



# High-resolution tracking data highlight the importance of fallow land during a seasonal habitat bottleneck for a steppe-land specialist

Ana Sanz-Pérez<sup>a,1,\*</sup>, Rocío Tarjuelo<sup>b,c</sup>, David Giralte<sup>a</sup>, Francesc Sardà-Palomera<sup>a</sup>, François Mougeot<sup>b</sup>, Carlos Santisteban<sup>a</sup>, Marcos Pérez<sup>a</sup>, Gerard Bota<sup>a</sup>

<sup>a</sup> Conservation Biology Group (GBiC), Landscape Dynamics and Biodiversity program, Centre de Ciència i Tecnologia Forestal de Catalunya (CTFC), Solsona, Catalonia, Spain

<sup>b</sup> Instituto de Investigación en Recursos Cinegéticos, IREC (CSIC-UCLM-JCCM), Ronda de Toledo 12, 13071 Ciudad Real, Spain

<sup>c</sup> Instituto Universitario de Investigación en Gestión Forestal Sostenible, Universidad de Valladolid e INIA, Palencia, Castilla y León, Spain

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## ABSTRACT

Farmland ecosystems are seasonally dynamic habitats shaped by meteorological fluctuations and anthropogenic land-use changes. Farmland birds may be seasonally constrained with limited foraging and breeding resources (so-called “resource bottlenecks”), especially when there is a loss of natural and semi-natural habitats. During spring, the growth of cereal crops makes a large proportion of arable land unsuitable for specialist steppe birds with narrow vegetation structure requirements. We investigated the existence of a seasonal bottleneck of suitable habitats for steppe birds using the endangered Pin-tailed sandgrouse (*Pterocles alchata*) as a model species. We used for first time lightweight GPS tags to study habitat selection and movement patterns throughout the cereal crop cycle during three years in north-eastern Spain. We also evaluated if conservation measures promoting suitable vegetation structures for steppe birds (Targeted Fallow Management, TFM) influenced habitat selection. Sandgrouse avoided cereal crops when cereal vegetation was high, resulting in a 30% reduction of suitable habitat area at the start of the breeding season. This proved the existence of a spring habitat bottleneck when sandgrouse only selected open natural habitats and fallows. Sandgrouse similarly selected TFM and conventionally managed fallows during and after the bottleneck, possibly because of their similar vegetation structure and the scarcity of alternative suitable habitats. Halting the ongoing loss of fallow land is paramount for the conservation of steppe birds like sandgrouse because they constitute a key refuge to buffer the impacts of seasonal habitat bottlenecks.

## 1. Introduction

Agricultural ecosystems have been profoundly intensified since the 20th century causing severe biodiversity loss (Kleijn et al., 2011) and dramatic declines of farmland bird populations (Burns et al., 2021). A major reason for these declines has been the rapid land use change, and particularly the loss of natural and semi-natural habitats that provide key resources for wildlife (e.g., fallow land; Traba and Morales, 2019; Van Buskirk and Willi, 2004). Farmland species are also challenged by a highly dynamic landscape, where seasonal fluctuations are induced by both anthropogenic – crop rotations, agricultural management, and crop cycles (Cardador et al., 2014) – and weather factors (Sardà-Palomera et al., 2012).

Wildlife populations occupying seasonal environments might undergo periods of severe resource scarcity (e.g., nesting sites or food limitations), termed as resource bottlenecks (Maron et al., 2015; Newton, 1994). Resource bottlenecks have proved ecologically disruptive by increasing energetic costs and threatening survival (Janke et al., 2015; Schlaich et al., 2016), ultimately limiting species distribution and abundance (Williams and Middleton, 2008). Resource bottlenecks may stem from within-year weather variability (e.g., rainfall seasonality; Williams and Middleton, 2008), and their effects can be aggravated when coupled with anthropogenic habitat modifications (e.g., seasonal agricultural practices; Maron et al., 2015; Zahn et al., 2007). Amongst the affected species pool, specialists are especially vulnerable as they are more sensitive to relatively small increases in stressors such as resource

\* Correspondence to: Ctra. Sant Llorenç de Morunys Km. 2, 25280 Solsona, Lleida, Spain.

E-mail address: [anasanz.asp@gmail.com](mailto:anasanz.asp@gmail.com) (A. Sanz-Pérez).

<sup>1</sup> ORCID ID: 0000-0003-2869-8693

limitations (Clavel et al., 2011; Parsons, 1995).

In agricultural systems, cereal steppes are landscapes dominated by cereal, pastures, and fallows (Sainz Ollero, 2013), subject to strong seasonal dynamics. During spring, the prompt development of tall and dense vegetation influences the distribution of farmland bird species (Cardador et al., 2014; Sardà-Palomera et al., 2012). The farmland bird guild with the worst conservation status in Europe are steppe birds (Burfield, 2005), which have their European strongholds in the cereal steppes of the Iberian Peninsula (Sainz Ollero, 2013). Steppe birds are habitat specialists, usually preferring low and sparse vegetation structures (Robleño et al., 2017; Sanz-Pérez et al., 2019). Vegetation growth within cereal crops in spring restricts the amount of suitable habitat available for some steppe bird species, that then concentrate in habitats with relatively stable vegetation structure throughout the year (Martín et al., 2010a). This habitat requirement is usually fulfilled by natural vegetation and fallow land, which provide undisturbed habitats for ground-nesting birds (e.g., Morales et al., 2013), and present cleared vegetation structures offering a good balance between predation risk and foraging opportunities (McMahon et al., 2010). Loss of fallow land over the last decades has been linked to steppe bird declines (Traba and Morales, 2019) and was suggested to exacerbate the impacts of a seasonal habitat bottleneck in cereal steppes (e.g., Tarjuelo et al., 2020a), which has yet to be demonstrated and quantified. Steppe birds could be especially vulnerable to spring habitat bottlenecks as they occur at the core of the breeding season, when meeting habitat and energetic requirements is key for reproductive success.

Here, we investigate the existence of a bottleneck in suitable habitat for steppe birds by using the Pin-tailed sandgrouse (*Pterocles alchata*) as a model species. Spain holds 92% of the European population of this medium-sized and ground-nesting steppe bird, where its breeding range is increasingly fragmented and its population has declined by 19% during 2005–2019 (Mougeot et al., 2021a). Non-cropped habitat loss (Tarjuelo et al., 2020a), agrochemical use (Lopez-Antia et al., 2018), and human impacts (Benítez-López et al., 2017) are likely drivers of sandgrouse population declines (see Mougeot et al., 2021b). As other steppe birds, Pin-tailed sandgrouse use different substrates in cereal steppes depending on the season (fallows, extensive pastures, cereal stubbles, and ploughed fields; Martín et al., 2010a; Tarjuelo et al., 2020a), but always conditional on low vegetation cover and/or height (Benítez-López et al., 2017). Understanding how highly threatened steppe birds such as sandgrouse cope with seasonal habitat fluctuations is key to promote steppe bird conservation and requires considering habitat selection as a dynamic process (Catry et al., 2012; Johst et al., 2001).

Habitat selection patterns of steppe bird species have been mostly studied based on discrete observations from field counts (e.g., Benítez-López et al., 2017; Tarjuelo et al., 2013) or radio-tracking data

(Martín et al., 2010a; Tarjuelo et al., 2020a). These methods provide valuable ecological insights but are usually characterized by low spatiotemporal resolution and might fail at characterizing the dynamic process of habitat selection (Guthrie et al., 2011). GPS technology overcomes these limitations by providing high resolution data that allows disentangling spatiotemporal variation in habitat selection and animal movements (Martín et al., 2009; Recio et al., 2011). Latest developments have allowed using GPS in light-weight birds (Recio et al., 2011), thus opening novel opportunities to improve existing habitat selection knowledge for secretive steppe bird species such as the Pin-tailed sandgrouse.

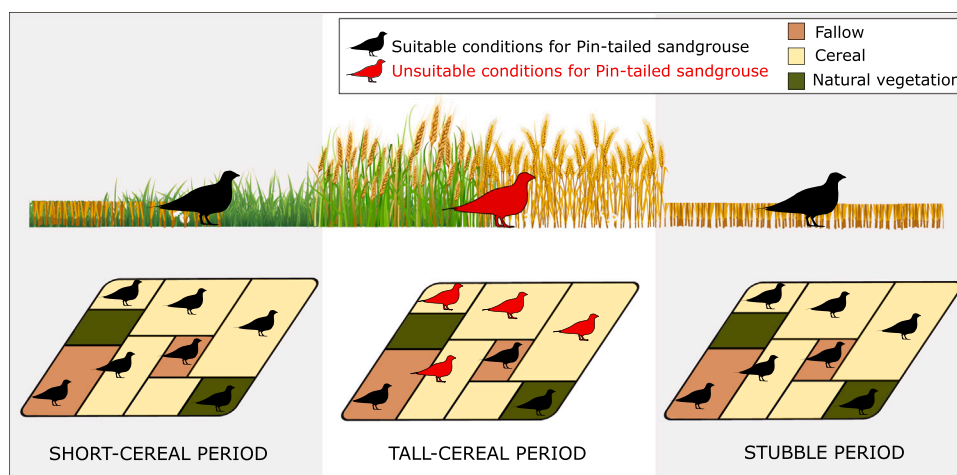
We used GPS data from 12 Pin-tailed sandgrouse during 2016–2019 to link habitat selection with seasonal changes in habitat suitability in a cereal steppe system from north-eastern Spain (Catalonia). Specifically, we aimed to confirm the existence of a habitat bottleneck, quantify the decrease of suitable area, and explore movement patterns as indicators of potential energetic costs during the bottleneck period. We built our habitat bottleneck hypothesis upon three different time periods defined by the vegetation characteristics of cereal crops, the dominant land-use (Fig. 1): Short-cereal period, Tall-cereal period, and Stubble period. We hypothesized that Pin-tailed sandgrouse would switch from positive selection to avoidance of cereal crops between the Short and Tall-cereal periods, because high cereal height makes it an unsuitable habitat for sandgrouse, and that birds would select again cereal crops after harvesting in early June (Stubble period). We expected fallows and natural vegetation to be strongly selected, especially during the Tall-cereal period when these habitats may buffer a landscape-level shortage of other suitable habitats.

The abundance of food resources and suitable vegetation structures for steppe birds in fallows can be jeopardized by conventional management practices, which often occur during the bird breeding season and are usually excessive to prevent weed growth (Giralt et al., 2018). Applying targeted agricultural practices in fallows – of moderate intensity, linked to species requirements and outside the breeding season – is a useful conservation tool to fulfill the ecological requirements of several steppe bird species (Sanz-Pérez et al., 2019), which can increase their abundance (Sanz-Pérez et al., 2021). Thus, we also aimed at disentangling differential habitat selection of fallows under conventional and targeted management, due to their relevance for bird conservation.

## 2. Material and methods

### 2.1. Study area

The study area was the cereal steppe of the Lleida plain (NE Spain) within the Special Protection Area (SPA) of ‘Secans de Mas de Melons-



**Fig. 1.** Graphic representation of the habitat bottleneck hypothesis for Pin-tailed sandgrouse. In the cereal steppe of our study area, fallow (brown), natural vegetation (green), and cereal (yellow) are the most abundant land uses. Black birds represent suitable conditions for this species, occurring in the three land uses during the Short-cereal period (left panel) and after harvesting in the Stubble period (right panel). Red birds represent unsuitable habitat conditions for this species, occurring in cereal fields when spring conditions promote tall and dense cereal vegetation, resulting in a Bottleneck in habitat suitability (Tall-cereal period; central panel).

Alfés' (0°40'E, 41°31'N; 6856 ha). This SPA holds an average population of ~ 167 (95% Confidence Interval = 77 – 327) breeding Pin-tailed sandgrouse (Giralt et al., 2019). The study area is a flat farmland with semi-arid Mediterranean climate (300–450 mm of annual rainfall; Calvet et al., 2004) dedicated to dry cereal cultivation, the habitat most commonly used by the study species in the Iberian peninsula (Mougeot et al., 2021a). The agricultural mosaic within the total home range of the studied Pin-tailed sandgrouse was dominated – on average across the three study years – by natural vegetation (i.e., shrubland or sparse shrubland; 25%), winter cereal crops (24%) and fallows (15%), interspersed with olive groves (9%), almond (7%), irrigated crops surrounding the SPA (6%), and human-related features (14%) (Fig. D1, Appendix D). We considered as fallow the agricultural land left uncropped during the full agricultural cycle of the study year, which develops green vegetation but could be subjected to management for limiting weed spread. Stubbles that are not sown in November are left uncropped during the whole year and therefore included in the fallow land use category. Rainfalls and warmer weather in spring trigger the development of vegetation in cereal crops until it dries around May. Cereal is harvested in the study area in early June (Cantero-Martínez and Moncunill, 2012).

The study area fosters a local conservation measure that consists of the agricultural management of fallow fields located in optimal locations (e.g., far from forest or irrigated crops; Mañosa et al., 2021) for vulnerable steppe bird species. This conservation measure named Targeted Fallow Management (TFM; Sanz-Pérez et al., 2019) is the compensatory measure of an irrigation project (Segarra-Garrigues) occurring inside the Special Protection Area (Mañosa et al., 2021) and provides 60% of the fallow land in the study area. TFM consists of the leasing of agricultural fields by the regional government that are left uncropped for one year (i.e., fallow fields). In a subset of the rented fallow fields, common agricultural practices (e.g., shredding, tillage; Cantero-Martínez and Moncunill, 2012) are applied once or twice per year from February to early April – before the breeding season – to increase the fallow surface with a vegetation structure that meets the specific requirements of different steppe birds, including the Pin-tailed sandgrouse (Giralt et al., 2018; Sanz-Pérez et al., 2019). The study area also includes fallow land conventionally managed by farmers (Conventional Fallow Management, CFM), mainly promoted by an Agri-environment Scheme Measure and as an Ecological Focus Area from Greening (Generalitat de Catalunya, 2020, 2019a). Fallows under CFM are usually ploughed and/or treated with herbicides more than two times per year, sometimes during the breeding season, and could therefore be completely cleared from weeds.

## 2.2. Data collection

We captured and marked 12 Pin-tailed sandgrouse with GPS-UHF loggers (PICA Ecotone, Gdynia, Poland) during 2016–2019. Birds were captured following the procedure described in Benítez-López et al. (2011) (See Appendix A). We used GPS locations from December 1st to August 31st in each of the three study years (December 2016 – August 2019; Table B1, Appendix B; Figure D1, Appendix B). We excluded GPS locations during September – November because birds moved to a different region where data on land-use at the same spatial resolution were not available. The GPS locations were obtained every 60 min between 5:00 a.m. – 7:00 p.m. UTC, when sandgrouse were active.

We selected important habitat variables for Pin-tailed sandgrouse habitat selection based on previous knowledge (Table 1; Benítez-López et al., 2017; Martín et al., 2010a; Tarjuelo et al., 2020a). Land uses were obtained from annual land-use maps and categorized as fallow, natural vegetation, olive, almond, irrigated fruit crops, rainfed cereal, other rainfed herbaceous crops (mainly peas, common vetch, and rapeseed), irrigated herbaceous crops, and forest (Table 1). We also considered topographic (slope) and human-related variables (distance to roads and dirt roads; Table 1). We categorized fallows as TFM or CFM by using the crop land-use map and a digitalized land use map from the TFM conservation measure (Table 1).

## 2.3. Study period division

To study differences in the habitat selection of Pin-tailed sandgrouse in relation to the cereal cycle, we defined three periods in accordance with our habitat bottleneck hypothesis. The selection of dates delimiting each period was done according to expert criteria based on knowledge of the cereal cycle in the study area (Cantero-Martínez and Moncunill, 2012). For the transition between the Short-cereal and Tall-cereal period, which depends on the growth of the cereal vegetation and is rather dynamic, the expert criteria were validated by a remote sensing approach. The Normalized Difference Vegetation Index (NDVI) can be used to estimate the density of green vegetation, being a good proxy for vegetation growth (Weier and Herring, 2000). We used NDVI data (European Space Agency, 2015) of the three study years (from mid-February to the end of April) to identify the time frame of cereal vegetation growth and determine a threshold date between the Short-cereal and Tall-cereal periods (See Appendix C for details on NDVI calculation and results). The date threshold between the Tall-cereal and Stubble periods was defined by harvesting time in the study area, which occurred within a short time-span (Cantero-Martínez and Moncunill, 2012).

**Table 1**

List of covariates used to model habitat selection of Pin-tailed sandgrouse in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain) from 2017 to 2019. The analysis column indicates whether the variable was used for analyses aimed at identifying the habitat bottleneck (1) or the importance of TFM for Pin-tailed sandgrouse habitat selection (2).

Name	Analysis	Description	Type	Source
Human				
Distance Roads (DistRoad)	1,2	Distance (logarithmic) from primary and secondary roads (m)	Continuous	1:50.000 Topographic map (ICGC, 2017a)
Distance Dirt Roads (DistDirt)	1,2	Distance (logarithmic) from dirt roads with > 2 m-width (m)	Continuous	1:50.000 Topographic map (ICGC, 2017a)
Habitat				
Crop land use	1	Presence/absence of fallow, olive, almond, irrigated fruit crops (Fruit.irri), cereal, other rainfed herbaceous crops irrigated herbaceous crops, (Herb.irri)	Dummy	DUN crop land use maps of 2017, 2018 and 2019 (Unique Agrarian Statement) (Generalitat de Catalunya, 2019b)
Vegetation land use	1, 2	Presence/absence of natural vegetation (NatVeg) and forest	Dummy	SIGPAC land use map of 2017 (Geographic Information System of Farming Land) (Generalitat de Catalunya, 2019c)
Fallow management land use	2	Presence/absence of TFM and CFM	Dummy	Annual DUN (Generalitat de Catalunya, 2019b) and maps of managed fallow fields (Sarda-Palomera et al., 2020)
Slope	1, 2	Slope in degrees	Continuous	DEM 25×25m (ICGC, 2017b)

Three periods were defined as follows: 1) Short-cereal period (1st December to 25th February), when cereal fields have been recently sown (November) and have low vegetation height and cover (~ less than 10 cm according to expert criteria; Large, 1954); during this non-breeding period, sandgrouse are still in flocks; 2) Tall-cereal period (8th March to 31st May), when cereals grow and reach a high and dense vegetation structure (more than ~ 20 cm; Large, 1954); this period coincides with the onset of the sandgrouse breeding (pair formation and early breeding); 3) Stubble period (10th June – 31st August), when cereal fields become stubbles after harvest; this period coincides with the peak of sandgrouse breeding season (laying and nesting). The above-mentioned period dates result from excluding a 5/6-day time window – and the GPS locations within – before and after the decided threshold dates between periods (i.e., 2nd of March between the Short and Tall cereal periods and 5th June between the Tall and Stubble periods; Appendix C), which were excluded to improve the separation of data from different periods and take into account inter-annual variations in cereal phenology.

## 2.4. Habitat selection analyses

We performed two separate habitat selection analyses to 1) identify and quantify a potential habitat bottleneck, and 2) determine the effect of fallow management (CFM vs. TFM) on Pin-tailed sandgrouse habitat selection. We tested whether aggregation of individuals – especially during winter when birds form larger flocks (Martín et al., 2010b) – could bias our habitat selection results by calculating the Coefficient of Association (Ca) of Cole (1949) using the R package ‘wildlifeDI’ (Long et al., 2014). These analyses showed that there was no association between the studied individuals during each period (all Ca < 0.5; Table B4, Appendix B).

### 2.4.1. Habitat bottleneck

First, we delimited individual home ranges to quantify habitat availability by creating 99% MCP from the GPS locations of each individual obtained across the three study periods (Table B2, Appendix B). Next, we generated the same number of random locations than bird locations for a given year and period (Table B1) within each individual MCP. We extracted the habitat characteristics of used and available (random) locations using the environmental and human covariates indicated in Table 1. Land-use data for random and used locations of a given year were extracted from their corresponding annual land-use maps (slope and road maps remained unchanged during the study period).

We quantified habitat selection patterns by using Resource Selection Probability Functions (RSPF) built with the R package ‘ResourceSelection’ (Lele et al., 2019). RSPFs are logistic regressions that yield absolute probabilities of use of a given resource by comparing the habitat features of used locations (1) with those of random or available locations (0) (Lele and Keim, 2006):

$$y(0,1) = \frac{\exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n)}{1 + \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n)}$$

where  $\beta_n$  are the coefficients estimated in the logistic regression and  $X_n$  denotes the set of covariates. We tested for multicollinearity (i.e., Pearson correlation > 0.4) and standardized continuous covariates. We used the land-use category ‘other herbaceous crops’ (Table 1) as the reference category. We added an ID-Year structure that accounted for the non-independence of observations belonging to the same individuals and years. We calculated non-parametric standard errors by bootstrapping within the RSPF (Lele et al., 2019) because this approach causes slight variations in standard errors between model iterations. Thus, we performed 100 RSPFs per period and computed the average standard error and p-values for each explanatory variable (see also Tarjuelo et al., 2020a). We used the beta coefficients of the RSPFs to

identify the habitats preferred (positive coefficient), avoided (negative) or used as available (non-significant coefficient). We then quantified the habitat bottleneck by calculating the land surface in ha under preference or avoidance during each year and period, and their respective proportions.

### 2.4.2. Role of Targeted Fallow Management

To evaluate the importance of TFM for Pin-tailed sandgrouse, we built one RSPF for each study period using only GPS locations falling within TFM or CFM fallows and natural vegetation areas. We constrained the definition of habitat availability (i.e., random locations) to these land uses and extracted the habitat characteristics of used and available locations (Table 1). We used natural vegetation as the RSPF reference category. We included the continuous variables that were significant in the first RSPF analysis to control for topographic and human-related effects on the species’ habitat selection (Table 1). We followed the same approach for bootstrapping, standard error, and p-value calculation.

## 2.5. Movement patterns

Movement parameters were calculated for each individual and period. We determined the proportion of locations in flight ( $n = 737$ ; Appendix B), and we calculated the field change rate by dividing the number of observations that change land-use when moving to the next field by the number of observations. We calculated core areas (areas of maximum utilization, in ha) by using a 50% kernel volume (‘ctmm’ R package; Fleming and Calabrese, 2021 Table B3, Appendix B), and the Euclidean distance between consecutive hourly positions (meters) as a movement index. We performed linear mixed models, using individual ID and year as random intercepts, to test if these movement-related variables differed among periods. We log-transformed the Euclidean distance variable to meet model assumptions. When models showed significant differences among periods, we performed post-hoc Tukey tests using the ‘emmeans’ function (Lenth, 2022).

## 3. Results

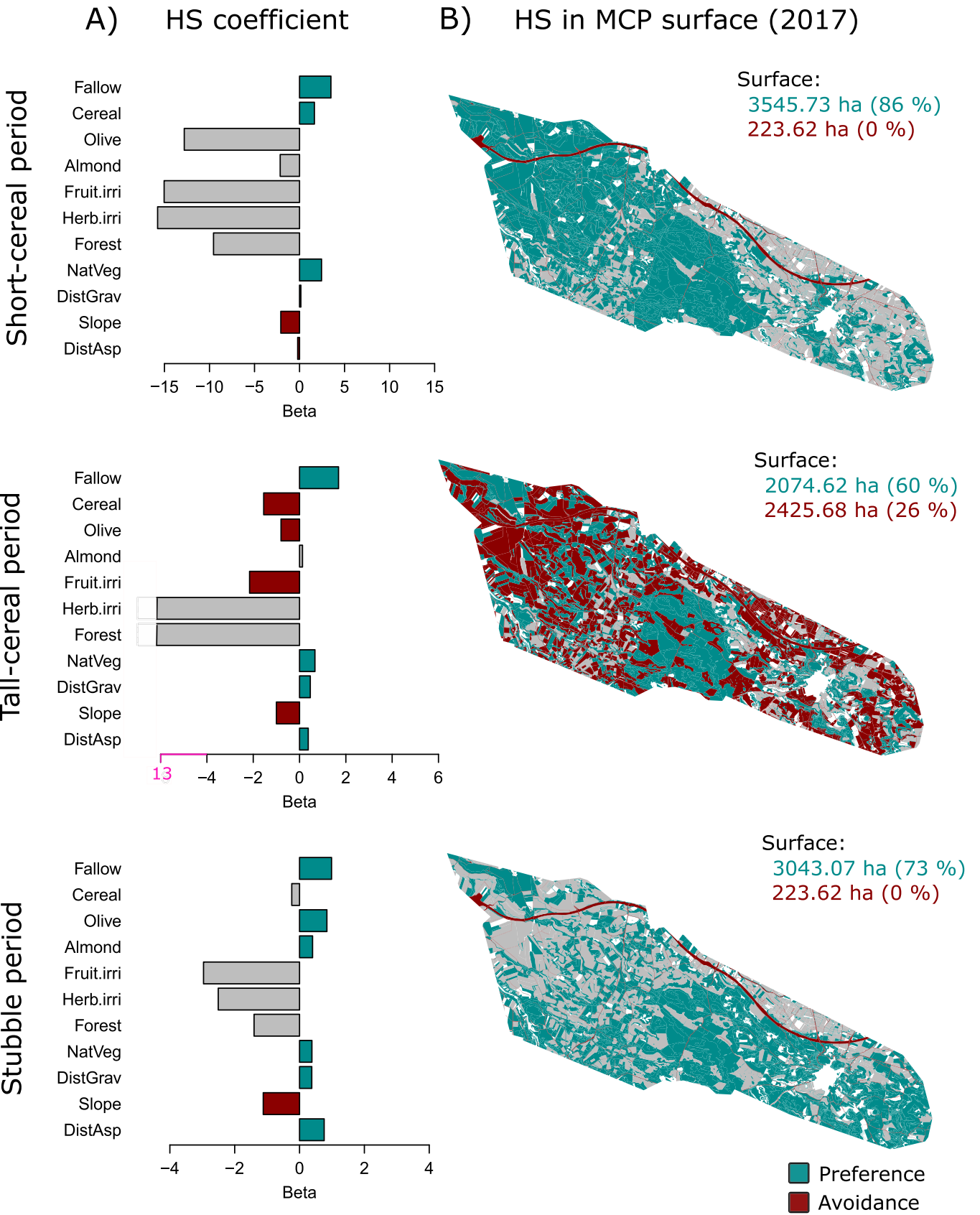
A total of 20,212 GPS locations were used to analyse habitat selection and movements (13% belonged to the Short-cereal, 48% to the Tall-cereal, and 39% to the Stubble period; Table B1, Appendix B). Average home range size of Pin-tailed sandgrouse was 1108 ha (SD = 646), which ranged from 776 (SD = 266) in the Short-cereal, to 1362 (SD = 805) in the Tall-cereal, and 970 (SD = 619) in the Stubble period (Table B2, Appendix B).

### 3.1. Identify and quantify the habitat bottleneck

Pin-tailed sandgrouse positively selected fallow and natural vegetation during all study periods (Fig. 2a; see Table D1 for standard errors), which were relatively abundant across study years (Fig. D1, Appendix D). Birds showed a positive selection towards cereal fields during the Short-cereal period but avoided them during the Tall-cereal period (Fig. 2a). The avoidance of cereal fields was no longer significant in the Stubble period, when this habitat was used as available (Fig. 2a). The beta coefficient of irrigated herbaceous and fruit crops, as well as forest remained negative but non-significant during the three periods, except for irrigated fruit crops in the Tall-cereal period (Fig. 2a, Table D1). Pin-tailed sandgrouse avoided olive crops during the Tall-cereal period but selected them during the Stubble period (Fig. 2a). Pin-tailed sandgrouse preferred flat terrain across periods, as well as locations far from roads and dirt roads, except in the Short-cereal period (Fig. 2a). The beta coefficients of distance to roads and dirt roads (DistDirt and DistRoad; Fig. 2a) increased throughout the three study periods.

The percentage of preferred habitat area within individual MCPs was on average 30% lower during the Tall-cereal period – when it consisted





**Fig. 2.** Results of the Habitat Selection analyses (HS) for the Short-cereal (upper panels), Tall-cereal (central panels) and Stubble (bottom panels) periods. Selection coefficients were used to identify and quantify a habitat bottleneck for Pin-tailed sandgrouse during 2017–2019. HS beta coefficients obtained from the RSPF of the three study periods are shown in the left panels (A; see Table 1 for variable acronyms and Table D1 for complete model output). The variable “other rainfed herbaceous crops” is the reference category, so its coefficient is not shown in the figure. The pink colour in the x-axis of the central panel denotes a different scale due to large coefficient values for forest and irrigated herbaceous crops. Right panels (B) show the land-use maps of 2017 distinguishing habitats that were positively selected (cyan blue), avoided (dark red), or used proportionately to their availability (grey) during each study period (see Supplementary Material for 2018 and 2019 maps). Maps cover the MCP built with 99% of bird locations in 2017–2019. The surface in hectares covered by preferred and avoided habitats is shown on top of each map. Percentages of avoided and preferred land-uses within the total MCP across the three study years (i.e., excluding continuous variables; see Table D2, Appendix D) are shown in brackets.

solely of fallow land and natural vegetation – than during the Short-cereal period, and it was 21.7% higher during the Stubble than the Tall-cereal period (Fig. 2b; Table D2; Fig. D2). By contrast, the percentage of avoided habitat area within individual MCPs increased from zero to 26% between the Short and the Tall-cereal period and decreased to zero in the Stubble period (Fig. 2b; Table D2).

### 3.2. Role of Targeted Fallow Management

The home range of Pin-tailed sandgrouse had on average 15% of fallow land – from which 9% was TFM and 6% was CFM – and 25% of natural vegetation (see study area section). The beta coefficients of TFM and CFM fallows were positive and similar throughout the three study periods (Table 2). During the three study periods, sandgrouse apparently preferred CFM over TFM. However, the effect of the two fallow types on the absolute probabilities of bird presence was notably lower during the Tall and Stubble periods than during the Short-cereal period due to the large negative intercepts (Table 2).

### 3.3. Movement patterns

There were statistically significant differences among periods for field change rate ( $F_{(2,10)} = 8.99$ ,  $p < 0.01$ ) and core areas ( $F_{(2,10)} = 5.07$ ,  $p < 0.05$ ), but not for the percentage of flying positions ( $F_{(2,10)} = 0.73$ ,  $p = 0.51$ ; Fig. 3) nor the Euclidean distances ( $F_{(2, 16718)} = 0.39$ ,  $p = 0.67$ ; Fig. 3). The rate of field change decreased from the Short-cereal period to the Stubble period, and the core areas were significantly smaller during the Stubble period as compared to the Tall-cereal period (Fig. 3; Table E1).

## 4. Discussion

The underlying effects of seasonally dynamic cereal steppes on the habitat selection and conservation of specialist steppe-land birds have been of particular interest (Benítez-López et al., 2017; Martín et al., 2010a; Tarjuelo et al., 2020a) and accurate GPS tracking data can improve the state-of-the-art on this question, especially when dealing with sensitive and secretive species (Recio et al., 2011). We used unprecedented high-resolution data on Pin-tailed sandgrouse to disentangle variation in movement and habitat selection linked to changes in crop phenology. Our results not only confirmed the existence of a

bottleneck in suitable habitat for sandgrouse at the start of its reproductive period, but also quantified a decrease in suitable habitat extent from 86% to 60% when cereal vegetation became tall, and suitable habitats were restricted to fallow land and natural vegetation. Optimal vegetation structures within fallows should be critical for steppe birds (Sanz-Pérez et al., 2019) – especially during the bottleneck – yet fallows under targeted conservation management were not preferred over fallows conventionally managed.

### 4.1. Bottleneck in suitable habitat: the role of fallow land and natural vegetation

Pin-tailed sandgrouse switched from preference to avoidance of cereal crops between the Short-cereal and Tall-cereal periods, supporting the habitat bottleneck hypothesis. Previous studies have suggested seasonal changes in habitat suitability for steppe birds in cereal croplands (Cardador et al., 2014) and the lack of suitability of tall cereal vegetation during spring for sandgrouse (Benítez-López et al., 2017; Tarjuelo et al., 2020a). Likewise, cereals after harvest (i.e., stubbles) were used but not selected by Pin-tailed sandgrouse, possibly because stubbles provide less protection from predators and are less suitable than other land uses such as fallow fields and natural vegetation (Martín et al., 2010b; Tarjuelo et al., 2020a). Cereal is a predominant land-use in our study area (Fig. D1, Appendix D), so large fluctuations in habitat conditions for steppe birds (> 20% in our study) occur when cereal vegetation develops.

Detecting the effects of such habitat fluctuations on wildlife requires pairing fine-scale data of both animal movements and resource dynamics – as we did here through identifying NDVI changes – which is often lacking in habitat selection studies (Hebblewhite and Haydon, 2010). Our high-resolution tracking data is, however, unbalanced because locations from the Short-cereal period were only available for four individuals due to long-distance overwinter movements of most of the breeding population. Future research should acquire more data during winter months, though our results are consistent with previous evidence (Martín et al., 2010a).

Preferred habitats for sandgrouse during the habitat bottleneck (Tall-cereal period) were only fallows and natural vegetation. They covered 60% of bird home ranges on average, though individual variability was high (36–93%). Most sandgrouse in Iberia live in dry farmland habitats, which are increasingly intensified. Our study population in Lleida –

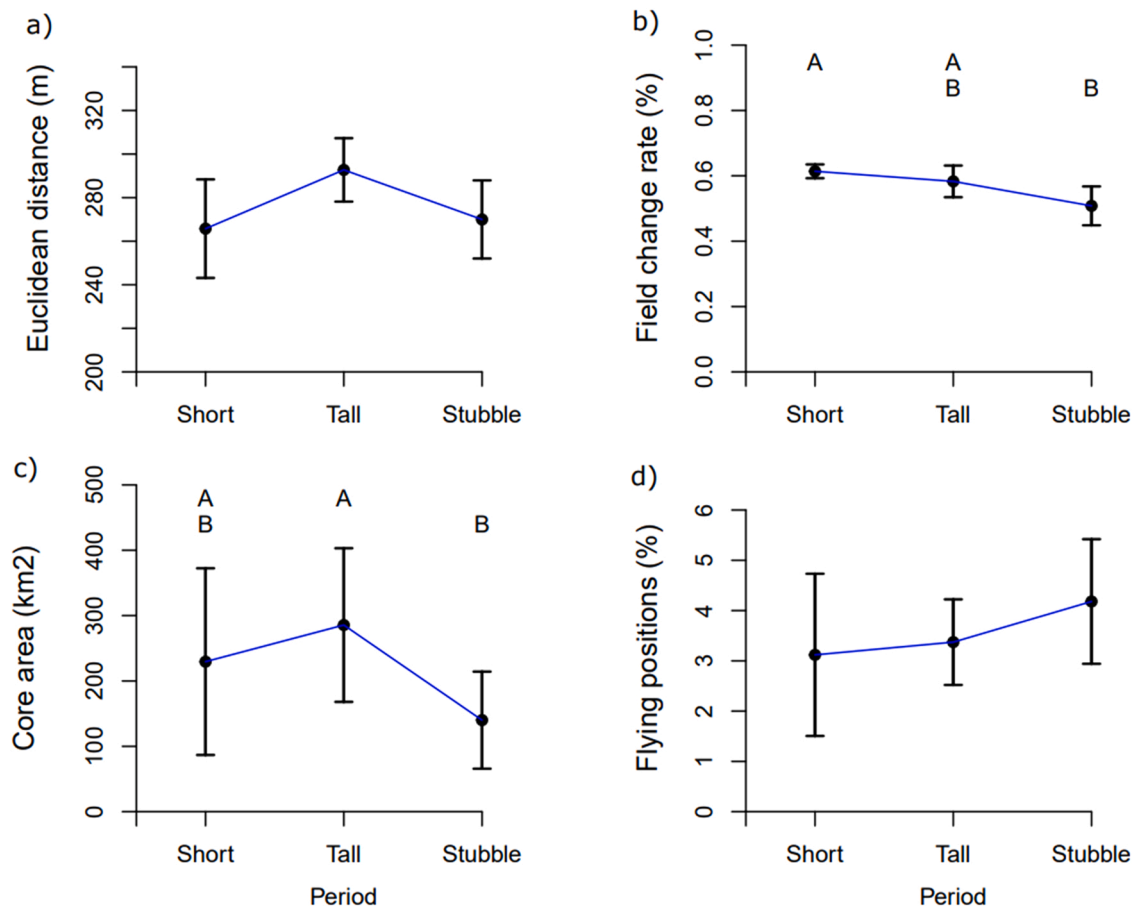
**Table 2**

Results from the RSPF analysis testing the role of Targeted Fallow Management (TFM) and Conventional Fallow Management (CFM) on Pin-tailed sandgrouse habitat selection. Averaged beta coefficients ( $\beta$  coef), Standard Errors (SE) and p-values are provided for the Short-cereal, Tall-cereal and Stubble periods. Significant p-values are indicated with an asterisk. The variable “Natural vegetation” is the reference category and therefore its effect is included in the intercept.

	Short-cereal period			Tall-cereal period			Stubble period		
	$\beta$ coef.	SE	p-value	$\beta$ coef.	SE	p-value	$\beta$ coef.	SE	p-value
Intercept	-3.36	3.84	0.38	-13.25	0.16	<0.01*	-10.07	0.47	<0.01*
CFM	0.78	0.18	<0.01*	1.34	0.04	<0.01*	0.67	0.04	<0.01*
TFM	0.62	0.23	<0.01*	0.92	0.03	<0.01*	0.52	0.03	<0.01*
DistDirt <sup>a</sup>	0.23	0.05	<0.01*	0.40	0.02	<0.01*	0.34	0.02	<0.01*
Slope	-1.82	0.26	<0.01*	-1.03	0.03	<0.01*	-1.03	0.05	<0.01*
DistRoad <sup>b</sup>	-0.06	0.05	0.24	0.27	0.01	<0.01*	0.33	0.01	<0.01*

<sup>a</sup> Distance to dirt roads

<sup>b</sup> Distance to roads



**Fig. 3.** Results on movement patterns analyses of Pin-tailed sandgrouse. Mean and 95% Confidence Interval (black dots and error bars respectively) are provided for the Short-cereal (Short), Tall-cereal (Tall), and Stubble periods for each movement variable: a) Euclidean distance (m), b) Field change rate, c) Core area (km<sup>2</sup>), and d) % of flying positions. Differences between periods according to Tukey test are indicated by different capital letters when period was significant (see also Table E1, Appendix E).

holding approximately 3% of the Spanish population of 2019 (Mougeot et al., 2021a) – shares the habitat characteristics of other dry farmland populations, except for the higher proportion of fallow land prompted by conservation schemes (TFM; Mañosa et al., 2021). Our results from a system with higher than average managed fallows warn about the increasingly adverse effects of seasonal habitat bottlenecks in most farmland regions where fallow land is disappearing, a trend associated with current steppe-bird populations declines (Traba and Morales, 2019).

#### 4.2. Human disturbance and general habitat selection patterns

In accordance with previous studies, Pin-tailed sandgrouse selected locations away from roads and dirt roads, confirming their sensitivity to human disturbances (Benítez-López et al., 2017; Tarjuelo et al., 2020a). This avoidance was weaker in the Short-cereal period (late winter), when human activity was likely lower and their gregarious behavior might reduce perceived predation risk (Borbón et al., 1999; Martín et al., 2010b), but stronger during the breeding period, when pairs use undisturbed and safe places for nesting (Mougeot et al., 2014). Pin-tailed sandgrouse avoided steep terrain and irrigated crops, confirming previous evidence on this behavior (Benítez-López et al., 2017; Martín et al., 2010a). Sandgrouse also preferred olive grove and almond crops in the Stubble period, as observed in other regions (see also Tarjuelo et al., 2020a), likely to rest and hide from the high temperature characterizing this period (Herranz and Suarez, 1999).

#### 4.3. Role of fallow management for habitat selection

Our results show that sandgrouse similarly selected TFM and CFM fallows, contrasting with the increasing number of studies proving the importance of managing vegetation structure for steppe birds (Hawkes et al., 2021; Robleño et al., 2017; Sanz-Pérez et al., 2019), and particularly for our model species (Sanz-Pérez et al., 2021). This could be due to several factors, such as the different scales at which the studies took place (presence/abundance data vs high-resolution tracking data). Also, the drastic reduction of suitable habitat during the Tall-cereal period greatly limits suitable options for habitat choice, constrained to fallows under targeted and conventional management, as well as natural vegetation. In addition, the TFM targeting species requirements for very short and sparse vegetation might end up in a vegetation structure similar of that yielded by CFM. However, this does not necessarily imply similar habitat quality of TFM and CFM, as other characteristics of TFM such as forbidden agricultural management during the breeding season might be critical for bird abundance (Sanz-Pérez et al., 2021).

#### 4.4. Movement behavior of Pin-tailed sandgrouse

Although models did not show a significant effect of period on the distance travelled between hourly consecutive positions, the average distance appeared to be greater during the Tall-cereal period. This pattern has been previously documented for other bird species during resource bottlenecks (e.g., Lapiedra et al., 2011; Schlaich et al., 2016) and for Pin-tailed sandgrouse during the breeding period in cereal steppes (Tarjuelo et al., 2020a), suggesting increasing travelled

distances as an adaptive strategy to exploit resources in fragmented landscapes (Fahrig, 2007). Indeed, if key resources become increasingly scant and dispersed in the cereal steppe matrix, as it is occurring with fallow land in most cereal steppes, birds might be forced to increase movements during nesting and fledgling care, which could impact productivity by increased probability of nest failure or low rates of chick survival. Average distances seemed to decrease in the Stubble period, when harvested cereal can be again used by sandgrouse, but additional data is needed to corroborate this pattern. The field change rate decreased from the Short-cereal period to the Stubble period and the core area was the lowest in the Stubble period, suggesting that birds reduced their occupied area as breeding progresses to trade-off resource acquisition and field-fidelity for nesting. Seasonal habitat bottleneck did not alter flying time, or, alternatively, hourly positions might not capture properly the flying behavior of this species.

#### 4.5. Conclusions and conservation implications

Fallows and natural vegetation play a critical role during the seasonal habitat bottleneck in cereal steppes, acting as refuges for steppe bird species at the start of the breeding season when a large fraction of the landscape turns unsuitable due to cereal growing. Conservation efforts should prioritize the increase of fallows with suitable characteristics for declining steppe bird species (see Tarjuelo et al., 2020b; Traba and Morales, 2019) to reduce adverse population-level consequences during the critical breeding period. Importantly, suitable fallows should be promoted in optimal sites (i.e., flat, undisturbed by humans, far from irrigation; see also Giralt et al., 2021) to ensure its success as a conservation tool for highly sensitive species such as the specialist Pin-tailed sandgrouse.

Seasonal resource fluctuations can affect survival (Janke et al., 2015; Schlaich et al., 2016) and have carry-over effects (Swift et al., 2020). A tendency towards greater displacements observed during the Tall-cereal period – coinciding with the habitat bottleneck – could be costly and encourages further research in other cereal croplands to address the fitness consequences of altered movement patterns as a response to scarce and patchy resources – particularly during the nesting period – in this and other steppe bird species. Ensuring availability of optimal habitats and fitness stability in seasonal landscapes is key to preserve steppe bird populations and should therefore become a priority in conservation planning.

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#### CRediT authorship contribution statement

Gerard Bota, François Mougeot, David Giralt, Francesc Sardà-Palomera, Rocío Tarjuelo, and Ana Sanz-Pérez conceived and designed the study. Rocío Tarjuelo and Ana Sanz-Pérez implemented the analysis with the contribution of Marcos Pérez. Ana Sanz-Pérez led the writing of the manuscript. Carlos Santisteban, Marcos Pérez, Francesc Sardà-Palomera, David Giralt, Gerard Bota, François Mougeot, performed fieldwork, with the help of Ana Sanz-Pérez and Rocío Tarjuelo. All the authors contributed to subsequent drafts and gave final approval for publication. Francesc Sardà-Palomera, David Giralt and Gerard Bota coordinated fieldwork and Gerard Bota secured funding.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

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#### Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108162.

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