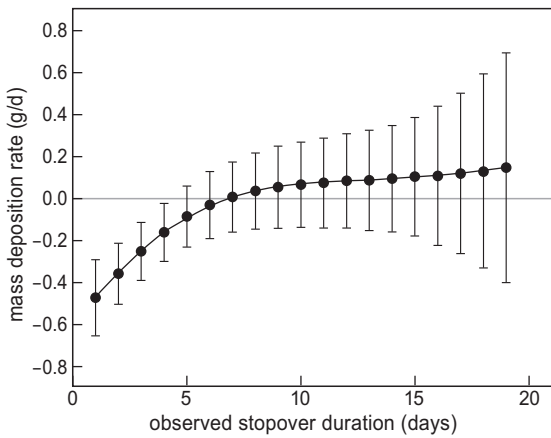


Figure 5. Predicted mean mass deposition rate (\pm 95% confidence interval) in relation to the number of days passed between the last and the first captured event (observed stopover duration). Non-linear line as obtained from a GAMM (Table 3).

Table 3. Results from a General Additive Mixed Model used to test for a linear effect of wing length, age and body mass at first capture event and a non-linear effect (smoothed) of date on mass deposition rate. Year was included as a random factor (r^2 conditional = 0.85, r^2 marginal = 0.05).

Predictor variables	$\beta \pm$ SE	P
Intercept	-0.182 \pm 2.056	0.930
Wing length	0.008 \pm 0.020	0.688
Age (Adults)	0.200 \pm 0.178	0.262
Initial body mass	-0.115 \pm 0.023	<0.001
Date	0.010 \pm 0.004	<0.001

Reference values β parameter estimates ($\beta = 0$): Age: first-year,

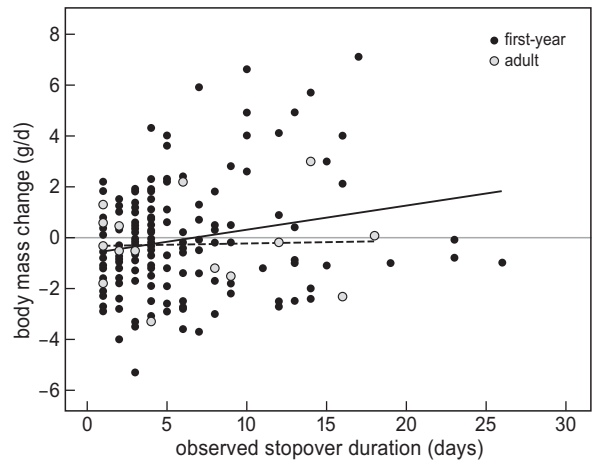


Figure 6. Body mass change in relation to the observed stopover duration between age classes of Red-backed Shrikes stopping over in the Pyrenees in autumn migration. A linear relationship is shown for first-year birds (solid line) and adults (dotted line).

CJS models assuming a constant p were higher ranked than those with an effect of age on p (Table 4). Therefore, we considered a constant p to test for the effect on transience and age-dependent transiency on φ . The top-ranking model, which best fitted the data, considered the presence of transients independently of age, though the second model, which considered constant φ , fitted the data equally well (Δ AICc > 2; Table 4). According to the first model the percentage of transients was 17.4% and the average probability for the individuals to stop-over for more than one day was 0.82 ± 0.012 (\pm SE), with a mean p of 0.10 ± 0.01 . In the second top-ranking model (Table 4), we obtained a $\varphi = 0.80 \pm 0.01$, with a mean p of 0.10 ± 0.01 . An additional separately analysed model did not reveal a significant effect of fuel on φ (Table 4, Figure 7).

DISCUSSION

This study provides relevant clues into the use of the Pyrenees as a stopover region for the Iberian population of the Red-Backed Shrike during its autumn migration. Using ringing data collected over more than a decade, we not only quantified the stopover use of this mountain area but also assessed its ecological and conservation significance for the southwestern Palae-arctic population of shrikes.

We provide evidence that the Pyrenees are used by the shrikes. Abundance peaked in late July, progressively decreasing up to late September; adults left the region earlier, with the last birds being captured by

mid-August, suggesting that they migrate faster and perhaps earlier within the season compared to first-years. Given that the sampling period often began at the end of July (Table S1), we cannot exclude that an unknown number of adults may have passed over the area even before, although field-based evidence shows that in the Atlantic region of Spain many adults still remain at their breeding sites in late July (JA pers. obs.). These findings align with existing theories that post-breeding migration is earlier in adults (Tryjanowski & Yosef 2002), and with records of the early departure of adult Red-backed Shrikes all over Europe (Lefranc & Worfolk 2022). First-year birds remained in the Pyrenees longer, supporting the idea of age-dependent stopover durations (Tryjanowski & Yosef 2002).

The relatively low fuel load and the near-zero observed fuel gain rate indicate that the Pyrenees do not act as a main refuelling area for the shrikes in autumn. Overall, it is likely that Iberian shrikes did not use the Pyrenees as a true staging zone *sensu* Warnock (2010), at least in adult birds, but rather as a transit stopover where they could rest before resuming their journey (Bäckman *et al.* 2017, Macías-Torres *et al.* 2022).

Despite the relatively low fuel accumulation observed, the Pyrenees still would play a relevant role in the migratory strategy of Red-backed Shrikes, albeit in a different capacity. The Pyrenees, and in particular their pastures at high altitude, offer an environment with a rich habitat mosaic of the preferred habitats of shrikes, such as grasslands and pastures with livestock (Olsson 1995, Vanhinsbergh & Evans 2002, Lizarraga 2004, Morelli *et al.* 2012, Tellería 2018a,b). The availability of such suitable habitats for foraging may be essential for the migratory strategy of the shrikes in Europe, apparently based on short flight bouts (Pedersen *et al.* 2020) relying on low but constant fuel loads, which is only possible when food availability is abundant and predictable along the route (Delingat *et al.* 2006, Arizaga *et al.* 2011), and has the advantage of avoiding the risk associated with being too heavy (Kullberg *et al.* 1996, Lind *et al.* 1999).

The high number of Red-backed Shrikes observed within the region, suggests that the Pyrenees are important for the passage of Iberian birds. Even though the area does not seem to be crucial for fuelling, it could still serve as an important resting area for transient birds at the beginning of migration. The high numbers

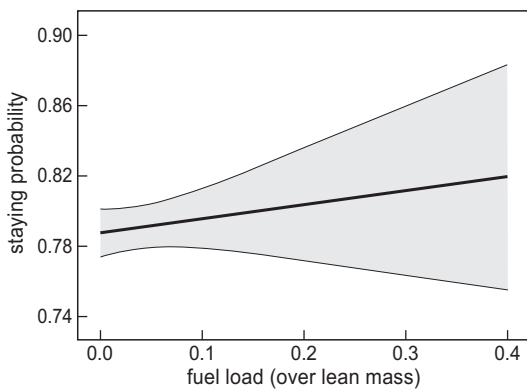


Figure 7. Predicted mean values of φ (\pm SE; probability to stay in relation to the fuel load of the bird during the initial capture event, according to the second CJS model ($\varphi(\text{fuel}), p$) shown in Table 4.

Table 4. Cormack-Jolly-Seber models used to test stopover probability, and its variation in relation to age and the presence of transients. Abbreviations: φ : apparent daily survival rate (i.e. the probability to stay), p : probability of recapture, AICc: small sample sizes-corrected Akaike values, Δ AICc: AICc difference in relation to the top-ranked model, np : number of parameters, FY: first-year birds, AD: adults, numbers 1 and 2 are relative to models assuming transients.

Models	AICc	Δ AICc	AICc weight	np	Deviance
φ_1, φ_2, p	2360.23	0.00	0.244	3	1120.46
φ, p	2361.21	0.97	0.150	2	1123.44
$\varphi_{\text{FY}}, \varphi_{\text{AD}}, p$	2362.96	2.73	0.062	3	1123.18
$\varphi, p_{\text{FY}}, p_{\text{AD}}$	2363.05	2.81	0.060	3	1123.27
$\varphi_{\text{FY1}}, \varphi_{\text{FY2}}, \varphi_{\text{AD1}}, \varphi_{\text{AD2}}, p$	2363.30	3.06	0.053	5	1119.48
$\varphi_{\text{FY1}}, \varphi_{\text{FY2}}, \varphi_{\text{AD}}, p$	2363.40	3.17	0.050	4	1121.61
$\varphi_{\text{FY}}, \varphi_{\text{AD1}}, \varphi_{\text{AD2}}, p$	2363.49	3.25	0.048	4	1121.69
$\varphi_{\text{FY}}, \varphi_{\text{AD}}, p_{\text{FY}}, p_{\text{AD}}$	2364.33	4.10	0.031	4	1122.54

Data subset to detect an effect of fuel load on φ

φ, p	2203.27	0.00	0.713	2	2199.26
$\varphi(\text{fuel}), p$	2205.09	1.82	0.287	3	2199.07

found in July may reflect concentrations of dispersing or local birds before the real start of their migration. The relatively high proportion of transients, particularly in adults, suggests that the Pyrenees may be especially relevant for first-year birds, acting to some extent as an important pre-migratory area. The high proportion of first-years can be very well explained simply by the fact that these first-year birds tend to be more numerous than adults in autumn migration (Tryjanowski & Yosef 2002).

From a conservation standpoint, our findings indicate that whilst the Pyrenees are probably not used as a main stopover zone for refuelling, they could still have a vital function, providing Red-backed Shrikes, particularly first-year birds, with an opportunity to rest and keep a balanced fuel load in the early phase of their first migration. All this underscores the importance of preserving and protecting the Pyrenean alpine grasslands. This is particularly relevant given the continued declines in Red-backed Shrike populations, particularly across much of Spain (main source population of the shrikes stopping over in the Pyrenees; Tellería 2018b), and the progressive loss of such open habitats due to the development of forest linked with the abandonment of rural areas (Arizaga *et al.* 2023). These sites, though not critical for fuel replenishment, seem to be important for the start of their long-distance migration and, even though not all stopovers are used for refuelling along the route in the same way, all stopovers fulfil a vital function. Moreover, many, if not all Spanish shrikes need to cross the Pyrenees, an area which could form an ecological barrier, and thus the occurrence of enough habitat for resting and/or refuelling is vital for these individuals to cross this barrier successfully.

ACKNOWLEDGEMENTS

We are grateful to Estació Biològica del Pallars Jussà for making the MigraVallFosca project possible and to Torre de Capdella council and Gratiud Pallars for the support for this project. This study would not have been possible without the collaboration of the meadow owners, casa Badia, casa Móra and cal Frare. Two anonymous referees and the associated editor Rienk Fokkema provided valuable comments that helped us to improve an earlier version of this work.

REFERENCES

- Alerstam T. & Lindström Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner E. (ed.) Optimal bird migration: the relative importance of time, energy and safety. Springer-Verlag Heidelberg, Berlin, pp. 331–351.
- Andueza M., Arizaga J., Belda E.J. & Barba E. 2013. The role of extrinsic and intrinsic factors on the departure decisions of a long-distance migratory passerine. *Ardeola* 60: 59–72.
- Arizaga J., Barba E., Alonso D. & Vilches A. 2010. Stopover of bluethroats (*Luscinia svecica cyaneacula*) in northern Iberia during the autumn migration period. *Ardeola* 57: 69–85.
- Arizaga J., Sánchez J.M., Díez E., Cuadrado J.F., Asenjo I., Mendiburu A., Jauregi J.I., Herrero A., Elozegi Z., Aranguren I., Andueza M. & Alonso D. 2011. Fuel load and potential flight ranges of passerine birds migrating through the western edge of the Pyrenees. *Acta Ornithol.* 46: 19–28.
- Arizaga J., Escamilla S., Castany J., Barragán A.M., Timor P., Silvestre R., Rebollo A., Adelantado J., Pupla B. & Cantos A. 2022. Flock structure and phenology of migration of the Common Linnet *Linaria cannabina* through eastern Spain. *Ring. Migr.* 37: 63–72.
- Arizaga J., Laso M., Rodríguez-Pérez J., Aizpurua O., García-Serna I., González H., Olano M., Webster B., Belamendia G., Zuberoigoitia I. & Carrascal L.M. 2023. Euskadiko hegazti habiagileen atlasa / Atlas de aves nidificantes de Euskadi. Sociedad de Ciencias Aranzadi, Donostia.
- Bäckman J., Andersson A., Pedersen L., Sjöberg S., Tøttrup A.P. & Alerstam T. 2017. Actogram analysis of free-flying migratory birds: new perspectives based on acceleration logging. *J. Comp. Physiol. A* 203: 543–564.
- Bani L., Massimino D., Orioli V., Bottoni L. & Massa R. 2009. Assessment of population trends of common breeding birds in Lombardy, Northern Italy, 1992–2007. *Ethol. Ecol. Evol.* 21: 27–44.
- BirdLife International 2021. European Red List of Birds. Publications Office of the European Union, Luxembourg.
- Bolshakov C., Bulyuk V. & Chernetsov N. 2003. Spring nocturnal migration of Reed Warblers *Acrocephalus scirpaceus*: departure, landing and body condition. *Ibis* 145: 106–112.
- Brandl R., Lubcke W. & Mann W. 1986. Habitat selection in the red-backed shrike *Lanius collurio*. *J. Ornithol.* 127: 69–78.
- Brochet A.-L. *et al.* & Butchart S.H. M. 2016. Preliminary assessment of the scope and scale of illegal killing and taking of birds in the Mediterranean. *Bird Conserv. Int.* 26: 1–28.
- Bryson U. & Pajjmans D.M. 2023. Red-backed Shrike (*Lanius collurio*) Linnaeus, 1758 on its non-breeding grounds: comparative biometrics, moult data and criteria to determine age and sex. *Namib. J. Environ.* 7D: 1–19.
- Bulyuk V.N. & Tsvey A. 2006. Timing of nocturnal autumn migratory departures in juvenile European robins (*Erithacus rubecula*) and endogenous and external factors. *J. Ornithol.* 147: 298–309.
- Burnham K.P. & Anderson D.R. 1998. Model selection and inference. A practical information theoretic approach. Springer-Verlag, New York.
- Butler P.J. 2016. The physiological basis of bird flight. *Phil. Trans. R. Soc. B* 371: 20150384.
- Catry T., Lourenço P.M. & Granadeiro J.P. 2018. Quantifying population size of migrant birds at stopover sites: Combining count data with stopover length estimated from stable isotope analysis. *Method. Ecol. Evol.* 9: 502–512.
- Chernetsov N. 2012. Passerine migration: Stopovers and flight. Springer, Berlin.
- Choquet R., Lebreton J.-D., Gimenez O., Reboulet A.-M. & Pradel R. 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating Capture–Recapture data. *Ecography* 32: 1071–1074.

- Delingat J., Dierschke V., Schmaljohann H., Mendel B. & Bairlein F. 2006. Daily stopovers as optimal migration strategy in a long-distance migrating passerine: the Northern Wheatear *Oenanthe oenanthe*. *Ardea* 94: 593–605.
- Franks S. *et al.* & Baillie S.R. 2022. Online atlas of the movements of Eurasian-African bird populations. EURING/CMS.
- Fransson T., Jakobsson S. & Kullberg C. 2005. Non-random distribution of ring recoveries from trans-Saharan migrants indicates species-specific stopover areas. *J. Avian Biol.* 36: 6–11.
- Harris T. & Franklin K. 2000. *Shrikes and Bush-shrikes*. Princeton University Press, Princeton.
- Jenni L. & Winkler R. 1994. *Moult and ageing of European passerines*. Academic Press, London.
- Josa P. & Castelló J. 2020. MigraVallFosca: Resultados del seguimiento de la migración posnupcial en una estación de anillamiento en el Pirineo. *Rev. Anilla*. 39: 6–14.
- Kaiser A. 1993. A new multicategory classification of subcutaneous fat deposits of songbirds. *J. Field Ornithol.* 64: 246–255.
- Knozowski P., Nowakowski J.J., Stawicka A.M., Dulisz B. & Górski A. 2024. Effect of management of grassland on prey availability and physiological condition of nestling of Red-Backed Shrike *Lanius collurio*. *Animals* 14: 1093.
- Kullberg C., Fransson T. & Jakobsson S. 1996. Impaired predator evasion in fat Blackcaps (*Sylvia atricapilla*). *Proc. R. Soc. B* 263: 1671–1675.
- Kuznetsova A., Brockhoff P.B. & Christensen R.H.B. 2017. lmerTest package: Tests in linear mixed effects models. *J. Stat. Soft.* 82: 1–26.
- Lefranc N. & Worfolk T. 2022. *Shrikes of the world*. Helm Identification Guides, London.
- Lind J., Fransson T., Jakobsson S. & Kullberg C. 1999. Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. *Behav. Ecol. Sociobiol.* 46: 65–70.
- Lizarraga A. 2004. *Ecología reproductora del alcaudón dorsirrojo (Lanius collurio) en Navarra*. University of Navarra Pamplona.
- Macías-Torres P., Alerstam T., Andersson A., Bäckman J., Thorup K., Töttrup A.P. & Sjöberg S. 2022. Activity patterns throughout the annual cycle in a long-distance migratory songbird, the red-backed shrike *Lanius collurio*. *Mov. Ecol.* 10: 55.
- Maggini I., Cardinale M., Sundberg J.H., Spina F. & Fusani L. 2020. Recent phenological shifts of migratory birds at a Mediterranean spring stopover site: Species wintering in the Sahel advance passage more than tropical winterers. *PLOS ONE* 15: e0239489.
- Molina B., Nebreda A., Muñoz A.R., Seoane J., Real R., Bustamante J. & Del Moral J.C. 2022. III Atlas de aves en época de reproducción en España. SEO/BirdLife, Madrid.
- Moreau R.E. 1972. *The Palaearctic-African bird migration systems*. Academic Press, London.
- Morelli F., Santolini R. & Sisti D. 2012. Breeding habitat of red-backed shrike *Lanius collurio* on farmland hilly areas of Central Italy: is functional heterogeneity one important key? *Ethol. Ecol. Evol.* 24: 127–139.
- Newton I. 2023. *The migration ecology of birds*. 2nd ed. Academic Press, London.
- Olsson V. 1995. The Red-backed Shrike *Lanius collurio* in southeastern Sweden: breeding biology. *Ornis Svec.* 5: 101–110.
- Panov E.N. 2011. *The true shrikes (Laniidae) of the World*. Ecology, behavior and evolution. Pensoft, Sofia-Moscu.
- Pedersen L. *et al.* & Töttrup A.P. 2020. Remarkably similar migration patterns between different red-backed shrike populations suggest that migration rather than breeding area phenology determines the annual cycle. *J. Avian Biol.* 51: e02475.
- Pradel R., Hines J.E., Lebreton J.D. & Nichols J.D. 1997. Capture-recapture survival models taking account of transients. *Biometrics* 53: 60–72.
- R Core Team 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- Salewski V., Falk K.H., Bairlein F. & Leisler B. 2002. Numbers, body mass and fat scores of three Palearctic migrants at a constant effort mist netting site in Ivory Coast, West Africa. *Ardea* 90: 479–487.
- Schaub M. & Jenni L. 2001. Stopover durations of three warbler species along their autumn migration route. *Oecol.* 128: 217–227.
- Schaub M., Pradel R., Jenni L. & Lebreton J.D. 2001. Migrating birds stop over longer than usually thought: An improved capture-recapture analysis. *Ecol.* 82: 852–859.
- Schaub M., Jenni L. & Bairlein F. 2008. Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. *Behav. Ecol.* 19: 657–666.
- Schmaljohann H., Eikenaar C. & Sapir N. 2022. Understanding the ecological and evolutionary function of stopover in migrating birds. *Biol. Rev.* 97: 1231–1252.
- Tellería J.L. 2018a. Distribution of the Red-Backed Shrike *Lanius collurio* at its western range boundary: patterns and conservation prospects. *Ardeola* 65: 221–232.
- Tellería J.L. 2018b. Old counts suggest the collapse of two red-backed shrike *Lanius collurio* populations. *Ardeola* 65: 283–290.
- Töttrup A.P., Klaassen R.H.G., Strandberg R., Thorup K., Kristensen M.W., Jargensen P.S., Fox J., Afanasyev V., Rahbek C. & Alerstam T. 2012. The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proc. R. Soc. B* 279: 1008–1016.
- Töttrup A.P., Pedersen L., Onrubia A., Klaassen R.H.G. & Thorup K. 2017. Migration of red-backed shrikes from the Iberian Peninsula: optimal or sub-optimal detour? *J. Avian Biol.* 48: 149–154.
- Tryjanowski P., Karg M.K. & Karg J. 2003a. Diet composition and prey choice by the red-backed shrike *Lanius collurio* in western Poland. *Bel. J. Zool.* 133: 157–162.
- Tryjanowski P., Karg M.K. & Karg J. 2003b. Food of the Red-backed Shrike *Lanius collurio*: a comparison of three methods of diet analysis. *Acta Ornithol.* 38: 59–64.
- Tryjanowski P. & Yosef R. 2002. Migration of the Red-backed Shrike *Lanius collurio* at the desert edge: a case study in Eilat (Israel). *Acta Ornithol.* 37: 73–78.
- Vanhinsbergh D. & Evans A. 2002. Habitat associations of the Red-backed Shrike (*Lanius collurio*) in Carinthia, Austria. *J. Ornithol.* 143: 405–415.
- Warnock N. 2010. Stopping vs. staging: the difference between a hop and a jump. *J. Avian Biol.* 41: 621–626.
- White G.C. & Burnham K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Stud.* 46: 120–139.

Wickham H., François R., Henry L. & Müller K. 2023. dplyr: A grammar of data manipulation (v. 1.1.3).
 Wood S.N. 2017. Generalized additive models: an introduction with R. CRC Press, Boca Raton.

SAMENVATTING

Om trekvogels effectief te kunnen beschermen is het belangrijk te weten op welke wijze de vogels tijdens de trek gebruikmaken van tussenstops. Wij hebben in 2010–2024 tijdens de najaarstrek in hooggelegen graslanden van de Centraal-Oostelijke Pyreneeën de leeftijdsamenstelling, de mate en snelheid van vetopslag en de verblijfsduur van doortrekkende Grauwe Klauwieren *Lanius collurio* van de Iberische populatie onderzocht. Eerstejaars klauwieren (91,5% van de gevangen vogels) verbleven niet langer in de tussenstopgebieden dan volwassen vogels. Beide leeftijdsgroepen hadden gemiddeld $0,0338 \pm 0,0536$ (SD) gram reserves opgeslagen (3,4% van het

lichaamsgewicht) en een minimale opvetsnelheid. Dit suggereert dat de Pyreneeën geen belangrijke opvetlocatie voor de soort zijn. Ze zijn, gezien de grote aantallen die passeren, wel een belangrijk doortrekgebied, vooral voor eerstejaars vogels aan het begin van de najaarstrek. Het mozaïek van weilanden en open habitats weerspiegelt de terreinvoorkeur van de soort om te foerageren. De resultaten van ons onderzoek kunnen wijzen op een trekstrategie door de Pyreneeën gebaseerd op korte afstandsvluchten met kleine energiereserves. Gezien de aanhoudende populatieafname en het verlies aan habitat, is het behoud van deze kruidenrijke graslanden cruciaal voor een veilige doorgang voor soorten als de Grauwe Klauwier. Onze resultaten ondersteunen de noodzaak om niet alleen belangrijke opvetlocaties te beschermen, maar ook rusthabitats aan het begin van trekroutes.

Corresponding editor: Rienk Fokkema

Received 11 April 2025; accepted 13 November 2025

SUPPLEMENTARY MATERIAL

Table S1. Sampling effort from 2010 to 2024 and number of captures and recaptures obtained in a constant-effort ringing site located in Aguiró. Abbreviations: PSD: potential sampling days, RSD: real sampling days (also expressed as a percentage over PSD), CAP: captures (number of birds first captured), REC: recaptures (number of within-season recaptures of birds first-captured previously), TOT: sum of the captures and recaptures.

Year	Date from	Date to	PSD	RSD	RSD (%)	CAP	REC	TOT
Variable sampling effort, until 5 h after dawn								
2010	26/07/2010	29/07/2010	4	4	100	27	0	27
2011	12/08/2011	14/09/2011	34	13	38.2	48	7	55
2012	13/08/2012	29/08/2012	17	7	41.2	11	2	13
Constant sampling effort, until 5 h after dawn								
2013	17/08/2013	18/09/2013	33	16	48.5	27	9	36
2015	16/08/2015	11/09/2015	27	19	70.4	36	14	50
2016	03/08/2016	19/09/2016	48	24	50.0	77	41	118
2017	02/08/2017	19/09/2017	49	24	49.0	79	24	103
2018	02/08/2018	29/09/2018	59	35	59.3	135	70	205
2019	05/08/2019	28/09/2019	55	38	69.1	176	81	257
2020	23/07/2020	12/09/2020	52	13	25.0	50	9	59
Constant sampling effort, until 4 h after dawn								
2023	13/08/2023	03/09/2023	22	15	68.2	28	4	32
2024	22/07/2024	23/09/2024	64	45	70.3	126	47	173