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Predation dynamics and breeding parameters of Mediterranean Short-toed Lark Alaudala rufescens and Thekla's Lark Galerida theklae nests in western Catalonia

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Agricultural intensification and changes in land use leading to habitat fragmentation are the main threats to steppe birds. Understanding nest predation and the factors driving it are essential tasks in the conservation and management of steppe bird species. This study investigates nest predation dynamics, hatching success, productivity and nest survival in two steppe-specialist lark species, the Mediterranean Short-toed Lark Alaudala rufescens and Thekla's Lark Galerida theklae, in Catalonia (NE Spain). We monitored 13 nests over a 7-week period and found that 80% of Mediterranean Short-toed Lark nests and 25% of Thekla's Lark nests fledged successfully. Predation during the nestling stage accounted for all detected nest failures, with predators including snakes, foxes and birds. Although predated nests were found below taller plants than successful nests, the vegetation composition in the area surrounding nests did not differ significantly between predated and successful nests. This study underscores the critical role of predation in the reproductive success of ground-nesting birds and highlights the key role played by habitat management practices that help sustain a short, open steppe vegetation structure favourable to these species. The effective conservation of steppe birds requires a detailed understanding of predation pressures and habitat preferences, which will improve their breeding success and prevent further population declines.

Key words: steppe-specialist birds, predation, ground-nest, breeding parameters, Catalonia, NE Spain.

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The current worldwide loss of biodiversity is largely the result of human-induced changes in land use (Cardinale *et al.* 2012) such that modifications in agricultural systems are today one of the major threats to birds globally (Pimm *et al.* 1995). More specifically, both the spread and intensification of agriculture after the Second World War have led to the loss of most permanent steppes in Europe (Goriup & Batten 1990) and as a direct consequence the populations of birds inhabiting these habitats have declined

dramatically throughout Europe. This is particularly true in Spain and Portugal, two countries that were once the main stronghold for steppe birds in the continent (Traba & Morales 2019).

In Spain – the western European country with the greatest abundance of steppe habitats and birds – natural steppes were historically used for extensive grazing, above all of sheep, a practice that benefitted steppe birds by maintaining a low open vegetation structure (Traba & Pérez-Granados 2022). However, the num-

ber of sheep in Spain decreased by 9.2 million (~37%) between 1992 and 2020 (Traba & Pérez-Granados 2022). During the same period, steppe birds in Spain declined dramatically in number and species diversity. Agricultural intensification and changes in land use have driven habitat loss and led to population isolation and fragmentation. Other threats include farming practices (Ponce et al. 2018), scrub encroachment, afforestation, infrastructure construction, and predation (Gómez-Catasús et al. 2019), the latter factor affecting over 80% of all nests (Pérez-Granados et al., 2017; Donald et al. 2002; Suarez & Manrique, 1992). Moreover, agricultural intensification has stimulated an increase in the abundance of mesopredators (Roos et al. 2018, Terraube & Bretagnolle 2018) and altered the dynamics of prey species (Bravo et al. 2023). For groundnesting birds, predation is the chief reason for nest failure (Praus et al. 2014, Yanes et al. 1996, Bravo et al. 2020) and high predation rates may threaten population viability (Suárez et al. 1993). For example, larks (Alaudidae) are highly vulnerable to many mammalian and avian predators (Suarez & Manrique 1992, Suárez et al. 1993, Yanes & Suárez 1996, Hódar 2006) including corvids (Bravo et al. 2020). However, the identity of predators is not always known and varies depending on the locality and the year (Suárez et al. 2005).

In studies of predation rates, nest-monitoring activities may increase predation risk and, above all in the case of ground-nesting passerines, frequent nest visits by researchers may attract predators or cause nest abandonment (Major 1990, Andresen 2015). Recent advancements such as the use of automatic cameras have helped reduce human presence around nests, and certain studies have reported that cameras do not appear to attract predators or influence survival rates over time (Pietz & Granfors 2000, Salewski & Schmidt 2022). Skagen et al. (1999) tried to further reduce the effects of disturbance by masking human scent with familiar odours, although without significantly reducing the predation of artificial nests. These findings highlight the complexity of understanding the effects of nest-monitoring but suggest that, even if cautious practices are employed, the impact on predation rates may not be detrimental.

The aim of this study was to identify the dynamics of nest predation and estimate demographic parameters such as hatching success, productivity and nest survival probability in two poorly known steppe-specialist larks, the Mediterranean Short-toed Lark Alaudala rufescens and Thekla's Lark Galerida theklae. Understanding these dynamics is crucial for the successful management of these species as it requires knowledge of their demographic parameters such as nest survival rates and productivity (Morales & Traba 2016). Both the Mediterranean Short-toed Lark and Thekla's Lark are key steppe specialists and play important roles in these ecosystems. In Catalonia (NE Spain) there are about 1000 breeding pairs of Mediterranean Short-toed Larks, distributed in two clusters almost 100 kilometres apart in the province of Lleida and the Ebro delta (Gordo & Anton 2021). In the province of Lleida there were probably only a few hundred individuals of this lark remaining by 2020 (Mañosa et al. 2020). By contrast, Catalonia supports between 11,400 and 29,200 pairs of Thekla's Larks, mainly in the xeric mountains and arid farmland found in the southern half of the region (Franch et al. 2021).

Materials and Methods

Study area and species

We conducted our study in the province of Lleida (Catalonia, NE Spain) in the Mas de Natural Reserve (41°29'99"N, Melons 0°42'76"E; mean elevation 186 m a.s.l.). The climate of this area is Mediterranean and moderately continental; precipitation is low, averaging 342 mm per year. The mean monthly temperature varies from 6 °C in January to 25 °C in July (Agencia Estatal de Meteorología 1983-2010). The reserve (1,431 ha) was declared a special protection zone for birds in 1988 and forms part of the Natura 2000 network (European Environment Agency 2019). It consists mainly of cereal cultivation, with some fallow and olive grove, as well as scattered patches of natural vegetation (mainly low shrubland).

The two target species of this study, Mediterranean Short-toed Lark and Thekla's Lark, nest on the ground (Pérez-Granados et al.

2017). They lay between two and five eggs per clutch and usually have multiple broods per year. The breeding period starts in March and lasts until June. Incubation lasts 11–14 days and nestlings remain in the nest for 8–10 days in both species (Suárez et al. 2009).

Data collection

Nests were searched for by walking across the study area in daytime (08.00–20.00) between 24 April and 24 June 2023 (9 weeks). Surveys consisted of checking bushes, observing bird behaviour and checking places where birds showing nesting behaviour landed. We also carried out dawn surveys (before sunrise) with the same approach but using thermal imaging binoculars (Pulsar, Accolade 2 LRF XP50 PRO) to detect birds. The coordinates of found nests were registered, and a camera trap was installed one metre away (Figure 1a). The camera was fixed with two cable ties to a wooden stick, the correct angle being created with a stone between camera and wooden stick if necessary.

We used two different brands of cameras, namely, Browning models BTC-6HDPX and BTC-5HDPX, and Bushnell model 119938C. Cameras were set up as follows: mode: *Trail*, capture delay: *Is*, picture size: 8 MP, multi shot: 3, smart IR: *on*, *night exposition*, *power save*, and *low sensitivity* (on cameras that allowed this setting). Camera images were analysed to extract key variables including hatching and fledging dates, predation dates and time, and predator species.

When installing cameras next to nests, we wore gloves and rubbed the cameras with white wormwood Artemisia herba-alba, a strongsmelling plant commonly found around nests that we hoped would at least partly cover our human scent. We flagged cameras with inconspicuous, natural markings (e.g. small piles of stones) placed at a distance of 5 metres. To minimise disturbance, we approached the cameras only every second to third day to check and replace batteries, and to adjust the camera if necessary (e.g. if it had been knocked out of focus by an animal). When approaching nest cameras, we walked irregularly, used gloves and rubbed our hands beforehand with white wormwood to reduce our scent. We spent as little time as possible at the nest site when setting the cameras and changing the SD cards. The camera was otherwise left untouched until the nestlings fledged or were predated. To confuse predators and to prevent them from associating the presence of a camera with the presence of a nest, we also installed 11 control cameras at randomly selected locations throughout the study area where no nests were present. When a nest camera was no longer operational, either because the nest had been predated or the chicks successfully fledged, it was left in place as a control camera. Conversely, control cameras were used to monitor new nests when discovered. Control cameras were relocated on a weekly basis to new random locations. Starting from the second week of the study, control cameras received the same treatments as the nest cameras (gloves and white wormwood).





Figure 1. a) Camera set up next to a nest in Mas de Melons (Lleida province, Catalonia, NE Spain. b) Vegetation sampling frame with the metal bar facing north and the nest in the middle.
a) Càmera instal·lada al costat d'un niu a Mas de Melons, província de Lleida, Catalunya, Espanya. b): Marc de mostreig de vegetació amb la barra metàl·lica orientada al nord i el niu al mig.

Once the monitored nests had been abandoned, we collected a series of additional habitat-related data based on Barrero *et al.* (2023). We identified the nest plant (i.e. the plant under which the nest was built) to species level, measured its height in cm, the percentage coverage (shading) of the nest, and characterised the type of habitat in which the nest was located (crop or fallow). In addition, we measured the percentage cover of bush, herbaceous, detritus, bare soil, rock, moss, faeces and stones within a 1-m²-vegetation frame centred on the nest (Figure 1b).

Statistical analyses

In addition to visual summaries of the data, we estimated the daily survival rate using the known-fate nest survival model in program MARK (Rotella 2006). We implemented the model using the R package RMark (Laake 2013). We fitted two alternative models, with and without the effect of lark species on survival, and compared them using the Akaike Information Criterion (AIC). Models whose AIC scores differ by ≤ 2 points are considered to be equally well supported, in which case we selected the model with the fewest parameters as the most parsimonious (Burnham & Anderson 2003). We repeated the analysis with data from only the nestling phase and from both incubation and nestling phases.

We described the habitat where the nests were found, recording the median area of the vegetation patch and the distance between the nest and nearest path, nest plant heights, percentage of nest coverage, and proportion of cover types in a 1-m² patch around the nest (bush, herbaceous, detritus, bare soil, rock, moss, faeces and stones). We then used T-tests for normally distributed data or Wilcoxon tests for non-normally distributed data to assess whether nest predation correlated significantly with nest plant height, nest coverage, or the cover type around the nest. We also performed T-tests or Wilcoxon tests for nest plant height, nest coverage and nest-surrounding parameters to check whether they differed between the two lark species.

Results

We found a total of 13 nests, five belonging to Mediterranean Short-toed Larks and eight to Thekla's Larks, and obtained a total of 502,112 videos and pictures (1.1 TB storage). Eight nests were found at the egg stage and four at the nestling stage. Hatching success was 100%; all predation events occurring during the nestling stage and none during incubation. The overall mean number (± SD) of fledged young per successful nest was 3.75 ± 1.04 for Thekla's Lark and 2.6 ± 0.55 for Mediterranean Shorttoed Lark. Predation caused five nests to fail in the two species (45%): one Mediterranean Short-toed Lark nest (9%) and four Thekla's Lark nests (36%). By contrast, of all the nests detected, four Mediterranean Short-toed Lark nests (36%) and two Thekla's Lark nests (18%) were successful. Of the successful nests, 80% of Mediterranean Short-toed Lark nests were successful and 33% of Thekla's Lark nests (Figure

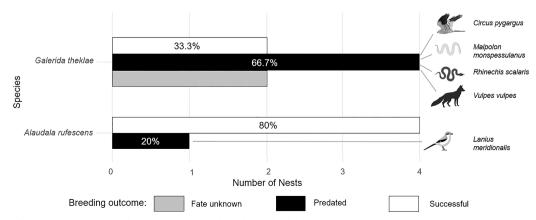


Figure 2. Percentages of nest outcomes and predators for both species. *Proporció dels resultats dels nius i depredadors per a les dues espècies.*

Table 1. Description of fledgling success and predation events in the monitored Mediterranean Short-toed Lark (MTSTL) and Thekla's Lark (TL) nests.

Descripció de l'èxit d'envol i els casos de depredació dels nius de terrerola rogenca (MTSTL) i cogullada fosca (TL).

Species	Predation or fledging date	Predation time	Initial number of		Fate		
			Eggs	Nestlings	Unknown	Fledged	Predator
MTSTL	25 May			2		Х	
MTSTL	25 May			2		Х	
MTSTL	2 June		3	3		Х	
MTSTL	5 June	9:15	3	3			Iberian Grey Shrike
MTSTL	7 June		3	3		Χ	
TL				3	X		
TL			4	4	Х		
TL	13 May	10:15		3			Montagu's Harrier
TL	28 May	16:02	5	5			Montpellier snake
TL	2 June		4	4		Х	
TL	5 June			2		Х	
TL	6 June	22:49		5			Ladder snake
TL	24 June	22:32	4	4			Red fox

2). Nest were predated by two species of snakes, the Montpellier Snake Malpolon monspessulanus and the Ladder Snake Rhinechis scalaris, as well as by a Red Fox Vulpes vulpes, a bird of prey (Montagu's Harrier Circus pygargus) and an Iberian Grey Shrike Lanius meridionalis. Predation events occurred throughout the breeding period from mid-May to late June (Table 1; Annex).

The nest fate was not determined at two nests due to SD card failure or incorrect camera setup. Model comparison suggested that there was no significant difference between the estimated survival for the two species, either for survival during the nestling phase or including the incubation phase (nestling phase only: AIC=39.2 and AIC=41.1, respectively, with and without a species effect; including incubation: AIC=44.7 and AIC=46.2). Therefore, we retained the model without the species effect for parsimony. Using this model for both species pooled, the daily survival rate of nests throughout both the incubation and the nestling phases was 0.963 (95% confidence intervals: 0.914-0.984), which gives a mean 0.55 probability of predation during a 21-day period. For the nestling phase only, the daily survival rate was 0.934

(95% CI: 0.855- 0.973) giving a mean 0.49 probability of predation during a 10-day period. If a nest was predated, usually all nestlings were eaten by the predator (see details of predation events in Table 1 and Figure 2).

Habitat and vegetation sampling around the nests

Nests were primarily found in natural vegetation patches and abandoned cultivated fields, predominantly old cereal fields; one nest was in an abandoned almond grove. These nesting sites were situated within a habitat matrix comprising cultivated fields, scrubland dominated by Salvia officinalis and Quercus coccifera, field margins, and fallow. All Mediterranean Shorttoed lark's nests (n=5) were found in natural vegetation patches dominated by white wormwood Artemisia herba-alba, sometimes classified as old fallows. By contrast, Thekla's Lark nests were located not only in natural vegetation (n=5) but also in abandoned cultivated fields characterized by low-structure vegetation, including chamaephytes and grasses (almond grove: n=1, fallow: n=2). Nests were located at distances ranging from 2 to 107 meters from tracks (median \pm SD: 24 \pm 32 meters). The area of the fields or vegetation patches where nests were found varied between 0.019 ha, the smallest, and 24.1 ha, the largest (median \pm SD: 2.8 \pm 6.8 hectares). All nests were built under shrubs. For Thekla's Larks, five nests were built under white wormwood, one under esparto grass Lygeum spartum, one under mountain rue Ruta montana and one under globe-fruited retama Retama sphaerocarpa. For Mediterranean Short-toed Larks, all five nests were built under white wormwood.

Data regarding means ± standard deviations of nest plant heights, percentage of nest coverage, amount of bush, herbaceous, detritus, bare soil, rock, moss, faeces and stones in a 1-m² patch around the nest for predated and successful nests of both species and for the nests of each species are provided separately (Table 2). The average height of all nest plants was 27.23 cm \pm 7 cm (mean \pm SD). The average plant height for predated nests was 35.25 cm \pm 2.39 cm, compared to 22.35 cm \pm 5.75 cm for successful nests. Nest plants were significantly taller for predated than for successful nests (t(df=6.91) = -4.98, p = 0.002, Fig. 3). However, we found no statistically significant difference between predated and successful nests in terms of surrounding vegetation structure or cover. Neither did we find any statistically significant differences between the two species in terms of nest plant height, nest coverage, bush, bare soil, rock, moss, faeces or stones. In the immediate surroundings of the nest, the proportion of herbaceous and detritus cover was significantly higher and lower, respectively, for Thekla's Lark than for Mediterranean Short-toed Lark (Wilcoxon rank sum test, w=5.5, p=0.035; Fig. 3).

Discussion

This work provides novel data that complement the scarce available information on key aspects of the reproductive ecology of two typical bird species found in the shrub steppes of the Iberian Peninsula. The level of scientific knowledge of these species is very limited in comparison with other more emblematic steppe birds (Morales & Traba 2016), even though the Iberian Peninsula hosts the bulk of the European population of both of these larks (Keller *et al.* 2020).

Our study observed a nest predation rate of 45% for both species, and our estimated survival indicated an overall 41% chance of nestlings surviving to fledging. This falls within the range of predation rates for steppe larks in similar habitats reported by Manrique and Suarez (1992) but is considerably lower than the 75-90% re-

Table 2. Means ± standard deviations of nest plant heights, and percentage nest, amount of bush, herbaceous, detritus, bare soil, rock, moss, faeces and stones cover in a 1-m² patch around nests for both predated and successful nests, and for the nests of each species separately, of the two studied lark species. Mitjanes ± desviacions estàndard de l'altura de les plantes del niu, % de cobertura del niu, quantitat de matolls, plantes herbàcies, detritus, sòl nu, roca, molsa, excrements de conill i pedres en un m² al voltant del niu per als nius depredats i no depredats d'ambdues espècies i per als nius de cada espècie per separat.

	Brood predated	Brood successful	All nests	MTSTL nests	TL nests
Nest plant height [cm]	35.25 ± 2.39	22.35 ± 5.75	27.23 ± 7	24.2 ± 8.38	29.13 ± 7.14
Nest coverage [%]	56 ± 23.82	59.67 ± 30.04	58.08 ± 28.56	70 ± 24.24	50.63 ± 29.95
Bush [%]	30.4 ± 19.96	38.5 ± 12.18	36.08 ± 15	34 ± 11	37.38 ± 17.73
Herbaceous [%]	3.8 ± 3.96	0.83 ± 0.75	2.08 ± 2.81	0.4 ± 0.55	3.12 ± 3.18
Detritus [%]	3.2 ± 4.97	8 ± 6.29	5.15 ± 5.71	10.6 ± 5.81	1.75 ± 1.49
Bare soil [%]	54.4 ± 28.57	40.5 ± 16.03	45.08 ± 22.76	47.4 ± 18.5	43.62 ± 26.2
Rock [%]	0.2 ± 0.45	2.33 ± 5.72	1.23 ± 3.85	2.8 ± 6.26	0.25 ± 0.46
Moss [%]	3 ± 6.71	1 ± 1.26	3.85 ± 8.6	0.6 ± 0.89	5.88 ± 10.68
Feces [%]	4.8 ± 4.15	8.33 ± 10.97	6.08 ± 7.85	3.6 ± 2.88	7.62 ± 9.68
Stones [%]	0.2 ± 0.45	0.5 ± 0.84	0.46 ± 0.66	0.6 ± 0.89	0.38 ± 0.52

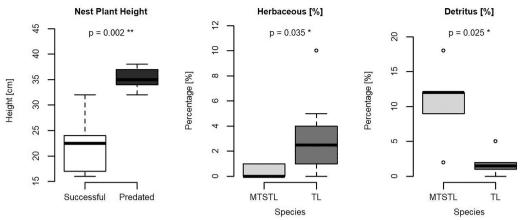


Figure 3. Boxplots of Nest Plant Height in both successful and unsuccessful nest and of Herbaceous Cover and Detritus Cover in Mediterranean Short toed Larks (MTSTL) and Thekla's Larks (TL). Thick solid lines indicate the median, boxes indicate the first and third quartiles, and whiskers indicate 95% percentiles. Diagrames de caixa de l'alçada de la planta del niu en nius reeixits i en nius no reeixits i de coberta herbàcia i de coberta de detritus en nius de terrerola rogenca(MTSTL) i de cogullada fosca (TL). Les línies sòlides gruixudes indiquen la mediana, els quadres indiquen el primer i el tercer quartils, els bigotis indiquen percentils del 95%.

ported by others (Yanes et al. 1996, Suárez et al. 2005). Notably, Suarez and Manrique (1992) observed around 50-80% of total nest losses during the incubation period in three species (Mediterranean Short-toed Lark, Thekla's Lark and Western Black-eared Wheatear). The effect of human scent around the monitored nests is not entirely clear (Weldon 2022), even if the precautions we took during camera trap placement during this study may have led to a low predation rate value. Our study included only a few nests during the pre-hatching stage and we observed no predation during the incubation period. These two factors, together with our small sample size, probably gives an overly optimistic estimates of survival when the prehatching phase is included. Future research should include an evaluation of the effects of masking human smell when installing cameras for studies of nest predation rate.

In previous studies that relied on the interpretation of tracks around daily monitored nests, predation events were mostly attributed to domestic dogs and foxes, but also to other predators such as snakes, ocellated lizards, hedgehogs and Iberian grey shrikes (Suárez & Manrique 1992, Yanes 2000). In our study, we observed no predation by domestic animals and only one confirmed predation by a Red Fox. This low level of predation by foxes was unexpected given the high density of this predator in

the study area (between 2 and 3 foxes/km²; own data) and its importance as a nest predator reported in other studies (Yanes & Suárez 1996). We observed one nest predation by an Iberian Grey Shrike. Although predation on small birds by this species has been previously reported (Hódar 2006), this is one of the few documented cases of predation by this shrike of a nest placed on the ground. In this instance, the predation of Mediterranean Short-toed Lark nestlings involved several consecutive visits to the lark's nest. Of the reptiles, two snake species were observed as predators, the Ladder Snake and the Montpellier Snake. Both are common in the study area and have previously been documented preying on lark nests in Spain (Yanes 2000, Pleguezuelos et al. 2007, Recuero et al. 2010).

Although nest predation is a key cause of reproductive failure, other factors also have an impact on nest survival. In agricultural landscapes, failure due to agricultural activities is a relevant cause of nest failure in ground-nesting birds (Ponce *et al.* 2018). However, in our study, although larks placed their nests on fallows, we detected no nest failure due to farming activities, probably because of the restrictive agricultural management employed on this nature reserve, which contributes to minimising this risk and reducing nest destruction as a factor influencing breeding success in this area.

Understanding the habitat characteristics around the nest of these lark species provides essential context for evaluating the factors influencing nest survival. Previous studies in the Ebro valley (NE Spain), Campo de Nijar and Cabo de Gata (SE Spain) of Mediterranean Short-toed Larks, Greater Short-toed Larks (Calandrella brachydactyla) and Thekla's Larks identified the habitat of those species as being characterised by a large proportion of bare ground and non-thorny chamaephytes, with little foliage, and 5–30 cm in height (Yanes et al. 1996, Serrano & Astrain 2005). Other studies in Castro Verde (S Portugal) and in the Caspian lowlands (W Kazakhstan) confirm these habitat preferences and indicate that there is a positive correlation between bare ground cover and the presence of Mediterranean Short-toed Larks but greater frequencies of Thekla's Larks in shrublands (Moreira 1999, Oparin et al. 2018). Yanes et al. (1996) reported that nesting Mediterranean Short-toed Larks selected bushes under 16 ± 5 cm in height, while Thekla's Larks preferred medium-sized bushes of 23 \pm 8 cm in height for their nests. Our results support these finding and highlight the distinct habitat preferences of these two species in the study area, albeit as long as the vegetation structure is as described above. The main habitat consisted in natural vegetation patches dominated by white wormwood, often resembling old fallow fields, which matches these species' preferences for areas with sparse vegetation and bare ground.

Understanding manageable habitat variables that influence survival rates is crucial for the conservation of ground-nesting birds. The vegetation surrounding nests is often considered a key factor mediating nest success since it offers protection from predators. However, while our study found higher predation rates in nests under taller plants, other studies report a dissimilar pattern (Guilherme et al. 2018, Smith et al. 2018, Bravo et al. 2022). This discrepancy could be explained by the fact that not only plant height but also plant density should be taken into account. In the case of the commonest plant observed in our study, white wormwood, taller plants tend to dry out and lose structural consistency. Therefore, further research is required to better understand this factor and its implications for these two species.

Steppe-specialised larks depend on the habitat structure traditionally created and maintained by extensive sheep grazing, which highlights the positive effect of pastoral activities on steppe bird abundance and diversity (Traba & Pérez-Granados 2022). Research by Morales et al. (2005) underlines the importance of maintaining open landscapes with sparse vegetation cover given that these types of habitats favour steppe bird populations by increasing foraging efficiency and reducing predation risk. An improved understanding of predation rates and their drivers will help further restoration efforts and recovery strategies.

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Resum

Estudi de la depredació de nius i paràmetres de reproducció de la terrerola rogenca *Alaudala rufescens* i la cogullada fosca *Galerida theklae* a l'oest de Catalunya

La intensificació agrícola i els canvis en l'ús del sòl, causant de la fragmentació de l'hàbitat, són les principals amenaces pels ocells esteparis. Comprendre com succeeix la depredació dels nius i els factors que la impulsen és essencial per a la conservació i gestió d'espècies estepàries en aquest entorn únic. Aquest estudi investiga la dinàmica de depredació dels nius, l'èxit de l'eclosió, la productivitat i la supervivència dels nius de dues espècies d'alàudids esteparis, la terrerola rogenca Alaudala rufescens i la cogullada fosca Galerida theklae, a Catalunya. Es van monitoritzar 13 nius durant un període de set setmanes i vam trobar que el 80% dels nius de terrerola rogenca i el 25% dels nius de cogullada fosca van tenir èxit. La depredació durant el període de pollets va provocar el fracàs del 45% dels nius, amb serps, guineus i ocells com a principals depredadors. La taxa de depredació observada és menor a estudis anteriors sobre espècies similars. Els nius depredats es van trobar sota plantes més altes que els exitosos, tot i que la composició de la vegetació de l'entorn no diferia significativament entre els nius depredats i els que van tenir èxit. Aquest estudi subratlla el paper crític de la depredació en l'èxit reproductiu dels ocells que fan el niu a terra i destaca la importància de les pràctiques de gestió de l'hàbitat que mantenen entorns esteparis oberts, favorables per a aquestes espècies. La conservació dels ocells esteparis requereix el coneixement detallat de les pressions per depredació i de les preferències d'hàbitat per millorar l'èxit reproductiu i evitar més declivis en aquestes poblacions vulnerables.

Resumen

Estudio de la depredación de nidos y parámetros de reproducción de la terrera marismeña *Alaudala rufescens* y la cogujada montesina *Galerida theklae* en el oeste de Cataluña

La intensificación agrícola y los cambios en el uso del suelo, causantes de la fragmentación del hábitat, son las principales amenazas para las aves esteparias. Comprender la depredación de los nidos y los factores que la impulsan es esencial para la conservación y gestión de las especies de aves esteparias en este entorno único. Este estudio investiga la dinámica de depredación de los nidos, el éxito de eclosión, la productividad y la supervivencia de los nidos de dos especies de aláudidos esteparios, la terrera marismeña Alaudala rufescens y la cogujada montesina Galerida theklae, en Cataluña, España. Monitoreamos 13 nidos durante un período de siete semanas y encontramos que el 80% de los nidos de terrera marismeña y el 25% de los nidos de cogujada montesina lograron criar con éxito. La depredación durante la etapa de pollos fue la causa del fracaso del 45% de los nidos, con serpientes, zorros y aves como los principales depredadores de los nidos. La tasa de depredación observada es inferior a estudios previos de especies similares. Los nidos depredados se encontraron bajo plantas más altas que los nidos exitosos, aunque la composición de la vegetación en el área circundante no difería significativamente entre los nidos depredados y los exitosos. Este estudio subraya el papel crítico de la depredación en el éxito reproductivo de las aves que anidan en el suelo y destaca la importancia de las prácticas de gestión del hábitat que mantienen entornos esteparios abiertos, favorables para estas especies. La conservación efectiva de las aves esteparias requiere el conocimiento detallado de las presiones de depredación y de las preferencias de hábitat para mejorar el éxito reproductivo y evitar mayores descensos en estas poblaciones vulnerables.

References

- Agencia Estatal de Meteorología (AEMET). 1983–2010. Standard climate values in Lleida. https://www.aemet.es/en/serviciosclimaticos/datosclimatologicos/valoresclimatologicos. Accessed on 10 May 2024.
- Andresen, C.H. 2015. The effect of human disturbance on nest predation rate of ground-nesting birds. Master thesis. Bø i Telemark: Telemark University College.
- **Arroyo, B.E.** 1997. Diet of Montagu's Harrier *Circus pygargus* in central Spain: Analysis of temporal and geographic variation. *Ibis* 139: 664–672. https://doi.org/10.1111/j.1474-919X.1997.tb04689.x
- Barrero, A., Caballero, B.C., Reverter, M., Gómez-Catasús, J., Bustillo-de la Rosa, D., Zurdo, J., Pérez-Granados, C. & Traba, J. 2023. Nest features and nesting niche segregation in five Iberian steppe passerines. Ardeola 70: 201-224.https://doi.org/10.13157/arla.70.2. 2023.ra4
- Benson, T.J., Brown, J.D. & Bednarz, J.C. 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. *J. Anim. Ecol.* 79: 225–234. https://doi.org/10.1111/j.1365-2656.2009.01604.x
- Bravo, C., Pays, O., Sarasa, M. & Bretagnolle, V. 2020. Revisiting an old question: Which predators eat eggs of ground-nesting birds in farmland land-scapes?. *Sci. Total Environ.* 744: 140895. https://doi.org/10.1016/j.scitotenv.2020.140895
- Bravo, C., Sarasa, M., Bretagnolle, V. & Pays, O. 2022. Detectability and predator strategy affect egg depredation rates: Implications for mitigating nest depredation in farmlands. Sci. Total Environ. 829: 154558. https://doi.org/10.1016/j.scitotenv.2022.154558.
- Bravo, C., Sarasa, M., Bretagnolle, V. & Pays, O. 2023. Hedgerows interact with forests to shape the abundance of mesopredators and their predation rate on eggs in farmland landscapes. Sci. Total Environ. 901: 165712. https://doi.org/ 10.1016/i.scitoteny.2023.165712
- Brinkert, A., Hölzel, N., Sidorova, T.V. & Kamp, J. 2016. Spontaneous steppe restoration on abandoned cropland in Kazakhstan: Grazing affects successional pathways. *Biodivers. Conserv.* 25: 2543–2561. https://doi.org/10.1007/s10531-015-1020-7
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. 2012. Biodiversity loss and its impact on humanity. Nature 486 (7401): 59-67. https://doi.org/10.1038/nature11148
- Burnham, K.P. & Anderson, D. 2003. Model selection and multi-model inference: A pratical information-theoretic approach. New York: Springer-Verlag.
- Donald, P.F., Pisano, G., Rayment, M.D. & Pain, D.J. 2002. The Common Agricultural Policy, EU enlargement and the conservation of Europe's farmland birds. Agric. Ecosyst. Environ. 89:

- 167182. https://doi.org/10.1016/S0167-8809(01) 00244-4
- **Donald, P.** 2010. *The Skylark*. London: Bloomsbury Publishing.
- Donázar, J.A., Naveso, M.A., Tella, J.L. & Campión, D. 1997. Extensive grazing and raptors in Spain. In Pain, D.J. & Pienkowski, M.W. (eds): Farming and Birds in Europe. Pp. 117–149. London: Academic Press.
- **European Environment Agency (EEA).** 2019. Secans de Mas de Melons-Alfés. https://eunis.eea. europa.eu/sites/ES0000021 #tab-designations. Accessed on 10 May 2024.
- Franch, M., Herrando, S., Anton, M., Villero, D. & Brotons, L. 2021. Atles dels ocells nidificants de Catalunya: Distribució i abundància 2015–2018 i canvi des de 1980. Barcelona: Institut Català d'Ornitologia / Cossetània Edicions.
- Gómez-Catasús, J., Reverter, M., Bustillo-de la Rosa, D., Barrero, A., Pérez-Granados, C., Zurdo, J. & Traba, J. 2023. Moderate sheep grazing increases arthropod biomass and habitat use by steppe birds. Agr. Ecosyst. Environ. 354: 108556. https://doi.org/10.1016/j.agee.2023.10 8556
- Gómez-Catasús, J., Garza, V., Morales, M.B. & Traba, J. 2019. Hierarchical habitat-use by an endangered steppe bird in fragmented landscapes is associated with large connected patches and high food availability. Sci. Rep. 9, 19010. https://doi.org/10.1038/s41598-019-55467-2
- Gómez-Catasús, J., Pérez-Granados, C., Barrero, A., Bota, G., Giralt, D., López-Iborra, G.M., Serrano, D. & Traba, J. 2018. European population trends and current conservation status of an endangered steppe-bird species: the Dupont's lark Chersophilus duponti. PeerJ 6: e5627. https:/ /doi.org/10.7717/peerj.5627
- Gordo, O. & Anton, M. 2021. Terrerola rogenca Alaudala rufescens. In Franch, M., Herrando, S., Anton, M., Villero, D. & Brotons, L. (eds.): Atles dels ocells nidificants de Catalunya: Distribució i abundància 2015–2018 i canvi des de 1980. Pp. 386–387. Barcelona: Institut Català d'Ornitologia / Cossetània Edicions.
- Goriup, P.D. & Batten, L. 1990. The conservation of steppic birds A European perspective. Oryx 24: 215–223. https://doi.org/10.1017/S0030605300 034931
- **Guilherme, J.L., Burnside, R.J., Collar, N.J. & Dolman, P.M.** 2018. Consistent nest-site selection across habitats increases fitness in Asian Houbara. *Auk* 135: 192–205. https://doi.org/10.1642/AUK-17-156.1
- Helldin, J.O., Liberg, O. & Glöersen, G. 2006. Lynx (Lynx lynx) killing red foxes (Vulpes vulpes) in boreal Sweden frequency and population effects. J. Zool. 270 (4): 657–663. https://doi.org/10.1111/j.1469-7998.2006.00172.x
- Herranz, J., Manrique, J., Yanes, M. & Suárez, F. 1994. The breeding biology of Dupont's Lark, Chersophilus duponti, in Europe. Avocetta 18: 141–146.
- Hernández, A. 1994. Seleccion de hábitat en tres especies simpátricas de alcaudones (real, Lanius excubitor L., Dorsirrojo, Lanius collurio L. y común, Lanius senator L.): Segregación interespecífica. Ecología 8: 395–413.

- **Hódar, J.A.** 2006. Diet composition and prey choice of the southern grey shrike *Lanius meridionalis* L. in south-eastern Spain: The importance of vertebrates in the diet. *Ardeola* 53: 237–249.
- Hurford, C., Wilson, P. & Storkey, J. 2020. The changing status of arable habitats in Europe: a nature conservation review. Cham: Springer International Publishing. https://doi.org/10.1007/ 978-3-030-59875-4
- **IUCN**. 2020. Thekla's Lark. In: IUCN Red List of Threatened Species. https://www.iucnredlist.org/species/22717387/166395300#population. Accessed on 10 August 2024.
- **IUCN**. 2021. Iberian Grey Shrike. In: IUCN Red List of Threatened Species. https://www.iucnredlist.org/species/22729533/200216423#population. Accessed on 10 May 2024.
- **Johnson, C.N.** 2010. Red in tooth and claw: How top predators shape terrestrial ecosystems. *J. Animal Ecol.* 79: 723–725. https://doi.org/10.1111/j.1365-2656.2010.01706.x
- Kaplan, E.L. & Meier, P. 1958. Nonparametric estimation from incomplete observations. J. Am. Stat. Assoc. 53, No. 282: 457–481.
- Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvanova, A., Kalyakin, M.V., Bauer, H.-G. & Foppen, R.P.B. 2020. European Breeding Bird Atlas 2: Distribution, Abundance and Change. Barcelona: Bird Census Council & Lynx Edicions.
- Laake, J. 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep. 2013-01, Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., Seattle, WA.
- **Major, R.E.** 1990. The effect of human observers on the intensity of nest predation. *Ibis* 132: 608–612.
- Mañosa, S., Bota, G., Giralt, D. & Estrada, J. 2020. The changing status of steppe-land birds in the Lleida Plain of Catalonia. In Hurford, C., Wilson, P. & Storkey, J. (eds.): The changing status of arable habitats in Europe: a nature conservation review. Pp. 291–316. Cham: Springer International Publishing.
- Morales, M.B. & Traba, J. 2016. Prioritising research in steppe bird conservation: a literature survey. Ardeola 63: 137–150.
- **Moreira, F.** 1999. Relationships between vegetation structure and breeding bird densities in fallow cereal steppes in Castro Verde, Portugal. *Bird Study* 46: 309–318. https://doi.org/10.1080/0006365 9909461144
- Oparin, M.L., Mamaev, A.B., Oparina, O.S. & Tro-fimova, L.S. 2018. Long-term dynamics of the community structure of larks (Alaudidae, Aves) in the Northwestern Caspian Lowland. *Biol. Bull. Russ. Acad. Sci.* 46: 1339–1346. https://doi.org/10.1134/S1062359019100236
- Pérez-Granados, C., López-Iborra, G. M., Garza, V. & Traba, J. 2017. Breeding biology of the endangered Dupont's Lark Chersophilus duponti in two separate Spanish shrub-steppes. *Bird Study* 64: 328–338. https://doi.org/10.1080/000636 57.2017.1359232
- **Pietz, P.J. & Granfors, D.A.** 2000. Identifying Predators and Fates of Grassland Passerine Nests Using Miniature Video Cameras. *J. Wildlife Manage*. 64: 71–87. https://doi.org/10.2307/3802976

- Pleguezuelos, J.M., Fernández-Cardenete, J.R., Honrubia, S., Feriche, M. & Villafranca, C. 2007. Correlates between morphology, diet and foraging mode in the Ladder Snake Rhinechis scalaris (Schinz, 1822). Contrib. Zool. 76: 179– 186.
- Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. 1995. The future of biodiversity. *Science* 269 (5222): 347–350. https://doi.org/ 10.1126/science.269.5222.347
- Ponce, C., Salgado, I., Bravo, C., Gutiérrez, N. & Alonso, J.C. 2018. Effects of farming practices on nesting success of steppe birds in dry cereal farmland. Eur. J. Wildlife Res. 64: 1–10. https://doi.org/10.1007/s10344-018-1167-0
- Praus, L., Hegemann, A., Tieleman, B.I. & Weidinger, K. 2014. Predators and predation rates of Skylark Alauda arvensis and Woodlark Lullula arborea nests in a semi-natural area in The Netherlands. Ardea 102: 87–94. https://doi.org/10.5253/078.102.0112
- Recuero, E., García-Martínez, G. & García-París, M. 2010. On a case of cannibalism in *Malpolon monspessulanus*. Bol. Asoc. Herpetol. Esp. 21: 42–43.
- Robleño, I., Bota, G., Giralt, D. & Recasens, J. 2017. Fallow management for steppe bird conservation: The impact of cultural practices on vegetation structure and food resources. *Biodivers. Conserv.* 26: 133–150. https://doi.org/10.1007/s10531-016-1230-7
- Roos, S., Smart, J., Gibbons, D.W. & Wilson, J.D. 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. *Biol. Rev.* 93: 1915–1937. https://doi.org/10.1111/brv.12426
- Rotella, J.J. 2006. Nest survival. In Cooch, E. & White, G. (eds.): Program MARK: a gentle introduction. Chapter 17. Available at: http://www.phidot.org/software/mark/docs/book/
- Salewski, V. & Scmidt, L. 2022. Nest cameras do not affect nest survival in a meadow-nesting shorebird. *Bird Conserv. Int.* 32: 127–136. doi:10.1017/S0959270920000659
- Sanz-Pérez, A., Tarjuelo, R., Giralt, D., Sardà-Palomera, F., Mougeot, F., Santisteban, C., Pérez, M. & Bota, G. 2022. High-resolution tracking data highlight the importance of fallow land during a seasonal habitat bottleneck for a steppe-land specialist. Agr. Ecosyst. Environ. 340: 108162. https://doi.org/10.1016/j.agee.20 22.108162
- Serrano, D. & Astrain, C. 2005. Microhabitat use and segregation of two sibling species of *Calan-drella* larks during the breeding season: conservation and management strategies. *Biol. Conserv.* 125: 391–397. https://doi.org/10.1016/j.biocon.2005.04.010

- Skagen, S.K., Stanley, T.R. & Dillon, M.B. 1999. Do mammalian nest predators follow human scent trails in the shortgrass prairie? Wilson Bull. 111: 415-420. http://www.jstor.org/stable/4164106
- Smith, J.T., Tack, J.D., Doherty, K.E., Allred, B.W., Maestas, J.D., Berkeley, L.I., Dettenmaier, S.J., Messmer, T.A. & Naugle, D.E. 2018. Phenology largely explains taller grass at successful nests in greater sage-grouse. *Ecol. Evol.* 8: 356–364. https://doi.org/10.1002/ece3.3679.
- Suárez, F., Hervás, I. & Herranz, J. 2009. Las alondras de España peninsular. Madrid: Dirección General Para la Biodiversidad. Ministerio de Medio Ambiente y Medio Rural y Marino.
- Suárez, F., Herranz, J., Yanes, M., Sánchez, A.M., García, J.T. & Manrique, J. 2005. Seasonal interannual variability in laying date, egg volume and hatching asynchrony of four lark species in Mediterranean Spain. Ardeola 52: 103-117.
- Suárez, F., Yanes, M., Herranz, J. & Manrique, J. 1993. Nature reserves and the conservation of Iberian shrubsteppe passerines: The paradox of nest predation. *Biol. Conserv.* 64: 77–81. https:// doi.org/10.1016/0006-3207(93)90385-E
- Suárez, F. & Manrique, J. 1992. Low breeding success in mediterranean shrubsteppe passerines: Thekla lark Galerida theklae, Lesser short-toed lark Calandrella rufescens, and Black-eared wheatear Oenanthe hispanica. Ornis Scand. 23: 24–28. https://doi.org/10.2307/3676423
- **Terraube, J. & Bretagnolle, V.** 2018. Top-down limitation of mesopredators by avian top predators: a call for research on cascading effects at the community and ecosystem scale. *Ibis* 160: 693–702. https://doi.org/10.1111/jbi.12581
- **Traba, J. & Pérez-Granados, C.** 2022. Extensive sheep grazing is associated with trends in steppe birds in Spain: Recommendations for the common agricultural policy. *PeerJ* 10, e12870. https://doi.org/10.7717/peerj.12870
- **Traba, J. & Morales, M.B.** 2019. The decline of farmland birds in Spain is strongly associated to the loss of fallowland. *Sci. Rep.* 9, 9473. https://doi.org/10.1038/s41598-019-45854-0
- **Weldon, P.** 2022. Does human scent bias the survival of bird nests? *Ibis* 164: 1–12. 10.1111/ibi.12966.
- Yanes, M. 2000. La depredación en nido de aláudidos almerienses. Almería: Instituto de Estudios Almerienses- Diputación de Almería.
- Yanes, M., Herranz, J. & Suárez, F. 1996. Nest microhabitat selection in larks from a European semi-arid shrub-steppe: The role of sunlight and predation. J. Arid Environ. 32: 469–478. https://doi.org/10.1006/jare.1996.0040
- Yanes, M. & Suárez, F. 1996. Incidental nest predation and lark conservation in an Iberian semiarid shrubsteppe. Conserv. Biol. 10: 881–887. https://doi.org/10.1046/j.1523-1739.1996.10030881.x

ANNEX

Camera trap images documenting the predation events of the five detected predators. Imatges de càmera trampa que documenten els esdeveniments de depredació i els cinc depredadors trobats.



On 13.5.2023 at 10:15 a Montagu's Harrier took 2 of the 3 nestlings from a Thekla's lark nest. One nestling was recorded to have survived the attack and left the nest but was not recorded again.

El 13/5/2023 a les 10:15, una arpella cendrosa va treure 2 dels 3 polls d'un niu de cogullada fosca. El tercer poll va sobreviure a l'atac i va abandonar el niu, però no es va tornar a observar.



On 28.5.2023 at 16:02 a Montpellier Snake ate 4 of 5 nestlings from a Thekla's Lark nest. One nestling was recorded to have survived the attack and left the nest but was not recorded again; the snake came back at 16:28.

El 28/5/2023 a les 16:02 una serp verda es va menjar 4 dels 5 polls d'un niu de cogullada fosca. Un poll va sobreviure a l'atac i va abandonar el niu, però no es va tornar a registrar i la serp va tornar a les 16:28.



On 5.6.2023 between 9:15-9:51 an Iberian Grey Shrike took all three nestlings from a Mediterranean Short-toed Lark nest. The Shrike returned three times and took one nestling on each occasion and returned one final time to check the empty nest.

El 5/6/2023, entre les 9:15 i les 9:51, un botxí es va emportar els tres polls d'un niu de terrerola rogenca. El botxí va tornar tres vegades i va agafar un poll en cada ocasió i va tornar una darrera vegada quan el niu ja era buit.



On 6.6.2023 at 22:49 a Ladder Snake ate all 5 nestlings from a Thekla's Lark nest.

El 6/6/2023 a les 22:49, una serp blanca es va menjar els 5 polla d'un niu de cogullada fosca.



On 24.6.2023 at 22:32-22:33 a Red Fox ate all 4 nestlings from a Thekla's Lark nest.

El 24/6/2023 a les 22:32-22:33, una guineu es va menjar els 4 polls d'un niu de cogullada fosca.