UNIVERSITAT DE BARCELONA

Integrating agriculture and conservation: The value of fallow land and its management for farmland and steppe bird conservation

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SUMMARY

Farmland bird populations – and especially the populations of specialist steppe birds – are declining dramatically as a consequence of habitat loss caused by agriculture intensification. Fallow (or un-cultivated) land presents open vegetation structures essential for the breeding and foraging of these species.

This thesis does not only demonstrate the importance of fallow land presence, but also how specific fallow management practices can improve the conservation of farmland and steppe bird populations, in a cereal steppe of north-eastern Spain. It also contributes to conservation planning at the monitoring stage, by showing the importance of accounting for imperfect detection when estimating farmland bird population trends. The applied guidelines provided here have great potential to be included within the upcoming European agricultural reform (CAP post-2020) and help prevent imminent bird population declines and extinctions.

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Integrating Agriculture and Conservation

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Integrando agricultura y conservación:
El valor de las tierras en barbecho y su gestión para la conservación de aves de medios agrícolas y esteparios

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Memòria presentada per **Ana Sanz Pérez**
per optar al grau de Doctor per la Universitat de Barcelona

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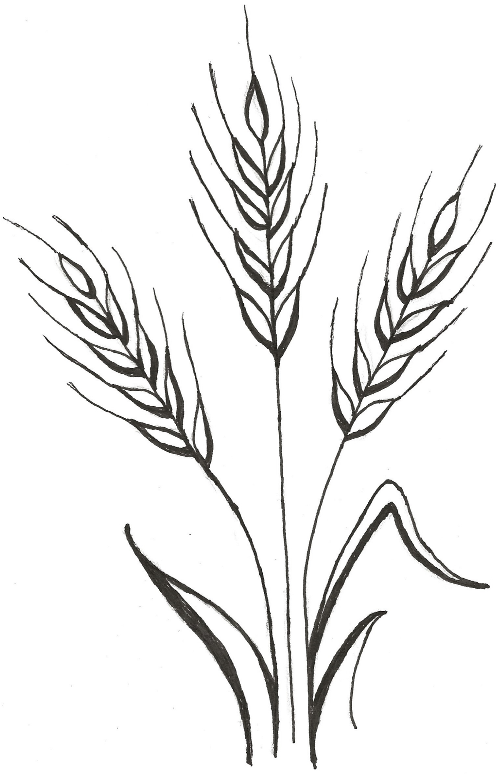
"There is a way that nature speaks, that land speaks.
Most of the time we are simply not patient enough,
quiet enough, to pay attention to the story."
— Linda Hogan

A mis padres, Pedro y Montse
A mi hermana María
A Cyril



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ABSTRACT (ENGLISH)

Extensive farmland ecosystems are widespread and biodiversity-rich, yet they face important human pressures since the beginning of agriculture intensification, which is leading them into a severe biodiversity crisis. As a result, farmland bird populations - particularly specialist species such as steppe birds - are declining dramatically. In Europe, steppe birds are associated with "cereal steppes", which are extensive agricultural landscapes where crop rotations include fallow fields. Fallows are key breeding and foraging habitats for farmland birds and usually present open vegetation structures essential for steppe birds. This thesis, situated in a cereal steppe in Catalonia (north-eastern Spain), evaluates the importance of fallow land and its management for enhancing farmland and steppe bird populations. Because population monitoring is key to evaluate the status of populations, I also explored the importance of accounting for imperfect detection when estimating farmland bird population trends. By using a Hierarchical Distance Sampling (HDS) model, I found that heterogeneous detection across observers and years could bias trend estimates when not accounted for. Through a HDS community model integrating data of 37 farmland bird species, I revealed the lack of efficiency of conservation measures applied in fallow fields, currently promoted by the European Common Agricultural Policy (Agri-Environmental Schemes and Greening), to increase farmland bird abundance. However, a local conservation measure targeted specifically at steppe birds (Targeted Fallow Management, TFM) – consisting of agricultural practices on fallows applied once or twice annually before the breeding season – enhanced steppe bird abundance. Through path analyses, I could disentangle the mechanisms behind TFM success and found that TFM fulfils species-specific requirements by modulating the vegetation structure. Finally, I used the first GPS data on the declining Pin-tailed sandgrouse (*Pterocles alchata*) to demonstrate the importance of fallow land during the breeding season, when cereal vegetation is tall and unsuitable for steppe birds causing a habitat bottleneck. This thesis provides applied guidelines for conservation planning, from population monitoring to mechanisms involved in the success of specific conservation measures. The key finding is the importance of promoting not only fallow-land presence, but also its management, to improve its conservation efficiency. These guidelines have great potential to be included within the upcoming European agricultural reform (CAP post-2020) and help prevent imminent population and species extinctions.

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RESUM (CATALÀ)

Els paisatges agrícoles són ecosistemes rics en biodiversitat, però des de mitjans del segle passat Europa pateix un procés d'intensificació agrícola que està causant la pèrdua d'aquesta biodiversitat a gran velocitat. Com a conseqüència, les poblacions d'ocells de medis agrícoles – en particular espècies especialistes com els ocells estèpics – pateixen un fort declivi. A Europa, els ocells estèpics estan estretament associats a les estepes cerealistes de la Península Ibèrica, que són paisatges oberts i plans on predomina el cultiu del cereal, en rotació amb guarets i altres cultius herbacis. Els guarets són hàbitats essencials per a l'alimentació i nidificació dels ocells de medis agrícoles, i normalment presenten una vegetació baixa en altura i cobertura que resulta òptima per els ocells estèpics. Aquesta tesi avalua la importància del guaret i la seva gestió per a la millora de les poblacions d'ocells agrícoles i estèpics. L'estudi es desenvolupa en una estepa cerealista de Catalunya (nord-est d'Espanya) en la qual s'apliquen mesures compensatòries per a la conservació d'ocells estèpics des de l'any 2015. En aquest context, la tesi també explora la importància de tenir en compte la detectabilitat per a l'estima de tendències poblacionals d'ocells en ecosistemes agrícoles, ja que el monitoratge és un aspecte essencial per avaluar l'estat de les poblacions. La tesi demostra l'eficiència d'una mesura de conservació d'àmbit local específicament dissenyada pels ocells estèpics, que consisteix en la gestió de guarets ("Targeted Fallow Management, TFM"). Mitjançant l'ús d'anàlisi de ruta ("Path analysis"), aquesta tesi revela el mecanisme ecològic d'actuació de la mesura TFM, que satisfà els requeriments específics de diferents espècies d'ocells estèpics mitjançant una gestió adequada de l'estructura de la vegetació. A més, TFM va resultar ser més eficaç que les mesures de conservació en guarets promogudes en el marc de la Política Agrària Comuna Europea (Greening i Mesures Agroambientals) per augmentar l'abundància de la comunitat d'ocells, especialment dels ocells estèpics. Aquests resultats s'han obtingut mitjançant l'aplicació de models jeràrquics de mostreig per distàncies ("Hierarchical Distance Sampling, HDS"). També s'utilitzen els models HDS per demostrar que l'existència d'una detecció heterogènia entre observadors i al llarg dels anys pot ocasionar estimes de tendències poblacionals errònies si no es té en compte la detecció imperfecta. Finalment, utilitzant dades GPS de ganga (*Pterocles alchata*), també es demostra la importància del guaret quan el creixement del cereal a la primavera ocasiona un coll d'ampolla en la quantitat disponible d'hàbitat òptim per aquesta espècie. Aquesta tesi proporciona recomanacions útils per la planificació de mesures de conservació, des de l'etapa inicial del monitoratge fins a comprendre quins són els mecanismes ecològics subjacents a les mesures de conservació més exitoses. La seva principal contribució és la importància d'una adequada gestió dels guarets per augmentar el seu valor com a eina de conservació. Aquestes recomanacions són especialment oportunes per poder ser incloses en la nova reforma de la Política Agrària Comuna, i així contribuir a la conservació d'aquestes espècies.

RESUMEN (CASTELLANO)

Los paisajes agrícolas son ecosistemas ricos en biodiversidad, pero desde mediados del siglo pasado Europa sufre un proceso de intensificación agrícola que está causando la pérdida de esta biodiversidad a gran velocidad. Como consecuencia, las poblaciones de aves de medios agrícolas – en particular especies especialistas como las aves esteparias – sufren un declive alarmante. En Europa, las aves esteparias están estrechamente asociadas a las estepas cerealistas de la Península Ibérica, que son paisajes abiertos y llanos en los que predomina el cultivo del cereal, en rotación con barbechos y otros cultivos herbáceos. Los barbechos son hábitats esenciales para la alimentación y nidificación de aves de medios agrícolas, y normalmente presentan una vegetación baja en altura y cobertura que resulta óptima para las aves esteparias. Esta tesis evalúa la importancia de las tierras en barbecho y su manejo para la mejora de las poblaciones de aves de medios agrícolas y esteparios. El estudio se desarrolla en una estepa cerealista de Cataluña (noreste de España) en la que se aplican medidas compensatorias para la conservación de aves esteparias desde el año 2015. En este marco, la tesis también explora la importancia de tener en cuenta la detectabilidad para la estima de tendencias poblacionales de aves en ecosistemas agrícolas, ya que el monitoreo es un aspecto esencial para evaluar el estado de las poblaciones. La tesis demuestra la eficiencia de una medida de conservación de ámbito local, específicamente diseñada para las aves esteparias, consistente en el manejo de barbechos ("Targeted Fallow Management, TFM"). Mediante el uso de análisis de ruta ("Path analysis"), esta tesis revela el mecanismo ecológico de actuación de la medida TFM, que satisface los requerimientos específicos de distintas especies de aves esteparias mediante una gestión adecuada de la estructura de la vegetación. Además, TFM resultó ser más eficaz que las medidas de conservación en barbechos en el marco de la Política Agraria Común Europea (Greening y Medidas Agroambientales) para aumentar la abundancia de la comunidad de aves, en especial de las aves esteparias. Estos resultados se han obtenido mediante la aplicación de modelos jerárquicos de muestreo por distancias ("Hierarchical Distance Sampling, HDS"). También se utiliza HDS para demostrar que la existencia de una detección heterogénea entre observadores y a lo largo de los años puede ocasionar estimas de tendencias poblacionales erróneas para ciertas especies, si no se tiene en cuenta la detección imperfecta. Finalmente, utilizando datos GPS de ganga ibérica (*Pterocles alchata*), también se demuestra la importancia del barbecho cuando el crecimiento del cereal en primavera ocasiona un cuello de botella en la cantidad de hábitat óptimo disponible para esta especie. Esta tesis proporciona recomendaciones útiles para la planificación de medidas de conservación, desde la etapa de monitoreo hasta comprender cuáles son los mecanismos ecológicos subyacentes a las medidas de conservación más exitosas. Su principal contribución es la importancia de una adecuada gestión de los barbechos para aumentar su valor como herramienta de conservación. Estas recomendaciones son especialmente oportunas para ser incluidas en la nueva reforma de la Política Agraria Común, y así contribuir a la conservación de estas especies.

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INTRODUCTION

GENERAL INTRODUCTION

1. Global change and the persistence of animal populations

Humans have inhabited earth for a short time span, but our activities have had disproportionate and long-lasting impacts on the global environment. We have entered into a new geologic epoch – the Anthropocene (Lewis and Maslin, 2015; Mendenhall et al., 2014) – characterized by the unprecedented pace of biodiversity loss leading us into the sixth mass extinction. Global biodiversity is highly threatened by climate change, air pollution and invasive species, with overexploitation and habitat loss as a result of agriculture intensification at the top of the threats list created by humans (Maxwell et al., 2016). Human development has caused the expansion of agricultural ecosystems, and several species have successfully adjusted to these new environments, leading to many anthropogenic species-rich ecosystems (Kleijn et al., 2006). Integrating biodiversity conservation into these human-dominated landscapes is essential but also challenging (Mendenhall et al., 2014), often constituting a source of conflict among stakeholders.

In addition to human factors, the presence, survival, and reproduction of an individual is determined by the available set of resources (food, shelter) and environmental conditions (biotic and abiotic; Gaillard et al., 2010). Animals are constantly facing the challenge to select habitats that maximize their fitness (Gaillard et al., 2010), so habitat selection (i.e., the disproportionate use of habitats relative to their availability; Johnson, 1980) is an essential evolutionary strategy (Morris, 2003). Hutchinson (1957) introduced the concept of ecological niche as a multi-dimensional space representing the various resources an individual, population or species needs to persist. Niche width is a key feature distinguishing between specialist and generalist species: while specialists depend on a particular habitat (narrow niche), generalists sustain themselves using a wide range of resources and thrive in heterogeneous environments (broad niche; Clavel et al., 2011).

Global change characterized by the rapid transformation of entire ecosystems has resulted in wildlife habitat loss, and has been particularly detrimental for specialist species, causing their population declines (Clavel et al., 2011). Altered habitats often confer an advantage to generalist species, which outcompete specialist species by colonizing the newly created niches (Clavel et al., 2011). Agriculture ecosystems have been widely transformed and intensified, constituting an illustrative example of biotic homogenization by promoting the existence of few generalist species (Gámez-Virués et al., 2015; Giralt et al., 2021). Deepening knowledge on species-habitat relationships in agriculture ecosystems is essential to design and implement effective conservation plans, especially for highly vulnerable specialist species.

1.1. Biodiversity conservation and food production: A crucial challenge of the 21st century

Around one quarter of Earth's terrestrial surface and half of the European land area is covered by cultivated land (European Commission, 2018; Millennium Ecosystem Assessment, 2005). Farmlands are the ecosystems interacting the most with human activities, as they directly overlap with the basic need of food production. Farmland biodiversity has a high cultural value and provides essential ecosystem services for food production (e.g., pollination, biological pest control, soil health; Erisman et al., 2016), yet its conservation status is among the poorest of all ecosystems (EEA, 2020; Pe'er et al., 2014).

Increasing food demands of a growing human population poses a great challenge for farmland biodiversity conservation (United Nations, 2017). The tipping point occurred in the 1960's with the explosion of the so-called "Green Revolution" and the implementation of the Common Agricultural Policy (CAP; Krebs et al., 1999). This revolution was characterized by economic and technological incentives to increase productivity, which triggered the transformation of traditional farming practices and resulted in the increase of large monocultures and agro-chemical use (Benton et al., 2003). The indiscriminate toxicity of widely used pesticides that persist in the food chain and accumulate at high trophic levels (Krebs et al., 1999; e.g., Lopez-Antia et al., 2016) was first highlighted in Rachel Carson's book *The Silent Spring* (1962), and remains a threat to farmland animal populations (Humann‐Guilleminot et al., 2019). Monoculture systems have decreased between-field and within-field habitat heterogeneity, and have compromised the quality and amount of suitable habitats (Benton et al., 2003; Wilson et al., 2005). The loss of natural and semi-natural habitats, such as fallow land (e.g., substituted by intensive irrigated crops), has also been a major cause of biodiversity declines during agriculture intensification (Traba and Morales, 2019).

1.2. The historical role of fallow land in agriculture and conservation

Fallow (or "set-aside") land is an arable land taken out of production temporarily to improve soil quality and maximize future productivity, and has traditionally been part of crop rotations in extensive agriculture systems. Fallow land has been a cornerstone in supporting plant and invertebrate biodiversity in farmlands, as well as providing key habitats for farmland birds (e.g., for foraging or nesting; Henderson et al., 2000; Van Buskirk and Willi, 2004). Agriculture intensification has maximized crop productivity and profit relative to traditional practices such as crop rotations (e.g., through pesticide use; Tarjuelo et al., 2020b). Thus, fallow land has been dissociated from productivity purposes. The loss of the agronomic role of fallow land, now viewed as solely serving environmental purposes, has reduced its economic appeal and hampered its endurance. This change of role is behind the dramatic loss of fallows (e.g., its surface in Europe declined by 31.9 % between 2010 and 2017; Tarjuelo et al., 2020b), which has been linked to animal population declines in farmlands (Traba and Morales, 2019; Van Buskirk and Willi, 2004).

1.3. The EU Common Agricultural Policy: A double-edged sword for conservation

Several conservation schemes have attempted to tackle the farmland biodiversity crisis (Abensperg-Traun et al., 2004; Kleijn et al., 2011). In Europe, the CAP played the double role of advocating intensification to maximize productivity, while also promoting conservation measures to minimize environmental impacts. The earliest conservation regimes appeared in 1992 with the MacSharry reform, which introduced the requirement of keeping 15% of cropland as fallow land (reduced to 10 % in 1996), and also Agri-Environmental Schemes (AES) (Oñate, 2005; Tarjuelo et al., 2020b). AES provide financial support to farmers adopting environmentally friendly practices and are still in use (Batáry et al., 2015). Other complementary reforms have attempted to reverse biodiversity loss with mixed results, such as the Rural Development Pillar (Pillar II, where AES are now included), the decoupling of subsidies from production (Oñate, 2005), and the implementation of so-called "greening" measures in the last programming period (2014-2020; Pillar I; European Comission, 2018). Greening consists of direct payments to farmers conditional on compliance with three requirements aimed at benefiting biodiversity: maintaining permanent grasslands, growing a minimum of three different crops, and establishing Ecological

Focus Areas (EFA) – landscape elements such as buffer strips or fallow – on 5% of arable land (European Commission, 2013).

Decades of research have significantly improved the knowledge on how to optimize the efficiency of CAP conservation measures (see Batáry et al., 2015), yet CAP is defined by its poor environmental performance (Kleijn et al., 2006; Pe'er et al., 2020, 2014). Key CAP shortcomings include poor targeting and insufficient funding for Agri-environmental Schemes, insufficient sets of indicators to promote result-based payments, and complex administrative burdens (Pe'er et al., 2020). CAP policy has particularly failed at promoting fallow land through its different reforms, such as the abolition of maintaining a mandatory 10% of fallow in 2008, or an unbalanced weighting system for EFA Greening options, leading farmers to choose productive crops such as nitrogen-fixing crops over fallow land (Tarjuelo et al., 2020b). As a consequence, animal populations inhabiting farmlands have experienced severe declines and range contractions since the inception of the CAP (e.g., farmland birds; Donald et al., 2001; Voříšek et al., 2010). The upcoming CAP reform (CAP post-2020; European Commission, 2019) is a new opportunity to reverse farmland biodiversity declines, and research on the effectiveness of CAP instruments is timely and crucial to support the inclusion of effective conservation measures at the European, national, and regional level.

2. Population monitoring as a pillar for conservation action

Biodiversity conservation depends upon the identification of threatened species, broadening knowledge on species ecological requirements, evaluation of management approaches, and documenting populations recovery (Bart, 2005). These essential conservation components have historically been supported by monitoring programs, which depend on robust sampling design to be informative. For instance, monitoring schemes provide the data on abundance, distribution, and population trends, which are the key features considered to categorize species at risk by the IUCN Red List assessment (Maes et al., 2015). Disentangling the mechanisms behind population declines requires going beyond population trends (Voříšek et al., 2010), thus, monitoring schemes that shed light on species-habitat relationships (e.g., habitat selection) or demographic parameters are key to inform conservation actions (Bart, 2005; e.g., Robinson et al., 2014). Monitoring schemes are also key to evaluate the efficiency of conservation efforts, which can then be continuously improved through adaptive management (Allen et al., 2011).

2.1. Bird population trend assessments

Evaluating the need for, and efficiency of, biodiversity conservation measures is often hampered by the difficulty of measuring population trends for a multitude of species. As a result, species or groups of species that can serve as indicators of overall biodiversity status, are a useful tool for biodiversity monitoring (Purvis and Hector, 2000). Birds are diverse, widespread, sensitive to environmental change and their ecology is well-understood, therefore fulfilling all the requirements to be suitable biodiversity indicators (Gregory, 2006). Moreover, their populations can be monitored by citizen science programs (Bart, 2005). Bird monitoring programs in Europe are numerous (PECBMS, 2018), and constitute a cornerstone to evaluate the performance of European conservation policy (Donald et al., 2007). The Pan-European Common Bird Monitoring Scheme (PECBMS, 2018) is an initiative that gathers information from national bird monitoring programs across Europe, produces multi-species indicators, and derives population trends from bird counts (Pannekoek and Strien, 2005). This initiative has been crucial to shed light on the contrasting population trends of European birds: while forest bird populations present relatively stable trends, common farmland bird populations have declined dramatically (Gregory et al., 2019; PECBMS, 2018).

Quantifying abundance is challenging because field observations are often imperfect, making it rarely possible to detect all individuals in a population (Kéry and Schmidt, 2008). Thus, failure to account for imperfect detection can result in erroneous abundance or population trend estimates (Kéry et al., 2009; Kéry and Schmid, 2004). Population trend estimates obtained from raw bird counts (i.e., not corrected for detectability) can be used as a robust indicator if detectability is constant over years, which is not always the case in bird surveys (Kéry and Schmidt, 2008). For instance, observers participating in bird monitoring programs might have different skills and thus be more or less likely to detect birds; this is particularly common within programs based on citizen science that rely on voluntary observers (Bart, 2005; e.g., Diefenbach et al., 2003). Weather conditions and vegetation might also differ among years, altering bird behaviour, and the observer sighting and hearing ability during surveys (Bas et al., 2008). Testing for heterogeneity in detection over time could ensure unbiased trend estimates, but the assumption of constant detection is rarely checked and likely often violated in bird surveys (Kéry et al., 2009; Rosenstock et al., 2002). Despite the risk of erroneous inferences about the true state of the population when not accounting for imperfect and varying detection (Kéry and Schmid, 2004), analyses ignoring detectability are common in most bird monitoring programs. This is also the case of the TRIM approach (TRends and Indices for Monitoring data; Pannekoek and Strien, 2005), which has proved useful to derive population trends from bird counts by fitting log-linear models within PECBMS, yet missing the detection process.

2.2. Incorporating detectability when estimating population trends: Hierarchical Distance Sampling

Imperfect detection can be explicitly accounted for by using an appropriate survey design and modelling approach. Hierarchical models are a useful framework to do so, as they describe the hierarchical processes that generate ecological field data: an observation process, describing the way in which we observe data (e.g., imperfect detection leading to counts of individuals that are different than the true number of individuals present), and that is conditional on the ecological process, which describes the true state of the population and is often of main interest in ecology (e.g., population size; Kéry et al., 2009; Kery and Royle, 2015). The additional information that must be collected in order to model the observation process separately from the ecological process can be of different nature (e.g., distance sampling; Buckland et al., 2001; replicated counts; Royle, 2004; capture-recapture; Williams et al., 2002), constituting different types of hierarchical models (Kéry et al., 2009).

Distance sampling is an efficient method for providing detection-corrected and unbiased abundance estimates of bird populations in a single survey (Buckland et al., 2001; Rosenstock et al., 2002), which reduces its costs as compared with other methods requiring multiple survey occasions (e.g., N-mixture, capture-recapture; Royle, 2004; Williams et al., 2002). Distance sampling consists of recording the perpendicular distance of an animal to the observer (or transect) and estimating the animal's probability of detection (p) as a function of distance (i.e., the detection function; Buckland et al., 2004, 2001). This framework was extended to allow for modelling spatial variation in the detection function and abundance as a function of site-specific covariates, termed Hierarchical Distance Sampling (Royle et al., 2004; Sollmann et al., 2016).

Even though farmlands are often perceived as open habitats where few environmental conditions can hamper detectability, they are in constant change (e.g., fast vegetation encroachment in spring; Cardador et al., 2014; crop rotations; Merriam, 1988; transformations due to agriculture intensification; Tscharntke et al., 2005), which may result in heterogeneous detection over space and time. Also, farmland hosts elusive bird species sometimes difficult to detect because of their ground-nesting and feeding behaviour (e.g., steppe birds; de Juana, 2005). Changing environmental conditions, together with potential observer effects and differences in species characteristics (e.g., body size) or behaviour, highlight the need to base farmland bird population trends on detectability-corrected abundance estimates, and hierarchical distance sampling is a well-suited and cost-effective method to do so.

2.3. The use of telemetry to study ecology and behaviour

The appearance of telemetry in the 1960s - that requires attaching a tracking device to the animal - provided researchers with a new tool to remotely track individuals, and has been key to gain information on elusive species (Martin et al., 2009). However, telemetry studies are costly and invasive, and therefore practically difficult to implement for large populations. As a consequence, they often require drawing inferences from a limited number of individuals that are assumed to be a representative sample of the population (Hebblewhite and Haydon, 2010). Telemetry studies are often used as a complement to large scale non-invasive monitoring to reveal key information from the movement behaviour of species (fine scale habitat selection, dispersal, migration…) that would not be attainable otherwise (Martin et al., 2009).

Given that land-use change is a major threat for farmland bird populations (Donald et al., 2006, 2001), deepening the knowledge on species-habitat relationships is key to understand and reverse their declines (Catry et al., 2012). Research on bird populations in agricultural habitats could greatly benefit from data at high spatio-temporal resolution, as farmland landscapes undergo high inter and intra-annual habitat transformations (Cardador et al., 2014). The recent adaptation of GPS technology to lightweight species provides a unique opportunity in the study of farmland bird habitat selection (e.g., Guthrie et al., 2011; Recio et al., 2011), allowing to obtain detailed information on individual movement and spatial distribution. For instance, high frequency relocations can help studying how farmland management influences foraging decisions (Catry et al., 2012; Johst et al., 2001). Linking individual space use with crop dynamics is especially needed to ensure that the resources defining the niche of farmland specialist species remains available over time (e.g., Tarjuelo et al., 2020a; Traba et al., 2015).

3. The case of steppe birds

The farmland bird guild with the most unfavourable conservation status at the European level are the so-called steppe birds (83% of all European steppe birds present unfavourable conservation status; Burfield, 2005), whose stronghold is found in the Iberian Peninsula (Santos and Suárez, 2005). Steppe birds have singular ecological and evolutionary characteristics related to their preference for structurally simple habitats (de Juana, 2005). Their highly specialized requirements in terms of vegetation structure (Figure 1; Robleño et al., 2017) are explained by the substantial time they spend on the ground (i.e., nesting and feeding; de Juana, 2005). Their micro-habitat selection patterns in terms of vegetation structure are determined by the trade-off between maximizing foraging efficiency, while minimizing predation risk (Traba et al., 2015; Whittingham et al., 2006). Indeed, the narrow and segregated niches of steppe birds have allowed their co-existence in steppe-like habitats and traditional agricultural landscapes (Traba et al., 2015).

The detrimental effects of agricultural intensification on this guild are exacerbated because of their specialist nature, which hampers their adaptation to the new habitats produced by modern agricultural practices, such as irrigated annual and permanent crops (Gámez-Virués et al., 2015). The adjustment of steppe birds to modern agricultural systems is further aggravated by their high sensitivity to human disturbances (e.g., human urbanization and infrastructure development; Santos and Suárez, 2005).

3.1. The Iberian cereal steppe

Steppe bird species are originally associated with natural steppes, nowadays only present in southern Russia, Ukraine and Kazakhstan (Sainz Ollero, 2013). They arrived on the Iberian Peninsula from the Afro-Asian steppes in the Quaternary, and their persistence was subsequently favoured by the Neolithic agricultural expansion (7,000 years ago; Santos and Suárez, 2005). The implementation of grazing and cultivation of cereal crops, together with the Mediterranean semi-arid climatic conditions, maintained these habitats treeless and structurally very resemblant to steppe-like habitats; thus, these areas are also referred to as "pseudo-steppes". The Iberian Peninsula is the major place in Europe where agricultural landscapes have maintained these climatic and structural conditions, explaining why it is a sanctuary for European steppe bird populations (Delgado and Moreira, 2000; Santos and Suárez, 2005).

The Iberian cereal steppe constitutes a landscape mosaic of crops, where extensive areas of cereal fields are still cultivated on a rotation basis. Crop rotations alternate cereal with legume crops or fallow land, and are also interspersed with pastures, permanent crops, and shrubland (Sainz Ollero, 2013). The schedule and spatial arrangement of agricultural practices (e.g., different cereal harvesting time; Catry et al., 2012), as well as changing weather conditions (i.e., fast vegetation encroachment in the rainy season; Cardador et al., 2014), confronts species with a patchy and dynamic pattern of suitable habitat (Johst et al., 2001). Steppe birds are able to cope with seasonally dynamic landscapes by shifting their habitat selection patterns towards patches with greater food availability and lower predation risk (Delgado and Moreira, 2000; Tarjuelo et al., 2020a). Non-cropped habitats generally offer suitable habitat conditions all year long, thus playing an essential role in maintaining steppe bird populations (Delgado and Moreira, 2000; McMahon et al., 2010).

3.2. Fallow land and its management for steppe bird conservation

Fallow land is perhaps the most important land-use element to make agricultural systems suitable for steppe birds and other farmland birds (McMahon et al., 2010; Van Buskirk and Willi, 2004). Indeed, the decline of steppe bird species in Spain has been linked to the loss of fallow land (Traba and Morales, 2019). Fallow fields support a greater abundance of food resources for steppe birds than cropped habitats (i.e., seeds, weeds and invertebrates; Evans et al., 2011; Henderson and Evans, 2000), and generally present a more open vegetation structure that minimizes predation risks (Whittingham et al., 2006). Thus, fallows are preferred habitats for steppe birds for breeding and nesting (e.g., Morales et al., 2013; Tarjuelo et al., 2020a).

An optimal vegetation structure is crucial for the success of fallow fields in hosting steppe bird species (e.g., Moreira, 1999). For instance, open vegetation is essential to ensure the accessibility of food items and favour early detection of predators (Wilson et al., 2005).

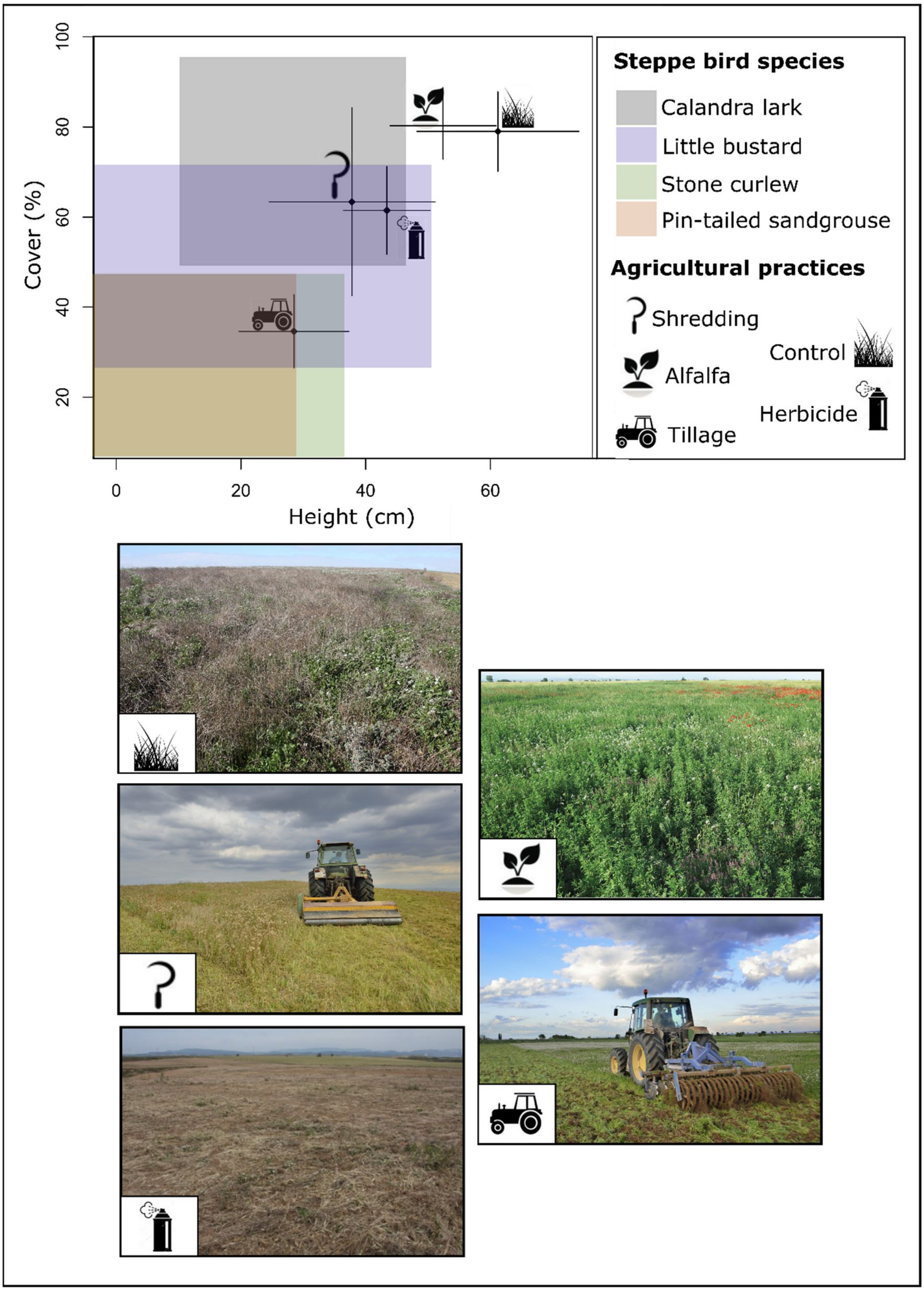

Figure 1. Range of habitat requirements in terms of vegetation structure according to bibliography (see Robleño et al., 2017), of the most important steppe bird species studied in this thesis (coloured rectangles). Average (and 95% Confidence Interval) of vegetation cover and height experimentally obtained across several fallow treatments are represented by black dots and crosses. Specific agricultural practices occurring between February and early April are represented by black silhouettes and depicted in the photos. These practices consist on cutting of the vegetation (Shredding), extensive alfalfa sowing (Alfalfa), chisel plough (Tillage), no treatment (Control), and glyphosate herbicide application (Herbicide)(Adapted from Robleño et al., 2017). Photos: Joan Estrada (Control, Alfalfa, Herbicide) and Jordi Bas (Shredding and Tillage).

However, decades of nitrogen fertilization in farmlands can prompt the over-development of above-ground biomass (Austin et al., 1993; Wilson et al., 2005), which can result in dense and tall vegetation if fallows are left unmanaged. On the other hand, farmers often over-use conventional management practices as they fear that wild weeds may hamper future crop productivity. This results in fields too cleared of vegetation, which jeopardizes the suitability of vegetation structures and food abundance (Giralt et al., 2018). Controlled and targeted agricultural management has the potential to provide optimal vegetation structure for bird species (Barré et al., 2018; Bracken and Bolger, 2006; Doxa et al., 2010), and different types of agricultural practices can potentially meet the specific requirements of steppe birds with segregated niches (Figure 1; Robleño et al., 2017; Traba et al., 2015).

4. Study area: The Lleida plain

This thesis is situated in the Lleida plain, a flat and dry area located in the eastern part of the Ebro-valley region, one of the major pseudo-steppe habitat regions in Iberia (north-eastern Spain; Figure 2; Sainz Ollero, 2013). The Lleida plain has a high conservation value for farmland bird species (Mañosa et al., 2021) and hosts > 80 % of the species considered as steppe-land birds in Spain (Traba et al., 2007). The landscape of this region historically consisted of a mosaic of annual and permanent traditional crops (wheat, barley, almond and olive trees, vineyards), fallow land and shrubland, that sustained endemic steppe wildlife communities due to its suitable habitat conditions (Mañosa et al., 2021). As in other regions from southern Europe and especially Iberia, these pseudo-steppe conditions have been threatened by several irrigation projects (Sainz Ollero, 2013). The largest impact of a system already damaged by agriculture intensification was the *Canal Segarra-Garrigues* irrigation project (2002-2010), aiming to irrigate most of the remaining pseudo-steppe habitats of the area (~70,000 hectares of land; Mañosa et al., 2021). This project triggered the mobilization of researchers, environmental, and ornithological organizations, given its severe implications for biodiversity protection (Brotons et al., 2004). As a consequence, the European Union forced the local government to implement several mitigation and compensatory measures for steppe bird populations (Mañosa et al., 2021).

4.1. Conservation actions and bird monitoring

The implementation of conservation actions in the area included a network of eight Special Protection Areas (SPA; belonging to the European protected areas network known as Natura 2000), where land use and human activities have been regulated in favor of steppe biodiversity (Mañosa et al., 2021). Conservation actions at the European level promoted within SPA have included Agri-Environmental Schemes (AES), where farmers commit voluntarily to conservation-friendly farming practices (e.g., no nocturnal work or herbicide application, promotion of fallow fields; Generalitat de Catalunya, 2020). AES in this region are intended to benefit the farmland bird community (Generalitat de Catalunya, 2020), and their voluntary nature sometimes results in low farmer uptake. An additional compensatory measure imposed by the EU was the leasing of arable fields maintained as fallow land in optimal areas for steppe birds by the Catalonian government (Mañosa et al., 2021; Sardà - Palomera et al., 2020), including fallow management to meet the specific requirements of different steppe bird species (Robleño et al., 2017). This regional conservation measure is referred to as “Targeted Fallow Management” (TFM) in this thesis.

The leasing and management of a large extent of fallow fields for conservation (an average of 2,914 ha/year during the last three years; Table 1) has brought the opportunity to perform the analyses presented this thesis. It especially allowed the study of ecological and conservation aspects of steppe bird communities by using a quasi-experimental set up at an unprecedented spatio-temporal scale. The study area of this thesis covers the eight SPAs of the Lleida plain (Figure 2), and data from the monitoring programs of the farmland and steppe bird communities occurring therein: I) the Farmdindis monitoring program, which has monitored population trends of local farmland bird species since 2010 and consists on a network of ~ 150 transects sampled every year during the birds' breeding season (Giralt et al., 2020); and II) a more specific program that aims at designing and evaluating the efficiency of the management actions (i.e., agricultural practices applied for steppe bird conservation) performed in the fallow fields leased by the Catalonian government (i.e., TFM in this thesis; Figure 2). TFM monitoring consists of bird surveys performed in the breeding season (point counts and zigzag sweep transects) and surveys of different measurements of habitat quality (i.e., orthopteran counts, vegetation plots) occurring annually since 2015 (Sardà - Palomera et al., 2020).

Table 1. Hectares of leased fallow fields per year since the start of the TFM compensatory measure in the study area (Lleida plain, Spain) from 2015 to 2020.

Year	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**
Area (ha)	920.43	1249.97	2198.98	2541.29	3058.55	3141.66

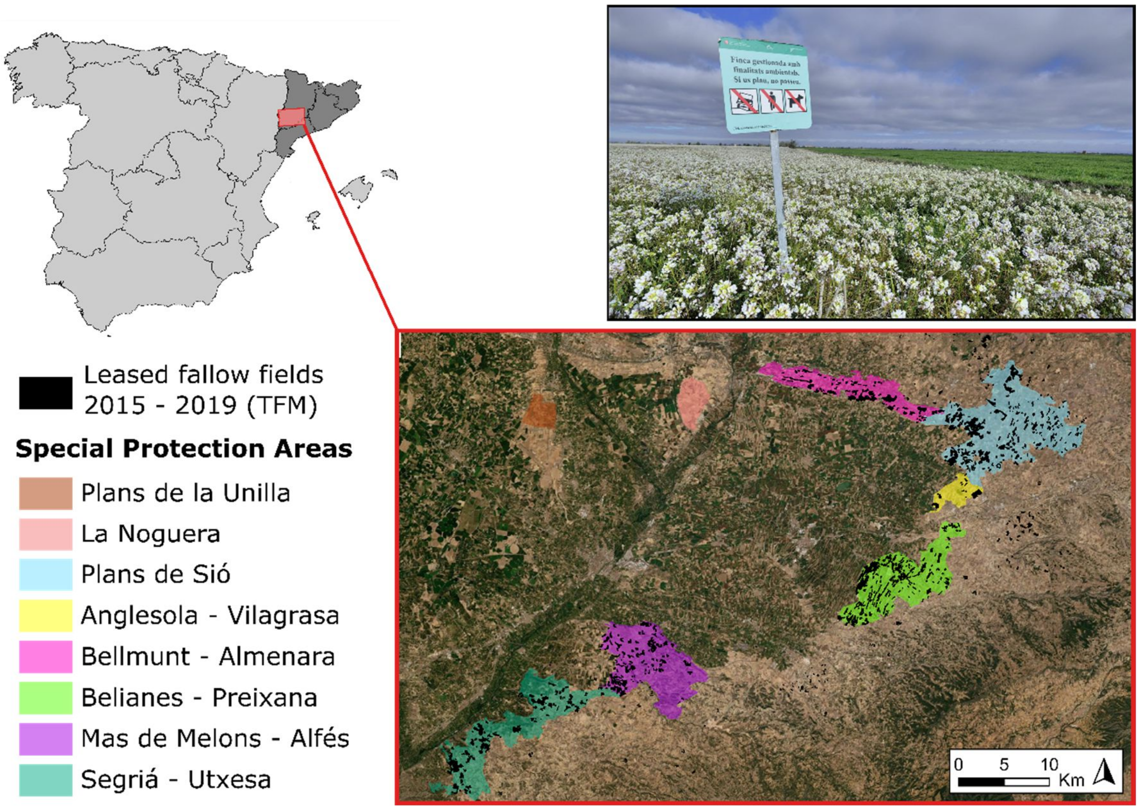

Figure 2. Location of the study area in the Lleida Plain (north-eastern Spain) and the eight SPA where data collection took place. Leased fallow fields from 2015 - 2020 as part of the compensatory actions for the *Segarra-Garrigues* irrigation channel (Targeted Fallow Management) are shown in black. At the top, a picture of one of the leased fallow fields with its identification sign in the study area (Photo: Jordi Bas).

4.2. Study species

This thesis focused on species from the farmland bird community in the study area (37 species), including – and making a special emphasis on – the endangered steppe bird guild. This thesis draws specific attention to four specialized steppe bird species occurring in the study area (Figure 3) that are ground-nesting species with different requirements (see Figure 1). These species benefit from the conservation measure promoting management actions on leased fallow fields (TFM).

The Little bustard (*Tetrax tetrax)* is a medium-sized steppe bird (40-45 cm; Cramp and Simmons, 2004) whose population declined by 50% from 2005 to 2016 in Spain, the core of its European distribution range (García de la Morena et al., 2018). The breeding male population of the Lleida plain was estimated to ~ 650 individuals in 2014, mostly occurring in the eastern SPAs (Bota et al., 2015). This species feeds on the ground, mostly on legume plants (Bravo et al., 2017). It is characterized by its sexual dimorphism, which results in niche segregation between sexes and leads to different needs for males and females in the breeding season: while females prioritize habitats that maximize concealment, males require food-rich patches and visibility for courtship (Morales et al., 2008).

The Stone curlew (*Burhinus oedicnemus)* is a medium-sized steppe bird (40-44 cm; Cramp and Simmons, 2004). It is a declining species (60 % population decline between 2002 and 2019; ICO 2019) with its core Catalonian populations inhabiting the pseudo-steppes of the Lleida plain (Mañosa et al., 2021). Despite it was only associated to natural steppes in its origins, it now thrives in arable land as long as open vegetation structure is available. Indeed, it is characterized by its strong preference for bare-ground soil, where visibility to detect predators and foraging opportunities (i.e., soil invertebrates) are maximized (Green et al., 2000).

The Calandra lark (*Melanocorypha calandra)* is a small steppe bird (18-19 cm) that mostly feeds on seeds and insects (Cramp and Simmons, 2004). Its populations occurs throughout the Lleida plain (Mañosa et al., 2021) and have increased by 31% in Catalonia since the last decade (ICO 2019). Compared to the rest of the steppe bird guild, this species shows a more generalist behaviour in terms of vegetation structure (McMahon et al., 2010), which sees to buffer the effects of agricultural intensification on its populations.

The Pin-tailed sandgrouse (*Pterocles alchata)* is a medium-sized steppe bird (31-39 cm; Cramp and Simmons, 2004) that mainly feeds on seeds on the ground (Martín et al., 2010). The breeding population in the Lleida plain consists of 60-80 individuals (Giralt et al., 2019). It is characterized by a high dependency on fallows and natural vegetation areas (i.e., sparse bushy or herbaceous vegetation; Benítez-López et al., 2017; Tarjuelo et al., 2020a), and its populations in the Lleida plain have experienced a slight increase since the start of TFM (Giralt et al., 2019).

Figure 3: Main steppe bird species studied in the Lleida plain (Catalonia) during this thesis. From left to right: Little bustard, Stone curlew, Calandra lark (Photos: Jordi Bas) and Pin-tailed sandgrouse with GPS tracking device (Photo: Lluis Culleré)

OBJETIVES AND STRUCTURE

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The ultimate objective of this thesis is to provide applied recommendations to improve the conservation status of the vulnerable farmland and steppe bird communities in Europe. I therefore focused on key steps involved in the conservation planning process, from the population monitoring stage to the design, implementation, and evaluation of conservation measures (Figure 3).

The specific objectives of this thesis are:

1. To evaluate the role of promoting not only fallow land, but also its management, for steppe bird conservation. Specifically, to study the potential of applying diverse agricultural practices on fallows (fallow management) to maximize the efficiency of fallow land as a conservation measure.
2. To analyse the efficiency of current conservation measures on fallow fields promoted by the European Common Agricultural Policy (CAP) and provide specific recommendations for the upcoming CAP reform.
3. To assess the importance of accounting for imperfect detection when estimating bird abundance and population trends in open agricultural landscapes, and to obtain robust abundance and population trend estimates for the farmland bird community of the Lleida plain.

These specific aims are addressed in detail by the four following chapters:

In **Chapter I**, I studied the importance of accounting for imperfect detection when estimating bird population trends. Heterogeneous detection across years and observers could bias population trend estimates if imperfect detection is not accounted for (Kéry and Schmidt, 2008). I tested if that was the case in open farmland landscapes by using the survey design of the Farmdindis monitoring program and species-specific Hierarchical Distance Sampling (HDS) models. HDS models also allowed me to obtain robust abundance estimates (within each SPA) and population trend estimates for the study species. Robust population trend estimates are key in monitoring programs, as population trends are the foundation for determining the conservation status of species (IUCN categories), and to evaluate the success of conservation measures (Figure 3).

In **Chapter II**, I used the same survey design and methodological approach to assess the effectiveness of conservation measures promoted by the European Common Agricultural Policy (CAP) for supporting farmland birds. I built a HDS community model to test the ability of large-scale (Greening, Agri-Environmental schemes) and regional (Targeted Fallow Management, TFM) conservation measures to increase the abundance of the farmland bird community. Among the three measures, TFM was the most specific management approach as it is specifically designed to meet the ecological requirements of target steppe bird species. Thus, I expected TFM to be more successful in increasing steppe bird – and possibly community – abundance, as compared with the other more generic conservation measures. My ultimate goal was to provide timely recommendations for the upcoming CAP reform (CAP post-2020).

In **Chapter III,** I aimed at quantifying the mechanisms involved in the success of TFM to support steppe bird populations, by focusing on Little bustard, Calandra lark, and Stone curlew. Steppe bird habitat selection is known to be influenced by vegetation structure, so different agricultural practices in fallow fields (applied a limited number of times, before the breeding season) could fulfil their requirements by shaping the vegetation (Figure 1; Robleño et al., 2017). Thus, I used path analyses to identify how bird occurrence in fallow fields was affected by different agricultural practices (fallow management) through changes in vegetation structure and food availability, as compared with unmanaged fallow fields. Because steppe birds have different ecological niches, I aimed at identifying the optimal agricultural practices fulfilling the requirements of each of the study species.

Finally, in **Chapter IV** I studied the role of fallow land and its management (TFM) on seasonal habitat selection patterns, using the Pin-tailed sandgrouse as a case study. I used the first GPS data obtained on this sensitive species to identify and quantify their habitat selection patterns in relation to the temporally dynamic availability of suitable habitat. Pin-tailed sandgrouse requires short vegetation cover and height, and the rapid development of cereal vegetation in spring reduces the amount of suitable habitat, likely creating a seasonal bottleneck in the availability of suitable habitats. Fallow land and natural vegetation present relatively stable and suitable vegetation all year long, thus, they could buffer the impact of the habitat bottleneck. I also aimed at identifying potential energetic drawbacks of the bottleneck by exploring the movement patterns of the studied individuals.

The four chapters of this thesis constitute the following original publications and submitted manuscripts:

Chapter 1:

Sanz-Pérez, A., Sollmann, R., Sardà-Palomera, F., Bota, G., Giralt, D., 2020. The role of detectability on bird population trend estimates in an open farmland landscape. *Biodiversity and Conservation,* 29, 1747–1765.

Chapter 2:

Sanz-Pérez, A., Sardà-Palomera, F., Bota, G., Sollmann, R., Pou, N., Giralt, D. The potential of fallow management to promote steppe bird conservation within the next EU agricultural reform. *Accepted in Journal of Applied Ecology*

Chapter 3:

Sanz - Pérez, A., Giralt, D., Robleño, I., Bota, G., Milleret, C., Mañosa, S., Sardà - Palomera, F., 2019. Fallow management increases habitat suitability for endangered steppe bird species through changes in vegetation structure. *Journal of Applied Ecology,* 56, 2166–2175

Chapter 4:

Sanz - Pérez, A., Tarjuelo, R., Giralt, D., Sardà - Palomera, F., Mougeot, F., Santisteban, C., Pérez, M., Bota, G. High-resolution tracking data reveals the importance of fallow land during a seasonal habitat bottleneck for a steppe-land specialist. *Manuscript in preparation*

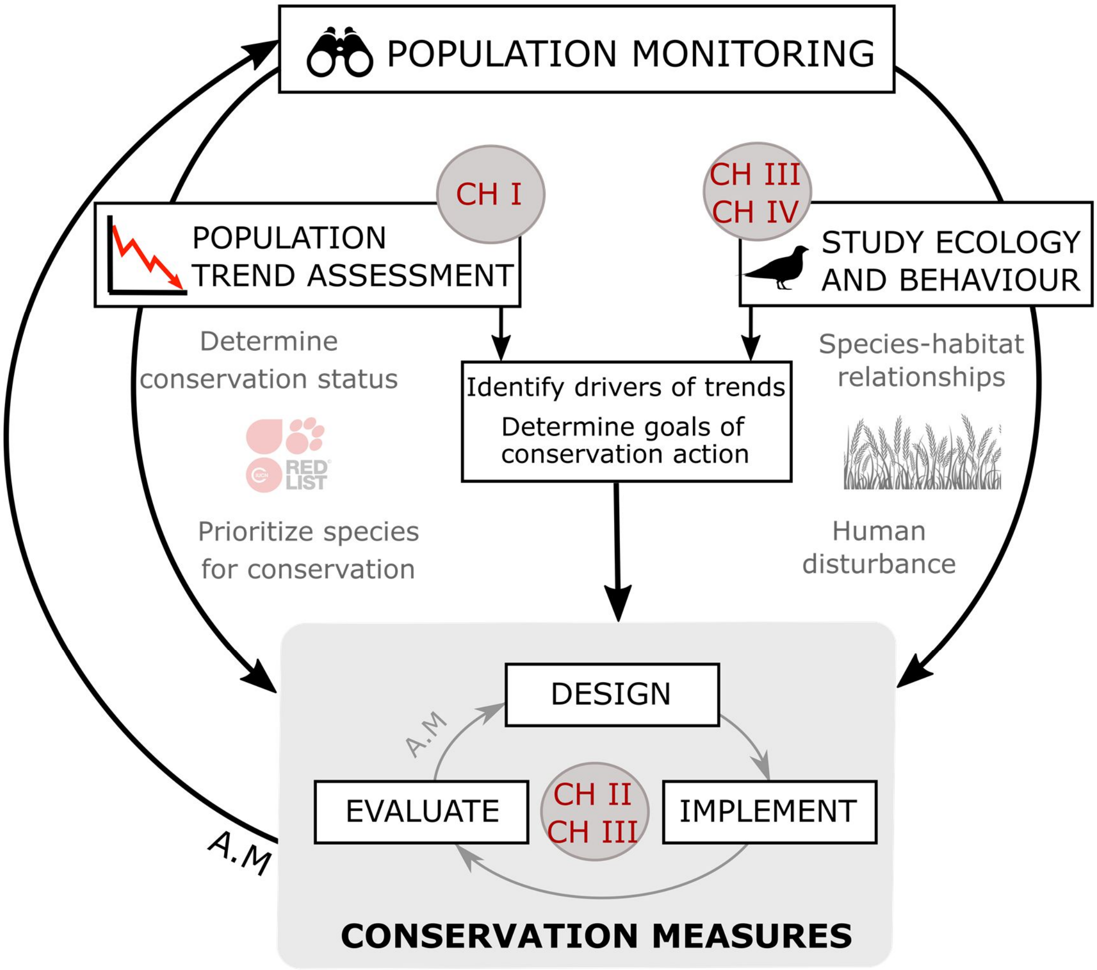

Figure 3. Contribution of this thesis to some of the key stages of conservation planning. The thesis chapters contributing to each stage are shown in red within the grey circles: I covered the importance of accounting for imperfect detection when estimating population trends within monitoring programs (Chapter I) and the ecological mechanisms behind population trends of vulnerable species (Chapter III and IV). Acknowledging the ecological reasons behind reliable population trend estimates is the base to design, implement, and evaluate species-specific conservation measures (Chapter II and III). The conservation planning process should be adjusted and improved through Adaptive Management (A.M).

Informe de los
DIRECTORES

INFORME DE LOS DIRECTORES

Como directores de la tesis doctoral “Integrating agriculture and conservation: The value of fallow land and its management for farmland and steppe bird conservation” realizada por Ana Sanz Pérez, presentamos el siguiente informe sobre la contribución de la doctoranda en las publicaciones en coautoría que componen la tesis:

Capítulo 1: Sanz-Pérez, A., Sollmann, R., Sardà-Palomera, F., Bota, G., Giralt, D., 2020. The role of detectability on bird population trend estimates in an open farmland landscape. *Biodiversity and Conservation,* 29, 1747–1765.

Contribución de la doctoranda: Participación en el diseño del estudio. Realización de análisis estadísticos y redacción del manuscrito.

Acerca de la revista: *Biodiversity and Conservation* en el Journal Citation Reports (JRC) de 2019 tiene un índice de impacto de 2.93. Se encuentra en el número 11 de 58 en el área de conservación (1° cuartil) y en el número 47 de 169 en el área de ecología (2° cuartil).

Capítulo 2: Sanz-Pérez, A., Sardà-Palomera, F., Bota, G., Sollmann, R., Pou, N., Giralt, D. The potential of fallow management to promote steppe bird conservation within the next EU agricultural reform. Accepted in *Journal of Applied Ecology*

Contribución de la doctoranda: Participación en el diseño del estudio. Realización de análisis estadísticos y redacción del manuscrito.

Acerca de la revista: *Journal of Applied Ecology* en el Journal Citation Reports (JRC) de 2019 tiene un índice de impacto de 5.84. Se encuentra en el número 4 de 58 en el área de conservación (1° cuartil) y en el número 15 de 169 en el área de ecología (1° cuartil).

Capítulo 3: Sanz - Pérez, A., Giralt, D., Robleño, I., Bota, G., Milleret, C., Mañosa, S., Sardà - Palomera, F., 2019. Fallow management increases habitat suitability for endangered steppe bird species through changes in vegetation structure. *Journal of Applied Ecology,* 56, 2166–2175

Contribución de la doctoranda: Participación en el diseño del estudio. Realización de análisis estadísticos y redacción del manuscrito.

Acerca de la revista: *Journal of Applied Ecology* en el Journal Citation Reports (JRC) de 2019 tiene un índice de impacto de 5.84. Se encuentra en el número 4 de 58 en el área de conservación (1° cuartil) y en el número 15 de 169 en el área de ecología (1° cuartil).

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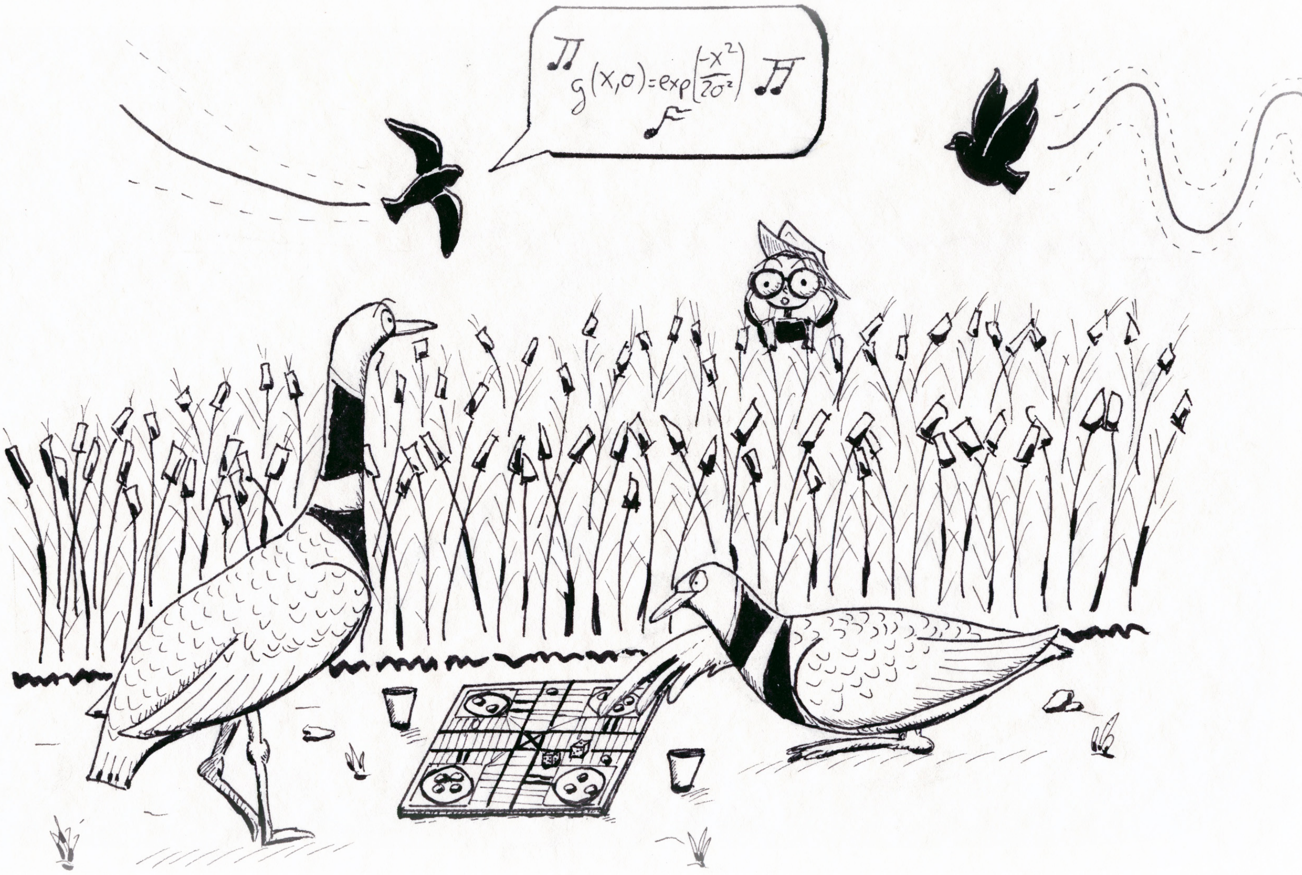
Chapter I:

The role of detectability on bird population trend estimates in an open farmland landscape

Biodiversty and Conservation, 2020. 29, 1747–1765.

Ana Sanz-Pérez, Rahel Sollmann, Francesc Sardà-Palomera, Gerard Bota, David Giralt



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The role of detectability on bird population trend estimates in an open farmland landscape

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ABSTRACT

Monitoring programs are key to determine bird population trends and to assess environmental policies, and therefore are central to conservation biology. The European approach commonly used to estimate bird population trends (TRends and Indices for Monitoring data, hereafter TRIM) has proved useful to fulfil this task, yet it fails to account for imperfect detection and assumes constant detectability across years. We tested the role of detectability for population trend estimation in an open Mediterranean farmland context, which is a dynamic landscape likely to undergo yearly changes in detectability, by using data of 30 bird species over a nine-year study period. We evaluated species-specific population trends under the TRIM approach and hierarchical distance sampling models (hereafter HDS) that estimate true abundance by accounting for imperfect detection. When comparing both methods, 13 species presented differences in population trend estimates between TRIM and HDS models. Moreover, detectability was not constant across the bird community: observer and year affected detection, and these effects varied among species. Our study highlights the importance of accounting for imperfect detection in bird monitoring programs to ensure reliable trend estimates, providing a first insight for an open farmland bird community. Aside from trend estimates, our HDS model may prove useful as a tool to obtain site-specific abundance estimates (for instance, within Special Protection Areas) and trend probabilities of bird populations.

Keywords: Detectability, Population trend, Farmland birds, Hierarchical distance sampling, TRIM, Abundance

INTRODUCTION

Wildlife populations are in decline globally and a proper understanding of population dynamics may be decisive for the ongoing battle against biodiversity loss (Pimm et al. 2014). Among others, farmland bird species have been severely affected by global change, with agricultural intensification being the major cause of their declines worldwide, and especially throughout Europe (Donald et al. 2001; Voříšek et al. 2010), where most of the exploitable surface is dominated by agriculture (Ormerod and Watkinson 2000). Conservation measures such as agri-environmental schemes (AES; Kleijn and Sutherland 2003) aim at buffering the negative impact of agriculture intensification on bird populations. Population monitoring is essential to detect population changes, evaluate the effectiveness of such measures and inform future conservation action (Donald et al. 2007).

Bird monitoring programs are numerous across Europe (Voříšek et al. 2010) and elsewhere (Bart 2005). Obtaining results on population trends at the continental scale is challenging because of variation in field methods among monitoring programs, which are usually organized at the national level. Despite the challenge posed by integrating this information, much progress has been made in the last two decades (e.g., for the U.S. and Canada: Bart 2005; for Europe: Voříšek et al. 2010). The Pan-European Common Bird Monitoring Scheme (PECBMS) was created as an initiative to pool population trend information from national bird breeding surveys across Europe and has provided robust evidence of farmland bird population declines (Voříšek et al. 2010).

PECBMS produces national and supranational indexes, as well as multi-species indicators (Klvaňová and Voříšek 2007), by using the TRIM software (TRends and Indices for Monitoring data; Pannekoek et al. 2005). TRIM provides a user-friendly interface (i.e., the TRIM program and the recently developed 'rtrim' package; Bogaart et al. 2018) and uses Generalized Estimating Equations (GEE) to fit log-linear models to bird count data, while dealing with overdispersion and serial correlation (Pannekoek et al. 2005). TRIM has proved useful for estimating species-specific population trends (e.g., Gómez-Catasús et al. 2018), linking population trends with their drivers (e.g., to quantify the effect of land abandonment on bird population declines; Herrando et al. 2014), and assesing conservation status for IUCN Red List assessments (Criterion A; Maes et al. 2015).

Although TRIM has been very useful for analysing time-series data of bird surveys, its population trend estimates are based on raw bird counts. Yet, birds cannot be counted with certainty because detection is always imperfect to some extent (Kéry 2008), and therefore accounting for probability of detection lower than 1 is necessary to ensure unbiased estimates of population size. Counts may provide reliable information about population trends if detection probability remains constant over time (Thompson 2002; Kéry and Schmid 2004). In spite of the broad consensus that the assumption of perfect or constant detectability is often violated in bird (and other wildlife) surveys (e.g., Diefenbach et al. 2003; Kéry et al. 2009), this assumption is rarely checked, and the effects of its violation are rarely evaluated (but see Camp et al. 2016).

Indeed, heterogeneity in detection over time may have a variety of sources, such as weather conditions (Bas et al. 2008), year-specific changes in bird behaviour (Newson et al. 2013), fluctuations in population sizes (Kéry and Schmid 2004) or differing observer skills (e.g., in monitoring programs that rely on volunteers; Diefenbach et al. 2003; Johnston et al. 2018). Likewise, spatial heterogeneity in detection may occur when surveys are placed in different habitat types (e.g., Kéry et al. 2009) or are subject to different treatments (Archaux et al. 2012). Detectability is also species-specific (Si et al. 2018), as it varies with factors such as body size (Anderson et al. 2015) or singing behaviour (Alldredge et al. 2007). Hence, homogeneous detectability of one species cannot always be extrapolated to the entire community.

Whereas techniques that fail to take detectability into account remain popular among bird studies and monitoring programs (Rosenstock et al. 2002; Klvaňová and Voříšek 2007), there are several modelling approaches that, when combined with appropriate survey designs, allow for estimation of population parameters taking into account imperfect detection. One of these approaches is distance sampling, which is a widely used technique to estimate abundance of wild animal populations (Buckland et al. 2004; see Rosenstock et al. 2002 for application in bird surveys). Distance sampling deals with the observation component of ecological field data (i.e., imperfect detection) by estimating the probability of detection (p) of an object as a function of its distance from the observer (i.e., the detection function; Buckland et al. 2001, 2004).

Hierarchical Distance Sampling (hereafter HDS; Royle et al. 2004) consists of the analysis of distance sampling data across multiple survey sites. HDS explicitly conditions the observation process on the underlying ecological process and further allows for modelling spatial variation in the detection function and abundance as a function of site-specific covariates.

Accounting for imperfect detection has proved important to obtain unbiased estimates of population trends in bird species (see Bart 2005 for marsh birds; Camp et al. 2016 for forest birds). However, few studies have tested the role of detectability for common birds (but see Newson et al. 2013), and to our knowledge none have focussed on the role of detectability on population trends of birds inhabiting open farmland landscapes, or specifically tested the effect of temporal variability in detection. While farmlands are open environments, which likely have a higher detectability than more closed habitat types (e.g., woodlands), these landscapes are dynamic and likely to undergo yearly changes (e.g., due to changes in crop types; Merriam 1988) that could cause variable detectability across years.

Here, we compare estimates of bird population trends in a farmland landscape from a TRIM and a HDS model, in order to test the effect of time-varying and imperfect detectability on trend estimates. Specifically, we studied the population trends of 30 bird species from 2010 to 2018 in an open farmland landscape of north-eastern Spain, where the coexistence of species of conservation interest has led to the designation of Special Protection Areas (SPA), and the application of generic (i.e., Agri-Environment Schemes, AES) and specific (e.g., Sanz-Pérez et al. 2019) conservation measures. Aside from the local monitoring program of our study (FarmDINDIS), that produces its own dataset, in this area there is a national (SACRE 2018) and a regional (ICO 2018) bird monitoring program that estimate population trends using TRIM. Our HDS model, which estimates true abundance and its changes across space and time, builds on the Binomial N-mixture model of Royle (2004) and the open-population HDS model of Sollmann et al. (2015), while also including the serial correlation structure from Johnson and Hoeting (2003) and an overdispersion parameter.

We predict that even in an open farmland landscape, bird detectability may vary among observers, weather conditions, and years, and that as a consequence, estimates of population trends will differ between TRIM and HDS models. Because of their different ecology and life-history traits that can influence detection, we expect different responses among species. In addition, we demonstrate how the actual abundance estimates from the HDS model can be used to assess population status of species of conservation concern within SPA. Evaluating the reliability of trend estimates from standard European bird monitoring programs is particularly important in agricultural landscapes, as farmland bird population trends are known to be bound to agricultural change (Gates and Donald 2000) and farmland is the dominant land surface in most European countries (e.g., 65% in Denmark; Ormerod and Watkinson 2000). Reliable trend estimates and true abundance information within SPA is timely now that the upcoming Common Agricultural Policy (CAP) reform (2021–2028) will bring new management regimes and conservation action.

MATERIAL AND METHODS

Study area and design

This study was conducted in the Lleida steppe plains (~ 3580 km2, NE Spain; Fig. S1, SI 1). The area is an open and flat agricultural landscape with semiarid Mediterranean climate and low annual rainfall (between 300 and 450 mm; Calvet et al. 2004), located 200–400 meters (m) above the sea level. Traditional agriculture practices in this area consist of extensive cultivation of winter cereal crops, annual fallow fields, and woody crops (olive and almond), interspersed with small patches of sparse natural shrub land.

From 2010 to 2018, a total of 191 line transects (Table S1; Fig. S1, SI 1) were sampled annually in May. Due to logistic limitations, only 57% of the transects was surveyed every year (transects were surveyed on average: Mean ± SD = 7.12 ± 2.95 years). Transects were 500 m long and were randomly placed throughout the whole study area, located on nonasphalted tracks to avoid trespassing on private farmland, and with a minimum separation of 1000 m to ensure independence of the data (Buckland et al. 2001). Eighty percent of the transects were located within Special Protection Areas (SPA) devoted to bird conservation (i,e., characterized by extensive agriculture; Fig. S1, SI 1; Brotons et al. 2004).

Bird surveys

Bird surveys were performed for the FarmDINDIS bird monitoring program, which aims at collecting information about local farmland bird populations and habitat characteristics in the study area. Bird surveys were conducted by 13 different professional observers (4 different observers on average per year; Table S1, SI 1) with experience in the identification of bird species in farmland landscapes. Observers conducted the surveys in the morning from 6 to 10 a.m. Surveys were not performed under the rain, when wind speed was above 20 km/h, or temperature was above 30 °C. Each survey was conducted by a single observer who walked at a slow pace (~ 1.5 km h − 1 with occasional pauses) along the line transect, and collected data of all bird species detected following a distance sampling protocol (Buckland et al. 2001). Birds were recorded on both sides of the transect when first observed, and the perpendicular distance from the transect line to a bird was visually estimated. Because distance sampling assumes independence of individual observations, but several of our study species often occur in groups, we considered groups of birds as the unit of observation, and recorded group size along with distance to the centre of the group. Observers recorded individuals detected visually or aurally, reported the mode of detection and marked the detection location on a map of the transect surroundings. Distance sampling assumes that distances are measured without error, which is unrealistic in a field setting. Grouping observations into distance bins can overcome distance estimation error; thus we assigned observations into five distance classes (0–25 m; 25–50 m; 50–100 m; 100–200 m; 200–500 m) with the guidance of a field map containing information on the borders of fields and type of crops surrounding the transect. The maximum truncation distance at which observations where recorded (i.e., the strip width) was 500 m. Aside from bird data, observers collected weather information at each transect that could affect the detection process, such as temperature, wind speed, clouds cover, and time of the day.

Trend assessment

We studied population trends of 30 bird species from 2010 to 2018 (Fig. 1). These species had different characteristics, ranging from small passerines (e.g., Great tit Parus major) to large non-passerines (e.g. Stone curlew Burhinus oedicnemus). We included in the analysis all species potentially breeding or foraging in the study area, with a minimum of 100 observations distributed across years. We evaluated population trends by using two different statistical approaches: a TRIM model, based on yearly population indexes derived from bird counts, and a HDS model based on abundance estimates corrected for imperfect and varying detection. For each species, we compared the population trend estimates provided by both models by assessing the direction of the trend coefficients (see below) and its significance. We considered trends significant when 95% Confidence Intervals (CI; TRIM) or 95% Bayesian Credible Intervals (BCI; HDS) did not contain zero. While we acknowledge that frequentist confidence intervals and Bayesian credible intervals do not have the exact same interpretation, we found this to be the most consistent way to assess statistical significance across the two approaches. To exploit the attributes of Bayesian trend estimation we also calculated the posterior probability of a negative trend for HDS results (Wade 2000). All analyses were performed in R version 3.5.1 (R Core Team 2018).

TRIM model

We fitted the log-linear time effects model (TRIM Model 3; Pannekoek et al. 2005), which estimates separate parameters (α, β) for each site *j* and year *t* and can be written as:

$$\ln(\mu_{jt}) = \alpha_j + \beta d_t + \gamma_t \quad (1)$$

where μ is the expected count (not corrected for detectability) at site *j* at time *t*, α is a fixed site (transect) effect, and d_t represents the centred year of study. In this version of the model, the temporal trend is decomposed into a linear trend parameter (β), that we used as an estimate of average population change, and a fixed effect (γ) that describes the deviations from the linear trend for each year. The parameter γ was set to zero in year 1 to make the model identifiable. This model investigates both whether the overall linear trend is significant and for which time-points significant deviations from the linear trend occur.

The estimation approach used by this TRIM model is generalized estimating equations (GEE) (Pannekoek et al. 2005). This method accounts for drawbacks typically found in trend analyses of counts such as overdispersion and serial correlation (Pannekoek et al. 2005).

We assessed the significance of the population trend for a given species by determining whether the 95% Confidence Interval (CI) associated with the overall trend parameter β overlapped zero (for comparison purposes with HDS). We extracted the total yearly expected counts and imputed counts (which equal the observed counts for surveyed site-year combinations and the expected count for un-surveyed site-year combinations, i.e., missing counts; Pannekoek et al. 2005) to plot expected and realized population trends (Fig. 2; Fig S3, SI 1). All TRIM analyses were performed with the 'rtrim' R package version 2.0.6 (Bogaart et al. 2018).

HDS model

We fitted a HDS model (Fig. S2, SI 1; Hobbs and Hooten 2015), where the process component describes local abundance N at a given transect *j* and year *t* as a random variable following a Poisson distribution:

$$N_{jt} \sim Poisson(\lambda_{jt}) \quad (2)$$

Here, λ_{jt} is the expected abundance of birds/bird groups and can be modelled as a function of an intercept and site-specific covariates. In order to obtain estimates of population change that were comparable with estimates from the TRIM approach, we built the following abundance model:

$$\log(\lambda_{jt}) = \alpha.site_j + \beta.year \times Year_t + \gamma.lam.year_t + w_{jt} \quad (3)$$

$$\alpha.site_j \sim Normal(\mu_{site}, \sigma_{site})$$

$$\gamma.lam.year_t \sim Normal(0, \sigma_{lam.year})$$

$$w_{j,1} = \varepsilon_{j,1}/\sqrt{1-\rho^2} \text{ for t = 1, and } w_{jt} = \rho * w_{j,t-1} + \varepsilon_{jt} \text{ for t >= 2}$$

$$\varepsilon_{jt} \sim Normal(0, \sigma_\varepsilon)$$

where $\alpha.site_j$ is a random site (transect) intercept, with hyperparameters μ_{site} and σ_{site} . Time is decomposed into a linear trend parameter ($\beta.year$), and a random year effect ($\gamma.lam.year_t$) that describes yearly deviations from the linear trend (i.e., by following a zero-mean normal distribution with variance $\sigma_{lam.year}$). The $Year_t$ covariate ranged from 0–8 (from the first to the 9th year of study). As for the TRIM model (see above), the parameter $\gamma.lam.year_t$ is set to zero for year 1 ($Year_t$= 0) to make the model identifiable. We accounted for serial correlation by using an autoregressive model of order 1 [AR(1) following Johnson and Hoeting (2003)]. This temporal structure was included in the parameter w, which accounts for both overdispersion and serial autocorrelation by partitioning the extra-residual variance into a serial correlation ($\rho * w_{j,t-1}$) and overdispersion (ε_{jt}) component. We estimated yearly expected and realized abundances (Fig. 2; Fig S3, SI 1) as derived parameters by summing λ or N, respectively, over all sites for a given year, and we estimated abundances within transects in SPA by summing λ over the sites belonging to each of the SPA for a given year (Table S5). Because our unit of observation was bird groups, we converted estimates of group abundance to actual abundance by multiplying λ_{jt} with average group size.

The observation model links the process (biological) model for N_{jt} (2,3) to the field data by introducing an observation error induced by imperfect detection. Specifically, the number of individuals (or groups) of a given species observed at transect *j* and year *t*, Y_{jt} , is described as a Binomial random variable:

$$Y_{jt} \sim Binomial(N_{jt}, p_{jt}) \tag{4}$$

where p is the probability of detection, which is estimated using the distance sampling framework. In distance sampling, p is assumed to be 1 at the transect line, and decreases from the observer as a function of distance *x* following a detection function (Buckland et al. 2001). We chose a half normal detection function as observation model:

$$g(x,\sigma) = exp\left(\frac{-x^2}{2\sigma^2}\right)$$

where σ is the scale detection parameter and can be modelled on the log scale as a function of an intercept and site-specific covariates. For some species, the half-normal detection function provided poor model fit and in these cases we used a hazard rate detection function instead:

$$g(\mathrm{x},\sigma)=1-exp\left(-\left(\frac{\mathrm{x}}{\sigma}\right)^{-\mathrm{b}}\right)$$

where b is the shape parameter. Preliminary analyses revealed that the most relevant detection covariates were observer identity and temperature (°C). Therefore, we fit the following model for σ:

$$\log\sigma_{jt} = \alpha.obs + \beta.temp \times Temp_{jt} + \gamma.sig.year_t \tag{5}$$

$$\alpha.obs \sim Normal\ (\mu_{obs}, \sigma_{obs})$$

$$\gamma.sig.year_t \sim Normal\ (0, \sigma_{sig.year})$$

We included observer as a random intercept ($\alpha.obs$) with hyperparameters μ_{obs} and σ_{obs} . $\beta.temp$ is the coefficient for the temperature variable ($Temp$) . In order to detect differences in detection probability among years (e.g., due to fluctuations in weather conditions or bird behaviour), we included the random effect $\gamma.sig.year_t$, with zero-mean and variance $\sigma_{sig.year}$.

Under the half-normal detection function and with binned distance observations, detection probability for each distance bin k can be calculated as the integral of $g(x)$ over the break points of k:

$$p_k = \frac{\int_{b_k}^{b_{k+1}} g(x)dx}{v_k}$$

where b are the $K + 1$ breakpoints of the K distance categories and v_k is the width of the k-th distance category (see also Sollmann et al. 2016). Under the hazard rate detection function, detection probability p for each distance bin k was approximated as p at the midpoint distance of the bin. In our study, v_k was 25, 25, 50, 100, and 300 m from the first to the fifth distance category, respectively. Because individuals are assumed to be uniformly distributed around the transects, the individual probability of occurrence in a distance bin Ψ_k is

$$\Psi_k = \frac{v_k}{strip\ width}$$

where the strip width is 500 m. Therefore, the cell probability of detection π_k is $p_k \times \Psi_k$, and the overall probability of detection (p_{jt} from the Binomial distribution, Eq. 4) is the sum over all π_k (see also Sollmann et al. 2015; Kéry and Royle 2016).

We conducted parameter estimation using a Bayesian MCMC approach in JAGS version 4.3.0 (Plummer 2003), accessed through the 'jagsUI' R package version 1.5.0 (Kellner 2018). JAGS model codes are available in SI 2 and SI 4. We used non-informative or weakly informative priors on all parameters. For the random effects, we chose uniform (− 10, 10) for μ_{site} and μ_{obs} , and uniform (0, 10) for σ_{site}, σ_{obs}, $\sigma_{lam.year}$ and $\sigma_{sig.year}$. We chose normal (0, 0.001) for $\beta.year$ and $\beta.temp$, where 0.001 is the precision, τ . Finally, we chose uniform (0, 3) and uniform (− 1, 1) for the overdispersion σ_ε and serial correlation ρ parameters, respectively. We ran three parallel Markov chains with a number of iterations ranging from 170,000 to 2,000,000, burn-in ranging from 5000 to 300,000, and thinning chains from 5 to 50 depending on the species (see SI 3 for further details on model convergence). With this, we ensured convergence of structural parameters of all the single-species models according to the Gelman-Rubin statistic (i.e., values < 1.1; Gelman et al. 2013).

We tested whether the abundance and detection components of the model fitted the data by using Bayesian *P*-values (Gelman et al. 1996) based on Freeman–Tukey residuals, and determined model lack of fit when Bayesian *P*-values were < 0.1 or > 0.9 (SI 3; see also Sollmann et al. 2016). The observation component with a half-normal detection function only fit the data for 7 species (Table S6, SI. 3). For 17 species, we improved model fit by using a hazard rate detection function for modelling detection (Table S6, SI 3; JAGS model code in SI 4). Changing the detection function did not result in a better fit for 6 species (Table S6, SI 3), which were therefore excluded from the analysis.

We reported parameter estimates as the posterior means and associated standard deviations. We also reported the 95% Bayesian Credible Interval (BCI), and considered parameters as significant when the 95% BCI did not overlap zero. Finally, for the trend parameter beta, we calculated the posterior probability of a negative population trend as the proportion of all posterior samples with values below zero (Fig. 5). Because posterior distributions for the standard deviation from the observer and year random effects (σ_{obs} , $\sigma_{sig.year}$) (uniform(0,10)), were skewed (Figs. 3, 4), we also reported the posterior mode (Figs. 3, 4) and used both (the mode and the mean) to draw conclusions about these variables. We considered that a given species had a higher variability among observers and/or years (i.e., as compared with the rest of the studied species), when both the SD estimates of the posterior mean and mode were above the 3rd quantile of the estimates distribution across all species (Table S3, SI 1).

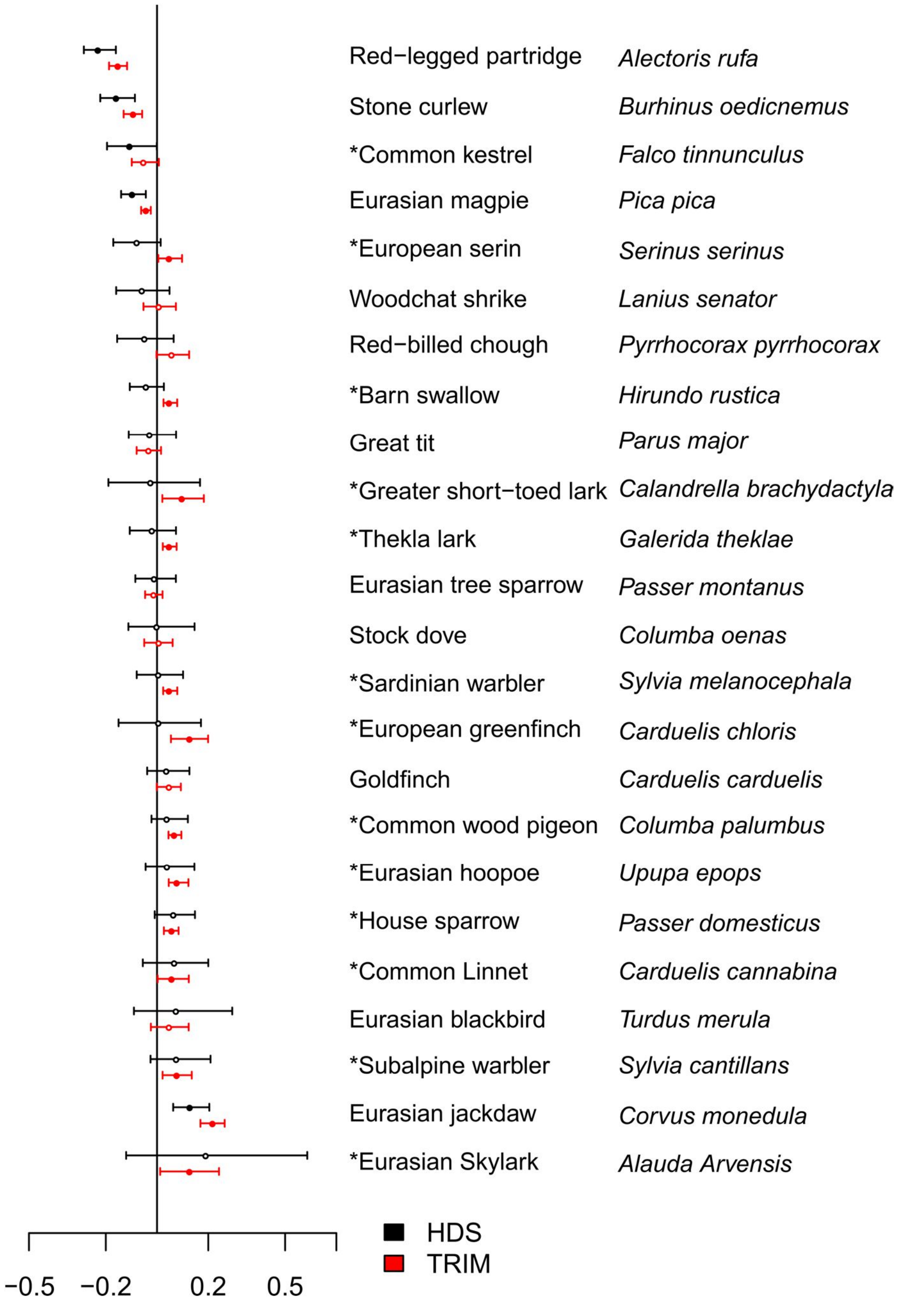

Fig. 1 Trend coefficient obtained by using HDS models (black) and TRIM models (red) on data of 24 bird species collected from 2010–2018 in Lleida (Spain). The trend coefficient of 6 species were discarded due to lack of model fit (Methods section). Filled circles show significant trends (95% Bayesian Credible Interval (HDS) or Confidence Interval (TRIM) not overlapping zero). Species for whom there are differences in the significance results obtained with both methods are indicated by an asterisk "*"

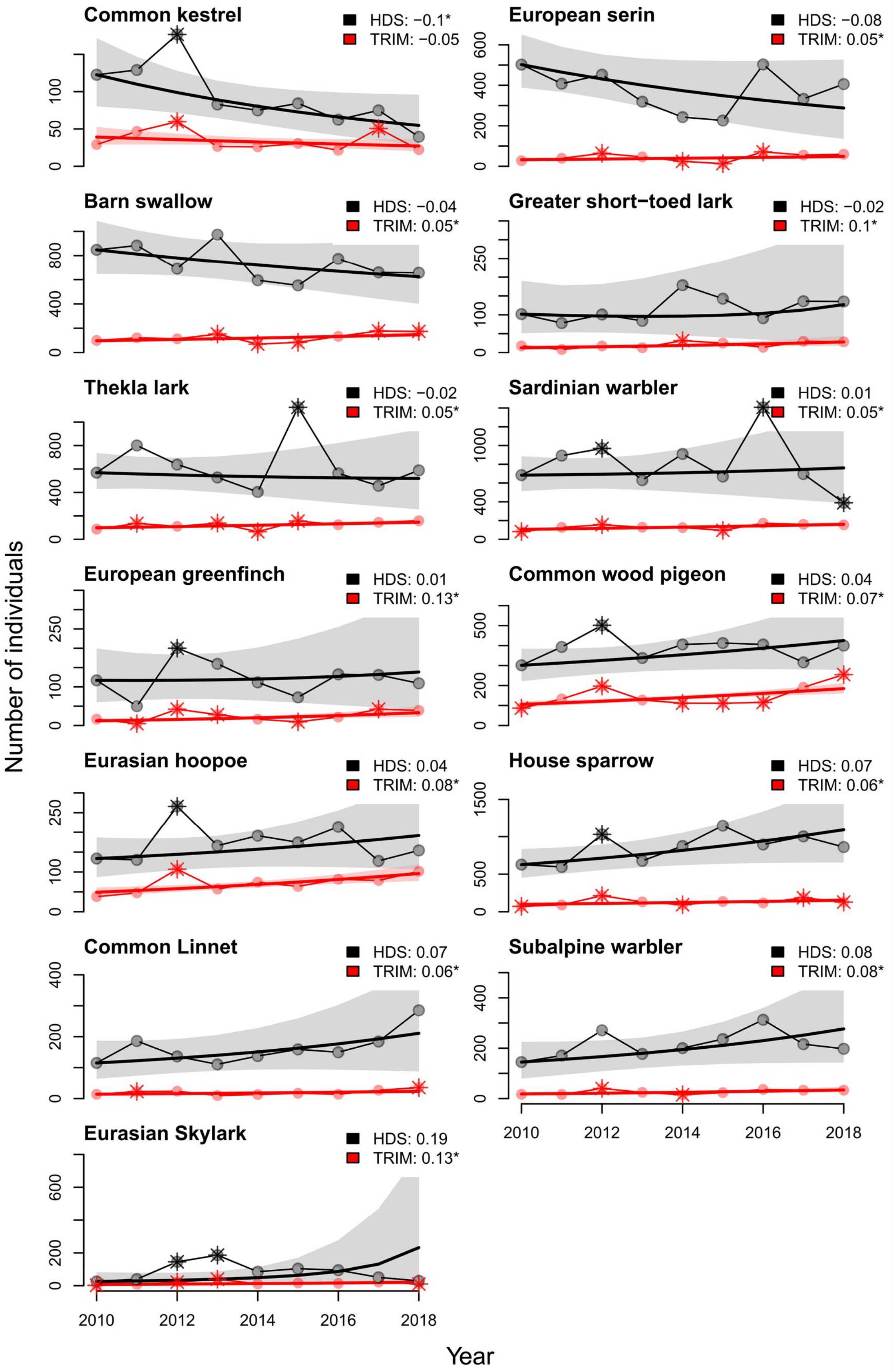
Common kestrel
HDS: −0.1*
TRIM: −0.05
European serin
HDS: −0.08
TRIM: 0.05*
Barn swallow
HDS: −0.04
TRIM: 0.05*
Greater short−toed lark
HDS: −0.02
TRIM: 0.1*
Thekla lark
HDS: −0.02
TRIM: 0.05*
Sardinian warbler
HDS: 0.01
TRIM: 0.05*
European greenfinch
HDS: 0.01
TRIM: 0.13*
Common wood pigeon
HDS: 0.04
TRIM: 0.07*
Eurasian hoopoe
HDS: 0.04
TRIM: 0.08*
House sparrow
HDS: 0.07
TRIM: 0.06*
Common Linnet
HDS: 0.07
TRIM: 0.06*
Subalpine warbler
HDS: 0.08
TRIM: 0.08*
Eurasian Skylark
HDS: 0.19
TRIM: 0.13*
Number of individuals
Year
2010
2012
2014
2016
2018
0
50
100
200
250
400
500
600
800
1000
1500

Fig. 2 Population trend of the species that showed different significant results for the trend coefficient when using HDS models (black) and TRIM models (red), based on data from 2010–2018 in Lleida, Spain. The population trend of each species is represented by a continuous line. The trend coefficients (on the log scale) are showed in the legend; asterisks beside the coefficients mark significant trends (i.e, 95% BCI (HDS) or CI (TRIM) not overlapping zero). The yearly abundance estimates from the HDS model are given by black dots, and the yearly expected counts from the TRIM model are given by red dots. Years from both models that present significant deviations from the linear trend are indicated by an asterisk

RESULTS

We evaluated the trends of 30 farmland bird species over 10 years, using data from a total of 1360 line transect surveys (Table S1, SI 1). Species occurrence on transects was variable, with Corn bunting *Emberiza calandra* and Crested lark *Galerida cristata* detected in the highest proportion of transects (mean of the proportions of transects where they were present per year = 82% and 79%, respectively; Table S2, SI 1), and Greater short-toed lark *Calandrella brachydactyla* and Eurasian skylark *Alauda Arvensis* the lowest (5% and 6%, respectively; Table S2).

Forty-three percent of all the analysed species (Common kestel *Falco tinnunculus*, European serin *Serinus serinus*, Barn swallow *Hirundo rustica*, Greater short-toed lark *Calandrella brachydactyla*, Thekla lark *Galerida theklae*, Sardinian warbler *Sylvia melanocephala*, European greenfinch *Carduelis chloris*, Common wood pigeon *Columba palumbus*, Eurasian hoopoe *Upupa epops*, House sparrow *Passer domesticus*, Common linnet *Carduelis cannabina*, Subalpine warbler *Sylvia cantillans* and Eurasian skylark *Alauda Arvensis*) showed different trend results when using TRIM and HDS models (Figs. 1, 2). In the case of Common kestrel, the HDS model returned significant negative trend estimates while the CI from the TRIM model overlapped zero, while the remaining 12 species presented the opposite pattern (the TRIM model returned significant trend estimates and the BCI from the HDS model overlapped zero; Figs. 1, 2). Three species showed a significant negative trend that was consistent across both approaches, one species showed a significant positive trend, and seven species showed non-significant trends (Fig. 1). Trend coefficients had the same signs across approaches for all species except European serin, Barn swallow, Greater short-toed lark, and Thekla lark (Figs. 1, 2), for which the trend was significantly positive when using TRIM, and marginally negative (i.e., with BCI overlapping zero) when using HDS. For the Woodchat shrike *Lanius senator* and the Red-billed chough *Pyrrhocorax pyrrhocorax*, the trend coefficients had different signs with no significant estimates with neither TRIM or HDS. The TRIM model resulted in a higher number of significant annual deviations from the linear trend than the HDS model (Fig. 2).

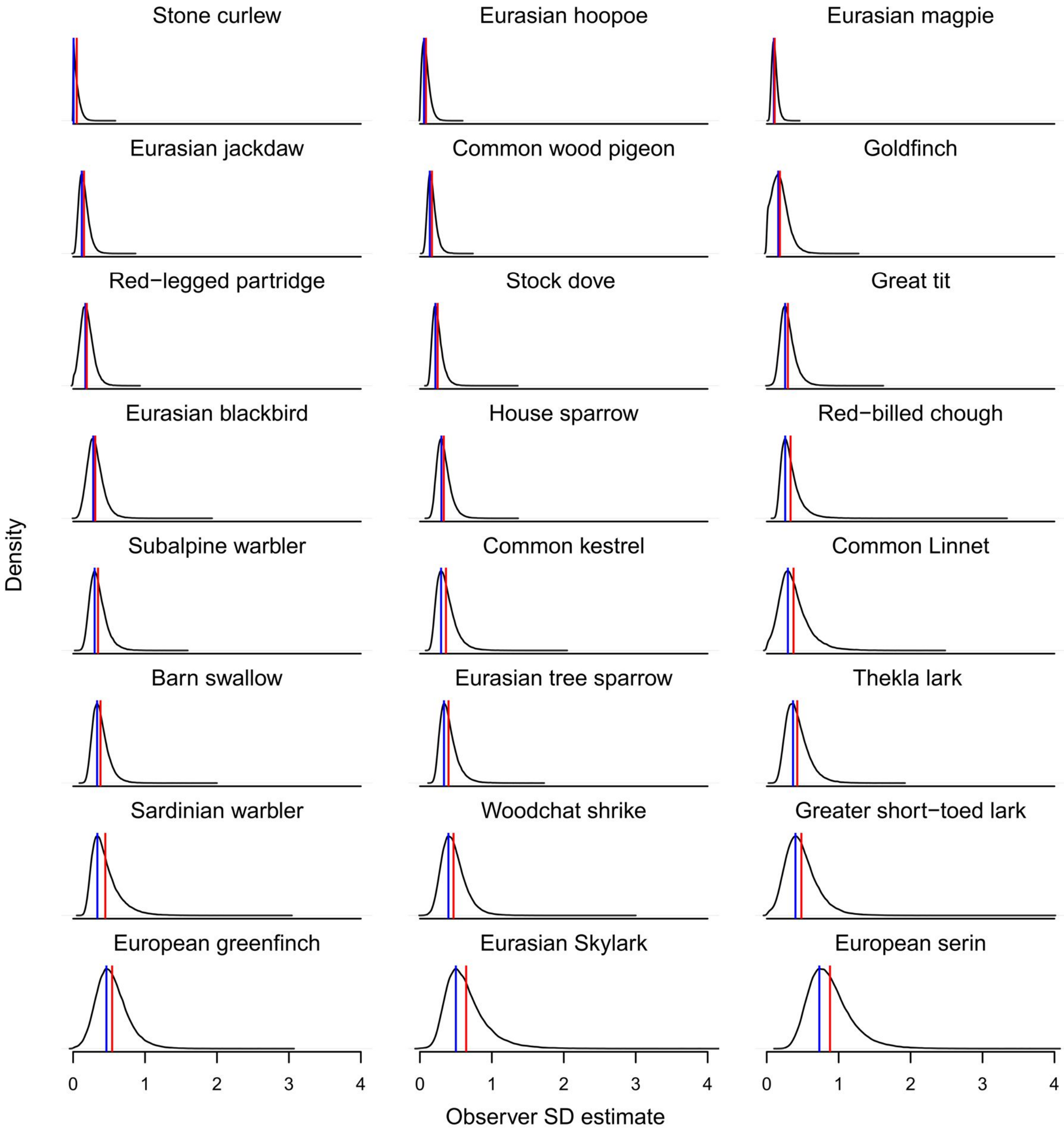

Fig. 3 Posterior distribution for the Standard Deviation (SD) of the observer random effects (σ_{obs}) from a Hierarchical Distance Sampling model fit to bird observation data from Lleida, Spain. The mean and mode of the SD estimate are indicated in red and blue, respectively. Species-specific plots are ordered according to increasing values of the mean observer SD estimate

Temperature did not affect the detection process of any of the studied species, and was therefore discarded from the observation model when it impaired convergence (Table S4, SI 1). The species that presented highest variability in detection among observers, based on estimates of the standard deviation of the observer random effect, were European serin, Eurasian skylark, European greenfinch, Greater short-toed lark, Woodchat shrike, Thekla lark and Sardinian warbler (Fig. 3). Likewise, the species that presented highest variability in detection across years were Eurasian skylark, Sardinian warbler, Red-legged partridge *Alectoris rufa*, European greenfinch, European serin and Thekla lark (Fig. 4).

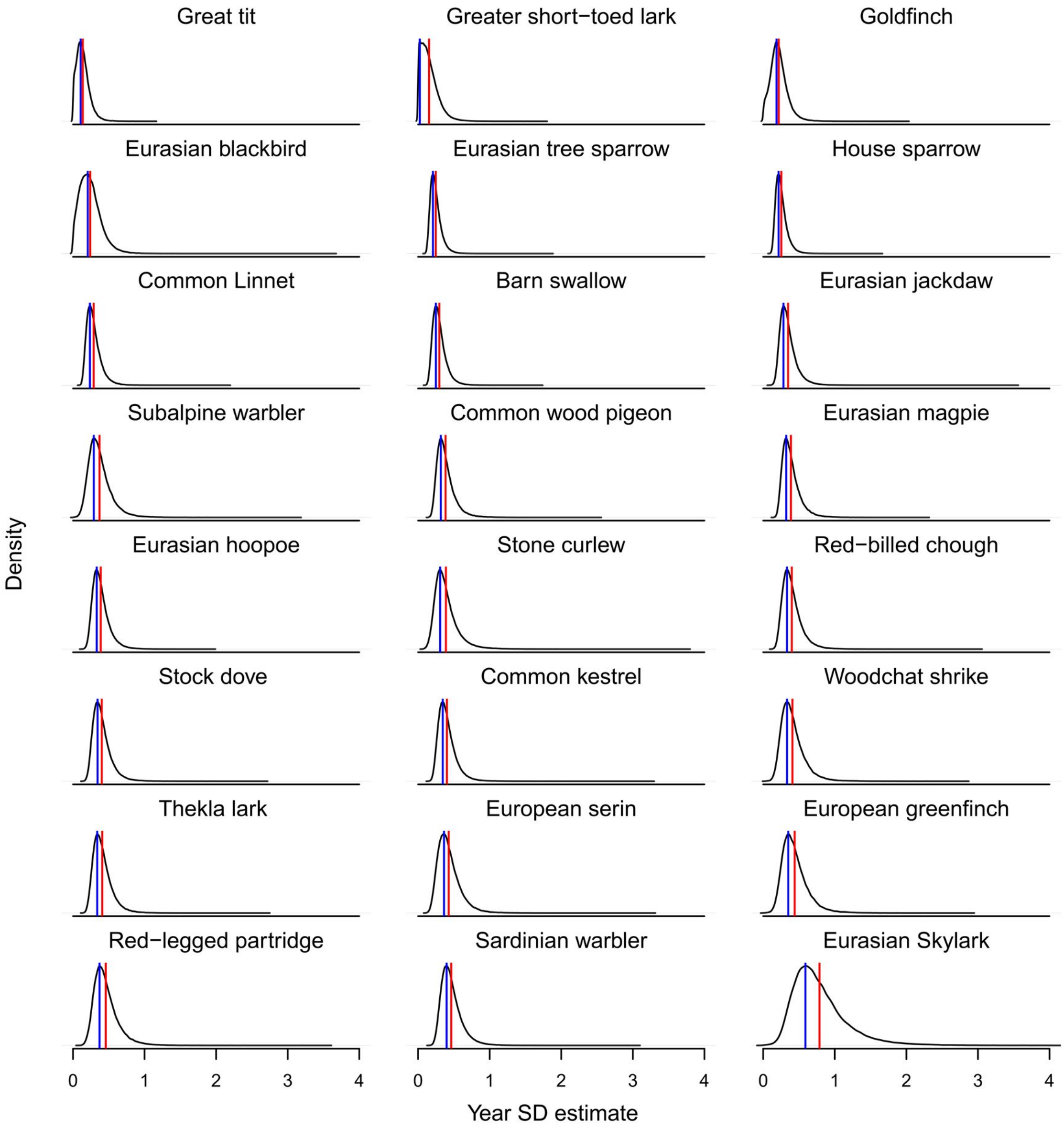

Fig. 4 Posterior distribution for the Standard Deviation (SD) of the year random effects ($\sigma_{sig.year}$) from a Hierarchical Distance Sampling model fit to bird observation data from Lleida, Spain. The mean and mode of the SD estimate are indicated in red and blue, respectively. Species-specific plots are ordered according to increasing values of the mean year SD estimate

DISCUSSION

Accounting for imperfect detection in monitoring programs has proved important to make inference about population trends of several taxa, including mammals (e.g., Moore and Barlow 2011), reptiles (e.g., Kéry et al. 2009) and birds (e.g., Bart 2005 for marsh birds; Berthiaume et al. 2009 for raptor birds; Camp et al. 2016 for forest birds). Our study occurred in a dynamic farmland landscape, where changes are common in terms of both human-related factors, such as crop rotations (Mas and Verdú 2003), and abiotic factors such as precipitation and temperature (Lobell and Field 2007). These changes have the potential to generate different spatial patterns in the vegetation structure on a yearly basis, which could influence the detection process on a specific transect (e.g., for ground-nesting species such as the Stone curlew, whose detection probability may depend on vegetation height; de Juana 2005). Our results showed that even in an open farmland landscape, where detectability could be expected to be high and relatively constant, detection varied considerably across species, and was affected by observer and year of study. Moreover, almost half of the studied species showed different population trend estimates when using HDS (i.e., accounting for imperfect detection) and TRIM models. Five of the species showing different population trend estimates (Eurasian skylark, Sardinian warbler, European greenfinch, European serin, and Thekla lark) were the ones presenting higher among-year variability in detection, meaning that temporal heterogeneity in detection could have biased some of the population trend estimates in our system. Yearly fluctuations in detection could be, for instance, associated with the singing behaviour of these and other species, which in turn may be influenced by factors such as weather conditions (Crick and Sparks 1999) or population size or density (Laiolo and Tella 2008), therefore adding extra variation to the detection process.

Another potential source of heterogeneity in detection commonly recognized in bird surveys is the variation in the skill level of observers (Ralph and Scott 1981; Diefenbach et al. 2003; Johnston et al. 2018). Observer effects are likely stronger in large-scale monitoring programs based on citizen science (Bart 2005; Voříšek et al. 2010) and relying on multiple volunteer observers with variable backgrounds. Our study was performed by hired professional observers, yet we found different degrees of observer variability among species. Moreover, our results point towards species mostly detected aurally (e.g., the Eurasian skylark, European greenfinch and Greater short-toed lark) showing higher detection variance among observers. Identifying bird species by their singing behaviour is more challenging than visually, so for most species differences in observer experience may be more pronounced. In contrast, temperature did not affect the detection process. Our field protocol avoided conducting census at very high temperatures, so temperatures where probably not extreme enough to affect bird activity in our study context. Care should be taken to extrapolate this conclusion to other areas or future years, as high temperatures have proved to affect bird singing and displaying activity (e.g., Gudka et al. 2019), and extreme temperatures due to climate change will affect the farmland dynamics (e.g., the yield of annual crops; Wheeler et al. 2000) and birds' ecology (Crick and Sparks 1999; e.g., Gudka et al. 2019 for displaying time).

In general, the TRIM model estimated more significant trends and more significant annual deviations from the trend than the HDS model. This can be explained by the different levels of uncertainty associated with trend estimates from the two approaches, with uncertainty from the HDS model being higher for all the studied species. These results are in accordance with other studies evaluating the effect of detectability on animal population trends such as the one of Camp et al. (2016) and Kéry et al. (2009); they are also expected, as incorporating a detection component into the model increases model complexity (i.e., the number of parameters), which translates to increased parameter uncertainty. Indeed, a higher uncertainty in HDS models seems to explain the different trend estimates between TRIM and HDS for 12 of the studied species. While these higher levels of uncertainty may seem undesirable from a management perspective, they likely provide a more honest representation of our state of knowledge of the studied species. Properly accounting for uncertainty when estimating trends is important for conservation, since underestimating uncertainty could lead to suboptimal decisions in a

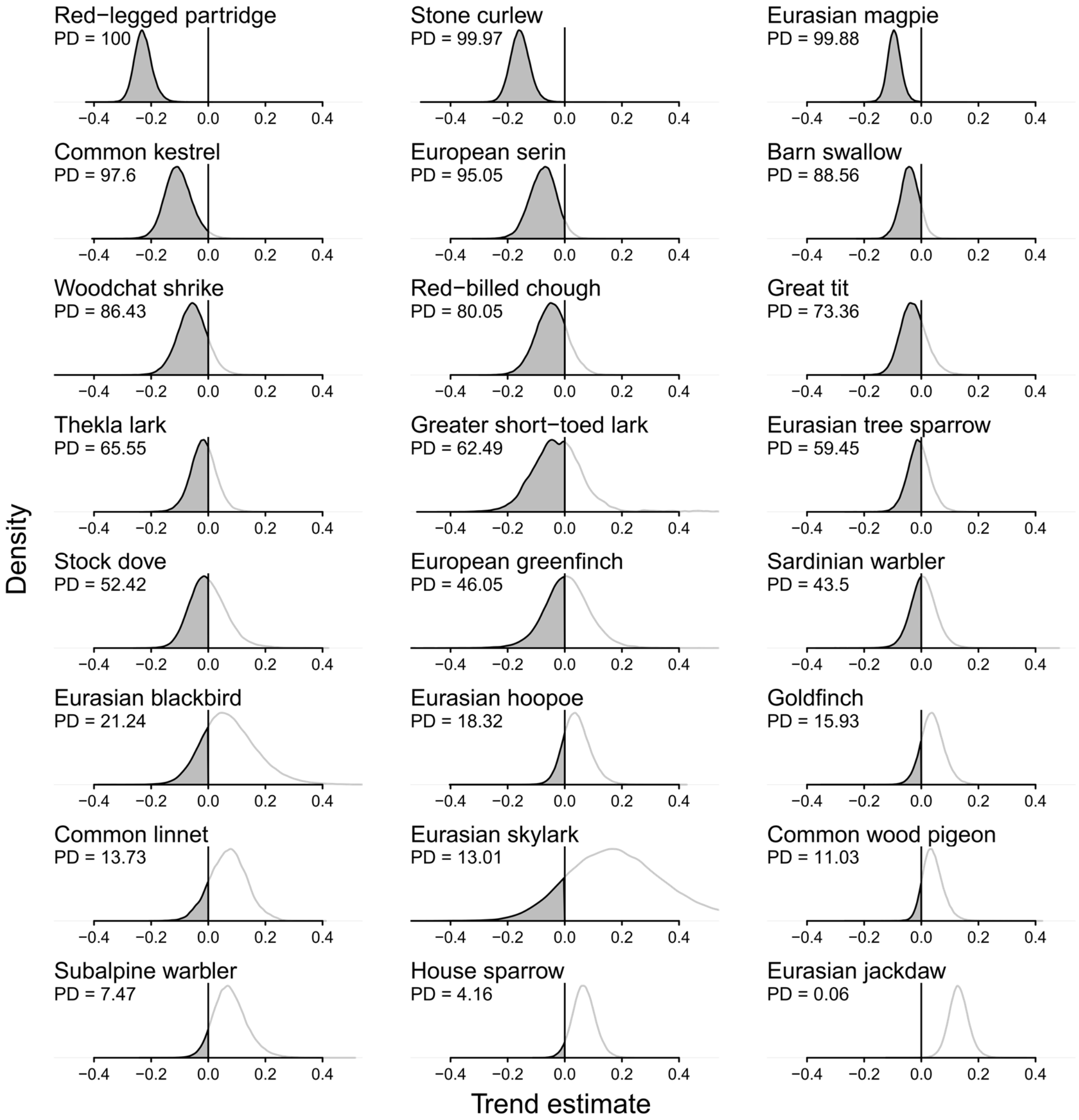

Fig. 5 Posterior distribution for the beta coefficient of the trend estimate from a Hierarchical Distance Sampling model fit to bird observation data from Lleida, Spain. The area under the curve of the posteriors below zero (i.e., probability of negative trend) is shaded in grey. The Probability of Decline (PD) is presented for each species. Species-specific plots are ordered according to increasing values of the trend estimate

decision-making framework (for example, by assigning an erroneous IUCN category to a species; Connors et al. 2014; Maes et al. 2015). Indeed, incorrectly classifying a population as decreasing will divert conservation funds from populations with higher extinction risk, while considering a population as stable when is declining could lead to the eventual loss of such population because remedial action is not taken (D'Eon-Eggertson et al. 2015).

The Bayesian HDS models also provided posterior probabilities for negative population trends (Fig. 5), which represent a continuous measure of the importance of the trend (i.e., rather than significance thresholds associated with frequentist methods; Wade 2000). For instance, the Woodchat shrike and the Great tit had non-significant trends with either HDS or TRIM models

(Fig. 1), but showed a probability of decline of 86% and 73% respectively (Fig. 5), which may prove useful to inform management decisions.

For 11 species, accounting for imperfect detection did not change trend estimates. Yearly fluctuations in detection may not be pronounced enough to be reflected on these population trends within the time frame of our study. Alternatively, the high visibility provided by open farmlands may have led to near-perfect detection of these species, thus making accounting for missed individuals less influential. Indeed, a preliminary analysis showed that a high truncation distance was required for the detection curve of some species to decrease, suggesting they remain highly visible even at several hundred meters' distance, so we recommend setting wide transect strips (e.g., up to 500 m, like in our study) for distance sampling study designs in open farmlands.

In addition to evaluating the effect of ignoring imperfect detection when estimating trends, the HDS approach presented here provides a tool to estimate and monitor true abundance (i.e., black dots in Fig. 2, S3; SI 1). The framework has been used to estimate abundance for a multitude of taxa (e.g., Moore and Barlow 2011 for Fin whales *Balaenoptera physalus*; Sollmann et al. 2015 for Scrub jays *Aphelocoma insularis*), and could be useful to address ecological questions regarding bird ecology in farmland landscapes. In our system, obtaining site-specific estimates of abundance could help evaluating the effectiveness of ongoing conservation actions (such as agri-environmental schemes; Cantero-Martínez and Moncunill 2012; Sanz-Pérez et al. 2019), and inform on how these management actions are contributing to increase the habitat suitability and the carrying capacity of Special Protection Areas (SPA). In fact, providing population abundance estimates in each SPA is one of the requirements of the Standard Data Forms (SDFs) for the European Commission (European Community Bird Directive 79/409/ECC and 147/2009/ECC; European Comission 2000). SDFs provide the list of all bird species relevant for a site to be officially designated as SPA. Having an updated SDF of the target species is essential to design site-specific conservation actions, as well as verifying the relevance of the target population in a wider context (Battisti and Fanelli 2015). We have provided an example of the potential of our HDS model in this sense by providing the site-specific abundance estimates within transects related to SPA areas in our study zone (Table S5, SI 1) for four of the studied species.

Conclusion

There is a global consensus that scientists play a key role not only in developing new methodologies, but also in questioning and evaluating current ones (Johnson 2008). Learning more about the detection process will garner insight in the role of detectability for abundance and trend estimation in different contexts, and advance towards the improvement of monitoring programs, which are a cornerstone of conservation biology. To our knowledge, this is the first study to test the role of imperfect and variable detection probability in population trend estimation in an open farmland bird community, and to evaluate the reliability of TRIM, the principal European approach for estimating bird population trends. For most of the studied species TRIM appears to be valid to determine trend direction and magnitude. However, if traditional significance levels are used to determine whether a population is in risk, TRIM may produce overly confident results because it ignores the added uncertainty due to imperfect detection, which is the case for 43% of our studied species. Therefore, we recommend that, even in open landscapes where visibility is high, monitoring programs should adjust their sampling designs to include detectability in their analysis.

Using methods that take imperfect detection into account in bird monitoring programs would ensure reliable trend estimates, which would pay off its more complex implementation in citizen-based surveys. In bird monitoring programs there is always a trade-off between making the surveys feasible and appealing to volunteers and using methodologies that provide accurate estimates. Collecting data that allows accounting for imperfect detection as well as its analysis is not always straightforward, and coordinators of monitoring programs are sometimes sceptical about accounting for detectability because they consider it irrelevant or find the analyses too complex. TRIM has an easy application, yet this is conditional on detectability being constant across years. Therefore, collecting data in a way that allows accounting for imperfect and variable detection (e.g., through distance sampling, which does not require temporal replicates; Buckland et al. 2001) and using methods that integrate detectability, is highly recommended.

Accounting for imperfect detection may be of even greater importance in habitats in which detection is lower, such as forests and shrublands, which also encompass big part of European monitoring efforts for common bird species (Klvaňová and Voříšek 2007), or mountain areas, which are important for regional monitoring programs (ICO 2018).

Ensuring unbiased population trends estimates is especially important for threatened species. Given the increase in agriculture intensification during the last decades, the farmland bird community is suffering from an abrupt decline (BirdLife International 2018). Thus, a proper assessment of their population trends and true abundance will be essential to correctly assign farmland bird species into IUCN categories and to design species-specific conservation actions.

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Author's contributions: R.S, D.G., F.S-P, and A.S-P conceived and designed the study, with G. B's suggestions. A.S-P and R.S implemented the analysis. A.S-P wrote the manuscript with the help of R.S, D.G., F.S-P and G.B. All authors contributed to subsequent drafts and gave final approval for publication. D.G coordinated fieldwork and G.B secured funding.

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Conflict of Interest: The authors have no conflict of interest to declare.

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APPENDIX

Supporting Information I

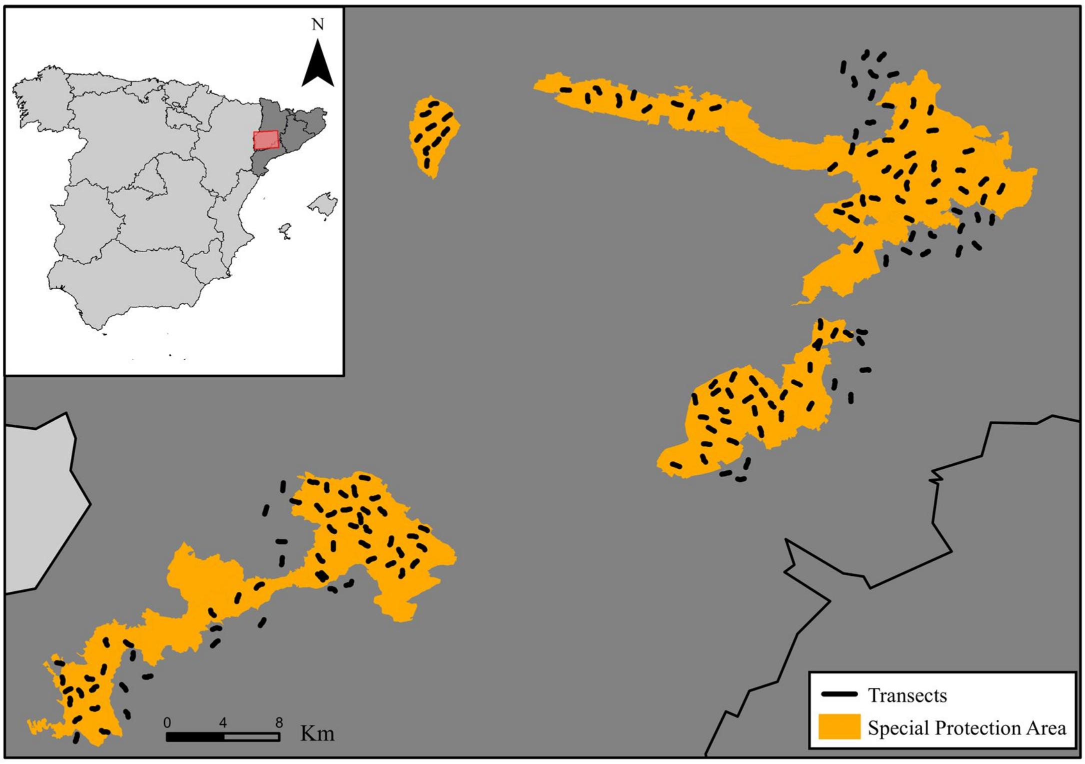

Figure S1. Study area and location of the line transects where bird surveys of farmland birds were performed from 2010 to 2018 in Lleida, Spain. The Special Protection Areas are represented by orange polygons.

Table S1. Yearly information on the number of line transects and observers that participated on the farmland bird surveys from 2010 to 2018 in Lleida, Spain

Year	Number of transects	Number of observers
2010	171	4
2011	151	8
2012	153	7
2013	152	4
2014	152	3
2015	147	5
2016	133	4
2017	151	4
2018	150	4
Total	1360	

Table S2. Proportion of transects with detection of each studied species each of the years of the study (2010 – 2018), where bird surveys were performed in Lleida, Spain. The mean proportion of each species presence is given as the average of the proportions for all years.

Species	2010	2011	2012	2013	2014	2015	2016	2017	2018	Mean %
Barn swallow	38.01	38.41	37.25	51.32	26.97	34.69	39.1	49.67	48	40.38
Calandra lark	47.37	61.59	69.28	63.82	55.26	55.78	69.17	70.86	73.33	62.94
Common kestrel	14.62	17.88	30.07	13.82	13.82	17.01	12.03	19.21	7.33	16.2
Common linnet	6.43	10.6	11.76	5.92	5.26	7.48	5.26	10.6	11.33	8.29
Common wood pigeon	32.75	46.36	59.48	40.79	42.11	39.46	42.86	50.33	54.67	45.42
Corn bunting	94.15	73.51	63.4	88.82	83.55	76.19	84.96	86.09	90	82.3
Crested lark	70.18	77.48	85.62	74.34	82.89	80.95	79.7	80.79	80.67	79.18
Eurasian blackbird	3.51	9.93	16.99	10.53	6.58	9.52	8.27	6.62	8	8.88
Eurasian hoopoe	15.79	23.18	41.18	25.66	32.89	27.89	31.58	27.81	32.67	28.74
Eurasian jackdaw	10.53	11.92	23.53	17.76	14.47	25.17	26.32	29.14	35.33	21.57
Eurasian magpie	75.44	69.54	74.51	66.45	59.21	60.54	44.36	60.93	55.33	62.92
Eurasian skylark	0.58	3.31	10.46	15.79	3.95	5.44	9.02	5.96	4	6.5
Eurasian tree sparrow	22.22	29.14	36.6	23.03	15.13	18.37	24.81	25.83	22.67	24.2
European bee-eater	32.16	43.71	45.75	30.26	29.61	34.01	32.33	45.7	38.67	36.91
European greenfinch	5.85	2.65	18.3	12.5	5.26	5.44	8.27	15.23	12	9.5
European serin	9.94	13.91	20.26	15.79	9.87	6.8	15.04	15.89	16.67	13.8
Goldfinch	11.7	15.23	23.53	17.76	10.53	12.93	14.29	18.54	20.67	16.13
Great tit	14.62	18.54	30.07	25	11.84	11.56	12.78	16.56	12.67	17.07
Greater short-toed lark	5.85	3.97	4.58	4.61	7.89	6.12	4.51	3.97	4	5.06
House sparrow	24.56	25.17	46.41	37.5	30.92	36.05	38.35	37.09	34	34.45
Little bustard	50.88	37.75	37.25	46.05	32.24	21.09	33.08	21.85	24.67	33.87
Red-billed chough	8.77	5.96	13.07	10.53	6.58	4.76	7.52	9.93	8.67	8.42

Table S3. Summary statistics of the distribution of SD estimates (mean and mode) of the observer and year random effects obtained across all species in the Hierarchical Distance Sampling models of 24 bird species in Lleida (Spain). The 6 species for which the detection model presented lack of fit was excluded from the summary statistics (see Methods section, main text). The 3rd Quantile values were used as a threshold to classify species with the highest SD estimates.

Variable	SD estimate	Min	1st Quantile	Median	Mean	3rd Quantile	Max
Observer	**Mean**	0.051	0.188	0.338	0.341	0.43	0.88
	Mode	0.006	0.168	0.294	0.283	0.344	0.731
Year	**Mean**	0.137	0.28	0.388	0.362	0.408	0.786
	Mode	0.024	0.231	0.318	0.294	0.344	0.589

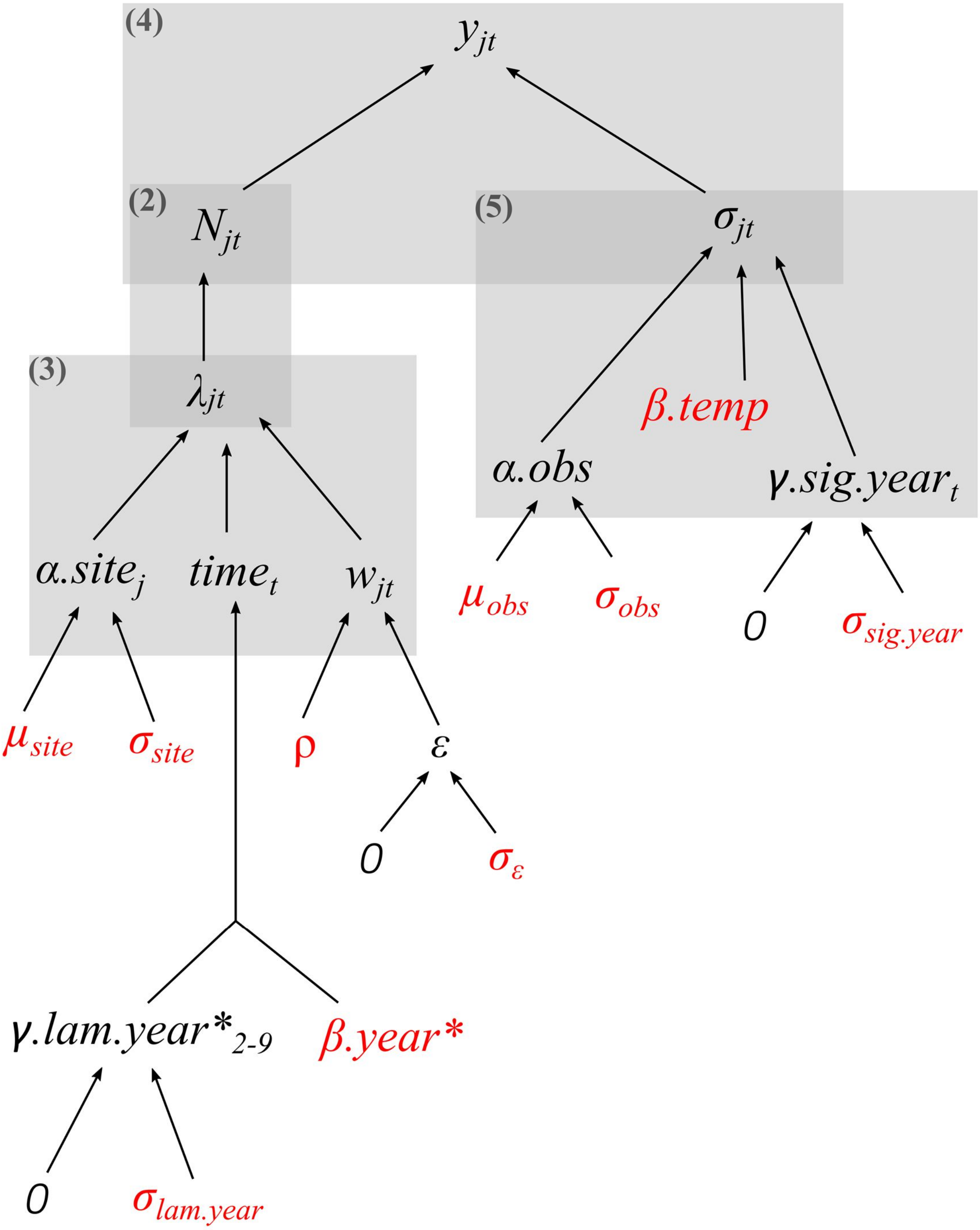

Figure S2. Bayesian network of the HDS model used to infer farmland bird population trends in Lleida (Spain) from 2010 to 2018. The shaded areas and numbers in brackets correspond to the equations representing the observation and process components in the methods section (main text). Priors are highlighted in red. The Bayesian network was inspired by Hobbs & Hooten (2015).

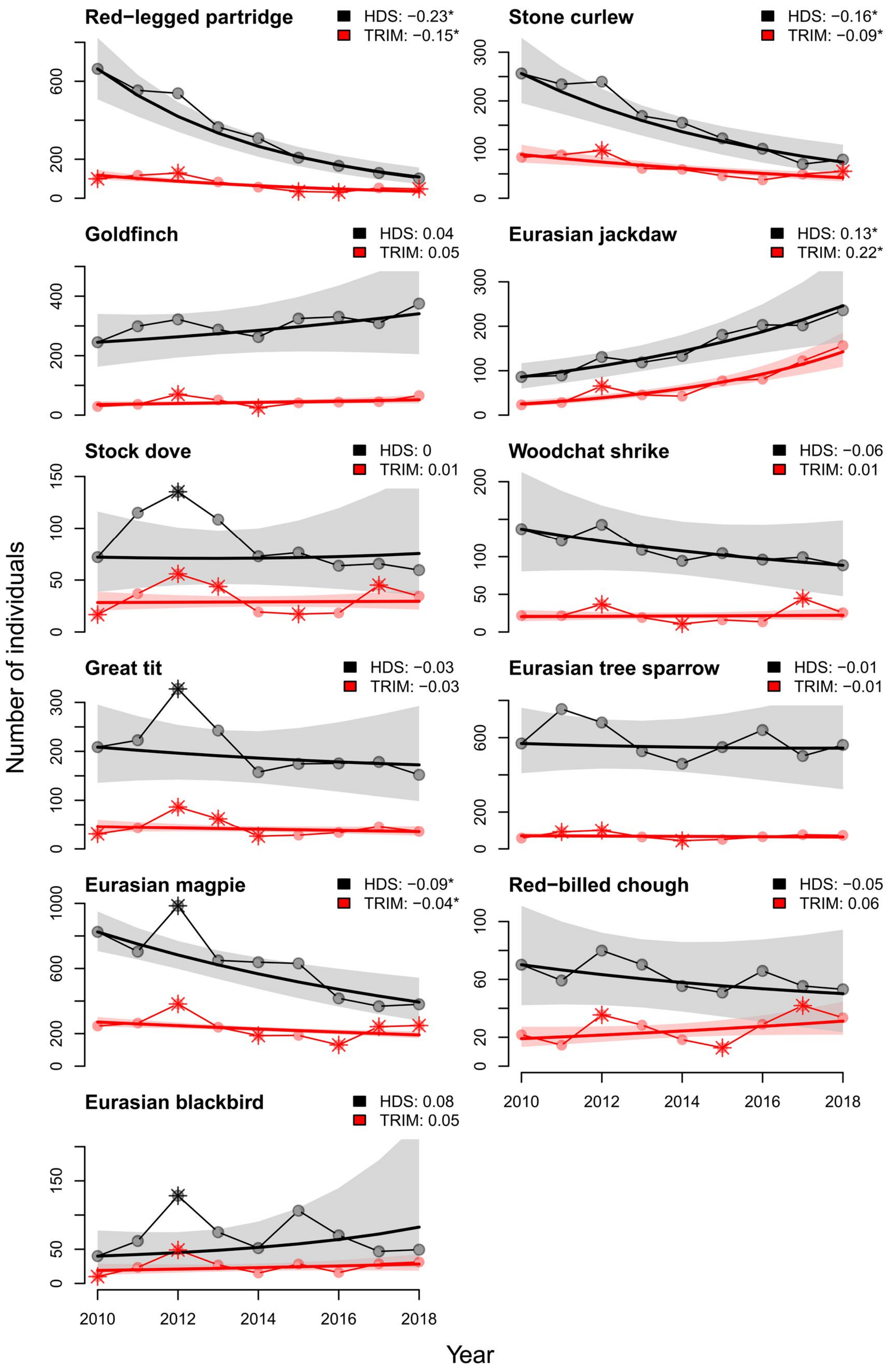
Red−legged partridge
■ HDS: −0.23*
🟥 TRIM: −0.15*
0
200
600
Stone curlew
■ HDS: −0.16*
🟥 TRIM: −0.09*
0
100
200
300
Goldfinch
■ HDS: 0.04
🟥 TRIM: 0.05
0
200
400
Eurasian jackdaw
■ HDS: 0.13*
🟥 TRIM: 0.22*
0
100
200
300
Stock dove
■ HDS: 0
🟥 TRIM: 0.01
0
50
100
150
Woodchat shrike
■ HDS: −0.06
🟥 TRIM: 0.01
0
50
100
200
Great tit
■ HDS: −0.03
🟥 TRIM: −0.03
0
100
200
300
Eurasian tree sparrow
■ HDS: −0.01
🟥 TRIM: −0.01
0
200
600
Eurasian magpie
■ HDS: −0.09*
🟥 TRIM: −0.04*
0
200
600
1000
Red−billed chough
■ HDS: −0.05
🟥 TRIM: 0.06
0
20
60
100
2010
2012
2014
2016
2018
Eurasian blackbird
■ HDS: 0.08
🟥 TRIM: 0.05
0
50
150
2010
2012
2014
2016
2018
Number of individuals
Year

Figure S3. Population trend of the 11 species (out of 24 species) that did not show different significant results for the trend coefficient when using HDS models (black) and TRIM models (red), based on data from 2010-2018 in Lleida, Spain. The population trend of each species is represented by a continuous line. The trend coefficients (on the log scale) are showed in the legend; asterisks beside the coefficients mark significant trends (i.e, 95% BCI (HDS) or CI (TRIM) not overlapping zero). The yearly abundance estimates from the HDS model are given by black dots, and the yearly expected counts from the TRIM model are given by red dots. Years from both models that present significant deviations from the linear trend are indicated by an asterisk.

Table S4. Posterior summaries for the coefficient of the temperature effect on the scale parameter of the detection function, σ (mean and 95% Bayesian Credible Interval) obtained from the HDS model fitted with data of 30 bird species during 9 years in Lleida, (Spain). The species models where temperature was not included for convergence purposes (see SI 3) are represented by a blank space.

Species	Temperature coefficient	Temperature BCI
Eurasian Skylark	-0.01	[-0.04 - 0.03]
Red-legged partridge	-0.02	[-0.03 - 0]
Stone curlew	-	-
Greater short-toed lark	0	[-0.04 - 0.03]
Goldfinch	0.01	[-0.01 - 0.03]
European greenfinch	0.01	[-0.01 - 0.04]
Common Linnet	0.02	[-0.01 - 0.06]
Eurasian jackdaw	0	[-0.01 - 0.01]
Stock dove	0.01	[-0.01 - 0.03]
Common wood pigeon	0	[-0.01 - 0]
Common kestrel	-	-
Crested lark	0	[-0.01 - 0.01]
Thekla lark	-	-
Barn swallow	-0.01	[-0.03 - 0.01]
Woodchat shrike	0	[-0.04 - 0.03]
European bee-eater	0.01	[0 - 0.02]
Calandra lark	-	-
Corn bunting	0	[-0.01 - 0]
House sparrow	-	-
Great tit	0	[-0.01 - 0.02]
Eurasian tree sparrow	-	-
Eurasian magpie	0	[-0.01 - 0]
Red-billed chough	0	[-0.02 - 0.02]
European serin	-	-
Starling sp.	0	[-0.01 - 0.01]
Subalpine warbler	0.03	[0 - 0.05]
Sardinian warbler	-	-
Little bustard	-	-
Eurasian blackbird	-	-
Eurasian hoopoe	-	-

Table S5: Site-specific abundance estimates (+/- SD) within SPA for four species. Abundance estimates for each SPA were obtained by summing up transect estimates

	SPA	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**
RED – LEGGED PARTRIDGE	AF	73.18 +/- 11.93	61.08 +/- 9.17	58.42 +/- 9.77	39.92 +/- 6.33	33.79 +/- 6.21	22.91 +/- 4.37	18.3 +/- 3.72	14.29 +/- 2.76	11.16 +/- 2.27
	AL	15.9 +/- 4.9	13.21 +/- 4.05	12.8 +/- 4.14	8.71 +/- 2.79	7.33 +/- 2.46	4.97 +/- 1.7	3.96 +/- 1.37	3.1 +/- 1.07	2.42 +/- 0.85
	BA	14.41 +/- 3.56	12.11 +/- 2.92	11.6 +/- 2.89	7.92 +/- 1.95	6.66 +/- 1.74	4.54 +/- 1.23	3.63 +/- 1.02	2.86 +/- 0.78	2.22 +/- 0.62
	BE	80.45 +/- 12.84	67.3 +/- 10.14	64.93 +/- 10.8	44.05 +/- 7.02	36.89 +/- 6.82	25.08 +/- 4.81	19.97 +/- 4.07	15.72 +/- 3.02	12.26 +/- 2.5
	BM	25.41 +/- 5.37	21.28 +/- 4.3	20.45 +/- 4.35	14.21 +/- 3	11.86 +/- 2.72	8.01 +/- 1.88	6.38 +/- 1.57	4.98 +/- 1.18	3.86 +/- 0.95
	GR	63.16 +/- 10.89	52.82 +/- 8.62	51.38 +/- 9.16	35.1 +/- 6.06	29.35 +/- 5.76	19.81 +/- 4.05	15.95 +/- 3.47	12.31 +/- 2.54	9.73 +/- 2.12
	SI	170.31 +/- 23.88	141.38 +/- 18.04	138.61 +/- 19.67	93.82 +/- 12.69	79.3 +/- 12.88	53.69 +/- 9.21	42.92 +/- 7.95	33.29 +/- 5.77	26.09 +/- 4.85
STONE CURLEW	AF	47.57 +/- 8.32	41.01 +/- 5.89	40.54 +/- 6.41	29.11 +/- 4.98	27.81 +/- 4.9	21.78 +/- 3.8	18.38 +/- 3.45	12.78 +/- 2.97	13.94 +/- 2.96
	AL	9.03 +/- 2.51	8.67 +/- 2.33	8.23 +/- 2.34	5.84 +/- 1.72	5.35 +/- 1.61	4.62 +/- 1.38	3.64 +/- 1.12	2.66 +/- 0.89	3.04 +/- 1
	BA	7.78 +/- 2	7 +/- 1.69	6.74 +/- 1.69	4.84 +/- 1.25	4.43 +/- 1.17	3.63 +/- 0.97	3.09 +/- 0.87	2.06 +/- 0.64	2.49 +/- 0.76
	BE	44.66 +/- 7.66	42.35 +/- 6.2	44.15 +/- 6.87	31.58 +/- 5.22	28.49 +/- 4.98	22.52 +/- 3.99	18.74 +/- 3.52	12.4 +/- 2.89	14.73 +/- 3.19
	BM	14.23 +/- 3.24	12.29 +/- 2.63	14.55 +/- 3.31	9.39 +/- 2.18	8.15 +/- 1.95	6.58 +/- 1.56	5.68 +/- 1.42	3.89 +/- 1.1	4.49 +/- 1.22
	GR	24.33 +/- 5.03	22.44 +/- 4.11	23.42 +/- 4.69	16.07 +/- 3.42	16.33 +/- 3.69	12.19 +/- 2.7	10.37 +/- 2.56	7.7 +/- 2.16	7.94 +/- 2.03
	SI	46.82 +/- 7.72	43.34 +/- 6.14	43.97 +/- 6.69	31.16 +/- 5.15	27.3 +/- 4.78	22.03 +/- 3.85	17.44 +/- 3.27	11.98 +/- 2.78	13.77 +/- 2.95
EURASIAN JACKDAW	AF	13.97 +/- 3.24	14.93 +/- 3.39	21.15 +/- 4.46	18.82 +/- 3.8	20.82 +/- 4.45	28.02 +/- 5.64	30.85 +/- 6.61	30.55 +/- 5.55	37.15 +/- 6.76
	AL	2 +/- 0.99	2.07 +/- 1.03	3.1 +/- 1.57	2.94 +/- 1.48	3.55 +/- 1.8	4.81 +/- 2.49	5.38 +/- 2.81	5.35 +/- 2.76	5.8 +/- 3.24
	BA	5.6 +/- 1.94	5.23 +/- 1.63	7.15 +/- 2.03	6.25 +/- 1.7	6.84 +/- 1.93	9.22 +/- 2.44	10.13 +/- 2.75	10.21 +/- 2.41	12.57 +/- 2.95
	BE	23.49 +/- 5.41	24.92 +/- 5.66	37.67 +/- 7.64	34.18 +/- 6.63	38.8 +/- 7.92	52.47 +/- 10.13	59.03 +/- 11.82	58.33 +/- 9.9	66.11 +/- 11.8
	BM	4.35 +/- 1.36	4.46 +/- 1.36	6.67 +/- 1.86	6.31 +/- 1.66	7.67 +/- 2.03	11.11 +/- 2.74	13.24 +/- 3.38	12.71 +/- 2.8	14.94 +/- 3.32
	GR	12.85 +/- 3.68	13.19 +/- 3.72	19.73 +/- 5.85	18.24 +/- 5.29	20.38 +/- 6.2	27.28 +/- 8.5	29.94 +/- 9.86	29.34 +/- 9.16	33.64 +/- 10.89
	SI	7.46 +/- 1.94	7.63 +/- 1.98	11.21 +/- 2.74	10.17 +/- 2.42	11.17 +/- 2.75	15.55 +/- 3.68	17.86 +/- 4.36	18.57 +/- 4.1	21.68 +/- 4.87
HOUSE SPARROW	AF	40.82 +/- 10.49	37.32 +/- 9.06	66.4 +/- 14.4	43.53 +/- 10.11	55.14 +/- 13.01	75.59 +/- 17.12	69.16 +/- 15.92	81.73 +/- 18.09	66.68 +/- 15.42
	AL	9.2 +/- 4.58	9.02 +/- 4.63	15.65 +/- 8.42	10.89 +/- 6	14.33 +/- 8.24	18.55 +/- 10.84	14.18 +/- 8.66	15.43 +/- 9.84	13.1 +/- 8.64
	BA	11.16 +/- 3.95	10.53 +/- 3.54	18.12 +/- 5.46	12.13 +/- 3.77	17.29 +/- 5.39	26.39 +/- 8.06	19.28 +/- 6.23	21.65 +/- 6.4	18.69 +/- 5.8
	BE	121.8 +/- 24.64	115.03 +/- 23.18	216.27 +/- 37.78	149.04 +/- 27.81	186.66 +/- 38.12	245.82 +/- 48.59	196.55 +/- 39.9	196.08 +/- 40.8	167.76 +/- 37.25
	BM	29.84 +/- 8.4	29.37 +/- 7.57	48.47 +/- 10.69	29.85 +/- 7.21	39.35 +/- 9.64	51.54 +/- 11.84	40.67 +/- 9.68	51.3 +/- 12.33	43.74 +/- 10.68
	GR	32.84 +/- 10.19	31.61 +/- 9.3	52.01 +/- 14.56	35.54 +/- 11.01	52.86 +/- 16.43	64.98 +/- 20.23	48.29 +/- 15.91	59.14 +/- 18.62	52.21 +/- 17.44
	SI	114.71 +/- 22.96	107.03 +/- 20.27	192.25 +/- 28.41	119.71 +/- 20.72	150.78 +/- 28.47	192.8 +/- 35.47	137.2 +/- 27.12	156.74 +/- 30.17	140.59 +/- 28.23

Supporting Information 2: JAGS model code

```
cat("model{
    # PRIORS FOR LAMBDA
    rho ~ dunif(-1,1) # Autorregresive parameter (serial AC)
    tau <- pow(sd, -2) # Prior for overdispersion in eps
    sd ~ dunif(0, 3)

    bYear.lam ~ dnorm(0, 0.001) # Prior for the trend

    # Random effects for lambda per site
    mu.lam.site ~ dunif(-10, 10)
    sig.lam.site ~ dunif(0, 10)
    tau.lam.site <- 1/(sig.lam.site*sig.lam.site)

    for (j in 1:nsites){
    log.lambda.site[j] ~ dnorm(mu.lam.site, tau.lam.site) }

    # Random effects for lambda per year
    sig.lam.year ~ dunif(0, 10)
    tau.lam.year <- 1/(sig.lam.year*sig.lam.year)

    log.lambda.year[1] <- 0
    for (t in 2:nyears){
    log.lambda.year[t] ~ dnorm(0, tau.lam.year) }

    # PRIORS FOR SIGMA
    bTemp.sig ~ dnorm(0, 0.001)

    mu.sig ~ dunif(-10, 10) # Random effects for sigma per observer
    sig.sig ~ dunif(0, 10)
    tau.sig <- 1/(sig.sig*sig.sig)

    # Random observer effect for sigma
    for (o in 1:nobs){
    sig.obs[o] ~ dnorm(mu.sig, tau.sig) }

    # Random effects for sigma per year
    sig.sig.year ~ dunif(0, 10)
    tau.sig.year <- 1/(sig.sig.year*sig.sig.year)
    for (t in 1:nyears){
    log.sigma.year[t] ~ dnorm(0, tau.sig.year) }

    for(i in 1:nind){
    dclass[i] ~ dcat(fct[site.dclass[i], year.dclass[i], 1:nG])

    # Bayesian p-value for detection component (Bp.Obs)
    dclassnew[i] ~ dcat(fct[site.dclass[i], year.dclass[i], 1:nG])
    Tobsp[i]<- pow(1- sqrt(fct[site.dclass[i], year.dclass[i],dclass[i]]),2)
    Tobspnew[i]<- pow(1- sqrt(fct[site.dclass[i], year.dclass[i],dclassnew[i]]),2)}
    Bp.Obs <- sum(Tobspnew[1:nind]) > sum(Tobsp[1:nind])

    # LIKELIHOOD
    # FIRST YEAR
    for(j in 1:nsites){
    sigma[j,1] <- exp(sig.obs[ob[j,1]] + bTemp.sig*tempCov[j,1] + log.sigma.year[year_index[1]])

    # Construct cell probabilities for nG multinomial cells (distance categories) PER SITE
    for(k in 1:nG){
    up[j,1,k]<-pnorm(db[k+1], 0, 1/sigma[j,1]^2) ##db are distance bin limits
    low[j,1,k]<-pnorm(db[k], 0, 1/sigma[j,1]^2)
    p[j,1,k]<- 2 * (up[j,1,k] - low[j,1,k])
    pi[j,1,k] <- int.w[k] / strip.width
    f[j,1,k]<- p[j,1,k]/f.0[j,1]/int.w[k]               ## detection prob. in distance category k
```

```
fc[j,1,k]<- f[j,1,k] * pi[j,1,k]
fct[j,1,k]<-fc[j,1,k]/pcap[j,1] }

pcap[j,1] <- sum(fc[j,1, 1:nG]) # Different per site and year (sum over all bins)
f.0[j,1] <- 2 * dnorm(0,0, 1/sigma[j,1]^2) # Prob density at 0
y[j,1] ~ dbin(pcap[j,1], N[j,1])
N[j,1] ~ dpois(lambda[j,1])
lambda[j,1] <- exp(log.lambda.site[site[j]] + log.lambda.year[year_index[1]] + bYear.lam*year1[1] +
                  w[j,1])
w[j,1] <- eps[j,1] / sqrt(1 - rho * rho)
eps[j,1] ~ dnorm(0, tau)

# Bayesian p-value on abundance component
Nnew[j,1]~dpois(lambda[j,1])
FT1[j,1]<-pow(sqrt(N[j,1])-sqrt(lambda[j,1]),2)
FT1new[j,1]<-pow(sqrt(Nnew[j,1])-sqrt(lambda[j,1]),2) }

# LATER YEARS
for(j in 1:nsites){
for (t in 2:nyears){
sigma[j,t] <- exp(sig.obs[ob[j,t]] + bTemp.sig*tempCov[j,t] + log.sigma.year[year_index[t]])

# Construct cell probabilities for nG multinomial cells (distance categories) PER SITE
for(k in 1:nG){
up[j,t,k]<-pnorm(db[k+1], 0, 1/sigma[j,t]^2) ##db are distance bin limits
low[j,t,k]<-pnorm(db[k], 0, 1/sigma[j,t]^2)
p[j,t,k]<- 2 * (up[j,t,k] - low[j,t,k])
pi[j,t,k] <- int.w[k] / strip.width
f[j,t,k]<- p[j,t,k]/f.0[j,t]/int.w[k]                ## detection prob. in distance category k
fc[j,t,k]<- f[j,t,k] * pi[j,t,k]
fct[j,t,k]<-fc[j,t,k]/pcap[j,t] }

pcap[j,t] <- sum(fc[j,t, 1:nG]) # Different per site and year (sum over all bins)
f.0[j,t] <- 2 * dnorm(0,0, 1/sigma[j,t]^2) # Prob density at 0
y[j,t] ~ dbin(pcap[j,t], N[j,t])
N[j,t] ~ dpois(lambda[j,t])
lambda[j,t] <- exp(log.lambda.site[site[j]] + log.lambda.year[year_index[t]] + bYear.lam*year1[t] +
                  w[j,t])
w[j,t] <- rho * w[j,t-1] + eps[j,t]
eps[j,t] ~ dnorm(0, tau)

# Bayesian p-value on abundance component (rest of years)
Nnew[j,t]~dpois(lambda[j,t])
FT1[j,t]<-pow(sqrt(N[j,t])-sqrt(lambda[j,t]),2)
FT1new[j,t]<-pow(sqrt(Nnew[j,t])-sqrt(lambda[j,t]),2)
}}
T1p <- sum(FT1[1:nsites,1:nyears]) #Sum of squared residuals for actual data set
T1newp <- sum(FT1new[1:nsites,1:nyears]) # Sum of squared residuals for new data set

# Bayesian p-value
Bp.N <- T1newp > T1p

# Derived parameters
for(t in 1:nyears){
popindex[t] <- sum(lambda[,t]) }

for(t in 1:nyears){
for(s in 1:nspa){
  popindex_zepa[s,t] <- sum(lambda[,t]*indexSPA[,s]) }}

# Expected abundance per year inside model
lam.tot[1] <- popindex[1] # Expected abundance in year 1
for (i in 2:nyears){
lam.tot[i] <- lam.tot[i-1] *
exp(bYear.lam)}}
```

Supporting Information 3: Bayesian p-values and model convergence

We used Bayesian P-values to test whether the abundance and detection components of the HDS model used to determine population trends of 30 bird species fitted the data (Gelman, Meng, & Stern, 1996). Only seven species had adequate model fit for their observation component when using the half-normal detection function (i.e., Bayesian *P*-values were > 0.1 or < 0.9; Methods section, main text; Value 1 from the Table S6). For the rest of the species, we improved model fit by using a hazard rate detection function (Value 2 from the Table S6, SI 3; JAGS model code in SI 4). The single-species models fitted with hazard rate detection functions presented convergence problems for some structural parameters. Therefore, we increased the number of iterations up to 2,000,000 for these single-species models, and performed some adjustments in the models in order to help model convergence (Value 3 from the Table S6). Namely, we restricted the prior distribution to normal (0,0.1) for the trend parameter $\beta.year$ for the Stock dove, Calandra lark, Eurasian hoopoe, Barn swallow, House sparrow, Eurasian tree sparrow, Common kestrel, Red-billed chough, Common linnet, European serin, Eurasian blackbird, European bee-eater and Thekla lark HDS models. We restricted the prior distribution to normal (0,0.1) for the temperature parameter $\boldsymbol{\beta.temp}$ for the Eurasian hoopoe, House sparrow, Eurasian tree sparrow, Common kestrel, Red-billed chough, European bee-eater, Thekla lark, and Greater short-toed lark HDS models. We restricted the prior distribution to normal (0,0.1) for the μ_{obs} for the Stock dove, Calandra lark, Eurasian hoopoe, Barn swallow, House sparrow, Eurasian tree sparrow, Common kestrel, Red-billed chough, Common linnet, European serin, Eurasian blackbird, European bee-eater, Thekla lark and Greater short-toed lark HDS models. We restricted the prior distribution to normal (0,0.1) for the μ_{site} for the Stock dove, Calandra lark, Barn swallow, House sparrow, Eurasian tree sparrow, Red-billed chough, European bee-eater and Thekla lark HDS models. We restricted the prior distribution to normal (0,0.1) for the shape parameter b from the hazard-rate detection function for the Little bustard, Stone curlew, Stock dove, Calandra lark, Eurasian hoopoe, Barn swallow, House sparrow, Eurasian tree sparrow, Common kestrel, Red-billed chough, Common Linnet, European serin, Eurasian blackbird, European bee-eater and Thekla lark HDS models. We used the conjugate distribution gamma (0.1,0.1) of the precision parameter tau for the σ_{obs} for the Stock dove, Common kestrel, Red-billed chough, European serin, and European bee-eater HDS models. We used the conjugate distribution gamma (0.1,0.1) of the precision parameter tau for the $\sigma_{sig.year}$of the species for the Stock dove, Calandra lark, Eurasian hoopoe, Barn swallow, House sparrow, Eurasian tree sparrow, Common kestrel, Red-billed chough, Common Linnet, European serin, European bee-eater and Thekla lark HDS models. We used the conjugate distribution gamma (0.1,0.1) of the precision parameter tau for the $\sigma_{lam.year}$ for the Stock dove, Calandra lark, Barn swallow, House sparrow, Eurasian tree sparrow, Red-billed chough, Common Linnet, European serin, European bee-eater and Thekla lark HDS models. We used the conjugate distribution gamma (0.1,0.1) of the precision parameter tau for the σ_{site} for the Calandra lark, Barn swallow, House sparrow, Eurasian tree sparrow, and Common Linnet HDS models. When adjusting the model parameters did not help reaching convergence for a species model, we removed the temperature parameter from the observation component (Value 4, Table S6)

Table S6. Bayesian p-values from the HDS abundance (Bp.N) and observation models (Bp.Obs) fitted with half-normal or hazard rate detection functions for the HDS models using data of 30 farmland bird species during 2010 – 2018 in Lleida, Spain. The Model column indicates the type of model used in the detection component (1 - Half-Normal; 2 – Hazard-rate; 3 – Hazard rate with adjusted parameters; 4 – Hazard rate with adjusted parameters and removal of temperature). Species presenting lack of fit with either of the two detection functions (Bayesian p-values < 0.1 or > 0.9, indicated by an asterisk) were excluded from further analyses.

Species	Bp.Obs	Bp.N	Model
Eurasian Skylark	0.878	0.539	1
Red-legged partridge	0.683	0.435	1
Stone curlew	0.646	0.462	4
Greater short-toed lark	0.32	0.49	1
Goldfinch	0.343	0.534	2
European greenfinch	0.304	0.497	1
Common Linnet	0.407	0.537	3
Eurasian jackdaw	0.127	0.526	3
Stock dove	0.596	0.488	3
Common wood pigeon	0.196	0.395	2
Common kestrel	0.887	0.471	4
Crested lark	0.063*	0.354	2
Thekla lark	0.1	0.353	4
Barn swallow	0.231	0.473	3
Woodchat shrike	0.191	0.51	1
European bee-eater	0.007*	0.429	3
Calandra lark	0*	0.161	4
Corn bunting	0*	0.186	2
House sparrow	0.371	0.442	4
Great tit	0.433	0.567	1
Eurasian tree sparrow	0.256	0.447	4
Eurasian magpie	0.438	0.277	2
Red-billed chough	0.612	0.581	3
European serin	0.166	0.438	4
Starling sp.	0.001*	0.424	2
Subalpine warbler	0.343	0.527	1
Sardinian warbler	0.1	0.477	4
Little bustard	0.983*	0.515	4
Eurasian blackbird	0.666	0.523	4
Eurasian hoopoe	0.257	0.477	4

Supporting Information 4: JAGS model with Hazard-rate detection function

```
cat("model{
    # PRIORS FOR LAMBDA
    rho ~ dunif(-1,1) # Autorregresive parameter (serial AC)
    tau <- pow(sd, -2) # Prior for overdispersion in eps
    sd ~ dunif(0, 3)

    bYear.lam ~ dnorm(0, 0.001) # Prior for the trend

    # Random effects for lambda per site
    mu.lam.site ~ dunif(-10, 10)
    sig.lam.site ~ dunif(0, 10)
    tau.lam.site <- 1/(sig.lam.site*sig.lam.site)

    for (j in 1:nsites){
    log.lambda.site[j] ~ dnorm(mu.lam.site, tau.lam.site) }

    # Random effects for lambda per year
    sig.lam.year ~ dunif(0, 10)
    tau.lam.year <- 1/(sig.lam.year*sig.lam.year)

    log.lambda.year[1] <- 0
    for (t in 2:nyears){
    log.lambda.year[t] ~ dnorm(0, tau.lam.year) }

    # PRIORS FOR SIGMA
    bTemp.sig ~ dnorm(0, 0.001)

    mu.sig ~ dunif(-10, 10) # Random effects for sigma per observer
    sig.sig ~ dunif(0, 10)
    tau.sig <- 1/(sig.sig*sig.sig)

    # Random observer effect for sigma
    for (o in 1:nobs){
    sig.obs[o] ~ dnorm(mu.sig, tau.sig) }

    # Random effects for sigma per year
    sig.sig.year ~ dunif(0, 10)
    tau.sig.year <- 1/(sig.sig.year*sig.sig.year)
    for (t in 1:nyears){
    log.sigma.year[t] ~ dnorm(0, tau.sig.year) }

    # PRIOR FOR BETA
    b ~ dunif(0, 100)

    for(i in 1:nind){
    dclass[i] ~ dcat(fct[site.dclass[i], year.dclass[i], 1:nG])

    # Bayesian p-value for detection component (Bp.Obs)
    dclassnew[i] ~ dcat(fct[site.dclass[i], year.dclass[i], 1:nG])
    Tobsp[i]<- pow(1- sqrt(fct[site.dclass[i], year.dclass[i],dclass[i]]),2)
    Tobspnew[i]<- pow(1- sqrt(fct[site.dclass[i], year.dclass[i],dclassnew[i]]),2) }
    Bp.Obs <- sum(Tobspnew[1:nind]) > sum(Tobsp[1:nind])

    # LIKELIHOOD
    # FIRST YEAR
    for(j in 1:nsites){
    sigma[j,1] <- exp(sig.obs[ob[j,1]] + bTemp.sig*tempCov[j,1] + log.sigma.year[year_index[1]])

    # Construct cell probabilities for nG multinomial cells (distance categories) PER SITE
    for(k in 1:nG){
    p[j,1,k]<-1-exp(-(midpt[k]/sigma[j,1])^-b)
    pi[j,1,k] <- int.w[k] / strip.width
    fc[j,1,k]<- p[j,1,k] * pi[j,1,k]                ## pi=percent area of k; drops out if constant
```

```
fct[j,1,k]<-fc[j,1,k]/pcap[j,1] }

pcap[j,1] <- sum(fc[j,1, 1:nG]) # Different per site and year (sum over all bins)

y[j,1] ~ dbin(pcap[j,1], N[j,1])
N[j,1] ~ dpois(lambda[j,1])
lambda[j,1] <- exp(log.lambda.site[site[j]] + log.lambda.year[year_index[1]] + bYear.lam*year1[1] +
                    w[j,1])
w[j,1] <- eps[j,1] / sqrt(1 - rho * rho)
eps[j,1] ~ dnorm(0, tau)

# Bayesian p-value on abundance component
Nnew[j,1]~dpois(lambda[j,1])
FT1[j,1]<-pow(sqrt(N[j,1])-sqrt(lambda[j,1]),2)
FT1new[j,1]<-pow(sqrt(Nnew[j,1])-sqrt(lambda[j,1]),2) }

# LATER YEARS
for(j in 1:nsites){
for (t in 2:nyears){
sigma[j,t] <- exp(sig.obs[ob[j,t]] + bTemp.sig*tempCov[j,t] + log.sigma.year[year_index[t]])

# Construct cell probabilities for nG multinomial cells (distance categories) PER SITE
for(k in 1:nG){
p[j,t,k]<-1-exp(-(midpt[k]/sigma[j,t])^-b)
pi[j,t,k] <- int.w[k] / strip.width
fc[j,t,k]<- p[j,t,k] * pi[j,t,k]              ## pi=percent area of k; drops out if constant
fct[j,t,k]<-fc[j,t,k]/pcap[j,t]  }

pcap[j,t] <- sum(fc[j,t, 1:nG]) # Different per site and year (sum over all bins)

y[j,t] ~ dbin(pcap[j,t], N[j,t])
N[j,t] ~ dpois(lambda[j,t])
lambda[j,t] <- exp(log.lambda.site[site[j]] + log.lambda.year[year_index[t]] + bYear.lam*year1[t] +
                    w[j,t])
w[j,t] <- rho * w[j,t-1] + eps[j,t]
eps[j,t] ~ dnorm(0, tau)

# Bayesian p-value on abundance component (rest of years)
Nnew[j,t]~dpois(lambda[j,t]
FT1[j,t]<-pow(sqrt(N[j,t])-sqrt(lambda[j,t]),2
FT1new[j,t]<-pow(sqrt(Nnew[j,t])-sqrt(lambda[j,t]),2)
}}
T1p <- sum(FT1[1:nsites,1:nyears]) #Sum of squared residuals for actual data set
T1newp <- sum(FT1new[1:nsites,1:nyears]) # Sum of squared residuals for new data set (

# Bayesian p-value
Bp.N <- T1newp > T1p

# Derived parameters
for(t in 1:nyears){
popindex[t] <- sum(lambda[,t]) }

for(t in 1:nyears){
for(s in 1:nspa){
  popindex_zepa[s,t] <- sum(lambda[,t]*indexSPA[,s]) }}

# Expected abundance per year inside model
lam.tot[1] <- popindex[1] # Expected abundance in year 1
for (i in 2:nyears){
lam.tot[i] <- lam.tot[i-1] *
exp(bYear.lam)}
}"
```

Chapter II:

The potential of fallow management to promote steppe bird conservation within the next EU Common Agricultural Policy reform

Journal of Applied Ecology (Accepted)

Ana Sanz-Pérez, Francesc Sardà-Palomera, Gerard Bota, Rahel Sollmann, Nuria Pou, David Giralt

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The potential of fallow management to promote steppe bird conservation within the next EU Common Agricultural Policy reform

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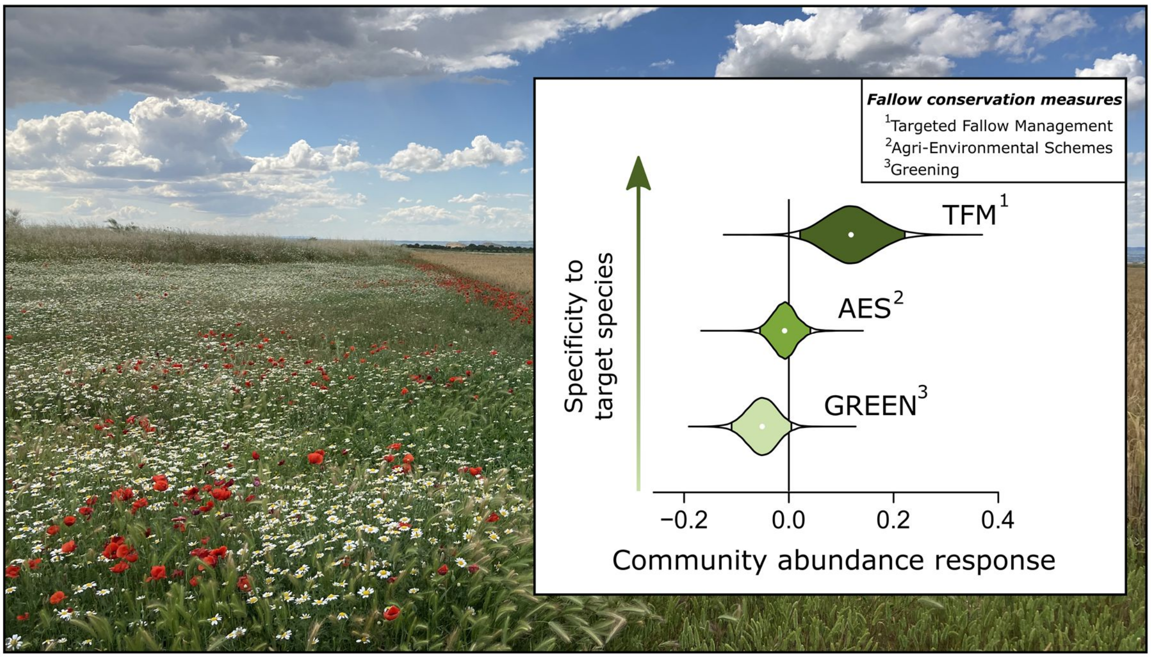
ABSTRACT

1. Agricultural intensification promoted by the European Common Agricultural Policy (CAP) has driven the decline of farmland and steppe bird populations. Policy tools to improve the environmental performance of the CAP – including Agri-Environmental Schemes (AES) and Greening – have often failed, and the new EU agricultural reform (CAP post-2020) offers a new opportunity to integrate effective measures addressing farmland bird declines. Fallow land and its management have proven beneficial for endangered steppe bird species by providing good quality habitat, and therefore has potential to become an effective conservation measure.
2. We used a Hierarchical Distance Sampling community model to evaluate the ability of different conservation regimes to increase the abundance of 37 bird species including endangered steppe birds and other farmland birds in 13,309 ha of fallow land in north-eastern Spain. The conservation regimes were based on different management prescriptions associated with AES, Greening and a local conservation measure promoting extensive fallow management targeting seven steppe bird species (Targeted Fallow Management, TFM).
3. The positive effect of conservation measures increased as their design was more targeted to specific species. TFM increased the abundance of target and other farmland species, while AES and Greening had either no effect or negative effects on bird abundance, respectively. Effects of other Greening conservation measures related to landscape heterogeneity such as crop richness and field size were variable across the community.
4. *Policy implications:* The success of TFM as a conservation tool highlights specific features of fallows and fallow management that enhance populations of endangered and common bird species. We translate our findings into specific guidelines that we recommend including within the new eco-schemes and AES present in the CAP post-2020.

Keywords: Detectability, Population trend, Farmland birds, Hierarchical distance sampling, TRIM, Abundance

GRAPHICAL ABSTRACT



INTRODUCTION

Farmland habitats cover approximately half of Europe's land surface (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011) and have long experienced biodiversity loss (Pe'er et al., 2014). Agricultural intensification has increased since the inception of the Common Agricultural Policy (CAP) in 1962 and has been the main driver of the steep decline in farmland bird populations in Europe (Voříšek et al., 2010).

Several reforms have attempted to counteract the environmental drawbacks of the CAP, starting in 1992 with the McSharry reform and the implementation of Agri-Environmental Schemes (AES), subsidies for farmers to compensate for the loss of income associated with environmentally friendly practices (Batáry, Dicks, Kleijn, & Sutherland, 2015). Subsequent reforms have attempted to complement AES (e.g., decoupling of subsidies from production; Oñate, 2005). However, it was not until the last programming period (2014-2020) that direct payments to farmers were introduced conditional on compliance with three mandatory "greening measures": maintaining permanent grassland, growing a minimum of three different crops, and establishing Ecological Focus Areas (EFA) – landscape elements considered important for biodiversity – on 5% of arable land (European Commission, 2013).

In spite of these efforts, European farmland biodiversity remains threatened (Pe'er et al., 2014). Fallow land is a critical EFA for biodiversity (Pe'er et al., 2017), yet its surface decreased by 18% between 2015 and 2018 (European Commission, 2018). AES have complemented EFAs in fostering fallow land, but have not stopped its decrease (Traba & Morales, 2019). Fallow loss is of great concern for farmland birds in Europe (Voříšek et al., 2010), and it has been linked to steppe bird population declines in Spain (Traba & Morales, 2019), as fallows are key for feeding, mating and nesting (de Juana, 2005). The Iberian Peninsula constitutes the European or global stronghold of many steppe bird populations (Burfield, 2005) as it harbours the so-called "pseudo-steppes", extensive areas of cereal fields alternated with fallows as part of a crop-rotation system (Sainz Ollero, 2013). Contrary to the large and continuous extent of the Iberian pseudo-steppe, other European pseudo-steppe areas in France, Italy, and the Pannonian region are small and isolated (Burfield, 2005). Fallow land in semi-arid farmlands outside Europe is also increasingly important to buffer the impact of agriculture (e.g., Central Kazakhstan; Kamp, Urazaliev, Donald, & Hölzel, 2011).

Steppe birds have narrow micro-habitat requirements, depending on specific vegetation height and cover, and food resources (Robleño, Bota, Giralt, & Recasens, 2017). Suitable vegetation structure is species-specific and can be achieved by applying different agricultural practices before the breeding season (Sanz - Pérez et al., 2019). Promoting the presence and management of fallow land linked to conservation goals on the future CAP Agenda is critical considering that several steppe bird species have become endangered (Burfield, 2005).

The new CAP post-2020 will downscale its legislation from the European to the Member State level, which will provide greater flexibility to address environmental needs (European Commission, 2019). Greening will be substituted by both compulsory and voluntary measures (incentives to adopt practices beneficial for the environment called “eco-schemes”; Pillar I; European Commission, 2019). Agri-Environmental Schemes will be developed by each Member State (Pillar II), enabling further flexibility at the regional scale (European Commission, 2019). The Pillar II will likely receive ~ 25% from the CAP post-2020 budget (European Council, 2020), and at least 30 % of the Pillar II budget will target environmental issues (European Commission, 2019). Using this budget to promote fallow presence and its management could contribute to halting farmland and steppe bird population declines (Tarjuelo, Margalida, & Mougeot, 2020). However, further evidence on the ability of fallow management to enhance bird abundance is critical to develop and advocate for science-based policy changes.

Here, we evaluate the effect of fallow management on the abundance of the farmland bird community of an Iberian pseudo-steppe (Lleida Plain, north-eastern Spain). Three types of conservation measures occur in the area, consisting of fallow fields with different management prescriptions: 1) Targeted Fallow Management (TFM), which is a regional conservation measure promoting extensive fallow management to benefit specific specialist steppe bird species (hereafter “target species”; Sanz - Pérez et al., 2019); 2) AES, which are also aimed at the steppe bird community but adopt more generic management prescriptions (Generalitat de Catalunya, 2020b); and 3) Greening EFAs, which are aimed at biodiversity in general (European Commission, 2013).

We used a Hierarchical Distance Sampling community model to test the effect of fallow surface under the three management regimes on the abundance of 37 farmland bird species of different conservation status. We predicted that the positive effect of conservation measures will increase as their design more explicitly focuses on the requirements of target species. Specifically, we expect that TFM has a positive effect on the abundance of steppe bird specialists (its target species), as it includes management guidelines to fulfil their ecological requirements (e.g., diverse agricultural practices to ensure optimal vegetation structure and food availability; Fig. 1). Although to a lesser extent than TFM, we expect AES to be more efficient than Greening in enhancing steppe and farmland bird abundance, as it includes beneficial management guidelines such as forbidden agricultural management during the breeding season (Fig. 1).

Landscape heterogeneity has shown similar or larger positive effects on biodiversity than farmland management, but with varying effects on the steppe bird community (Concepción & Díaz, 2011; McMahon, Giralt, Raurell, Brotons, & Bota, 2010), as steppe birds are often specialists of homogeneous landscapes (Filippi-Codaccioni, Devictor, Bas, & Julliard, 2010). Greening measures have promoted crop richness and the preservation of field borders, aiming at increasing overall biodiversity through landscape heterogeneity. We therefore also investigated the effects of crop richness and field size on the abundance of the farmland bird community.

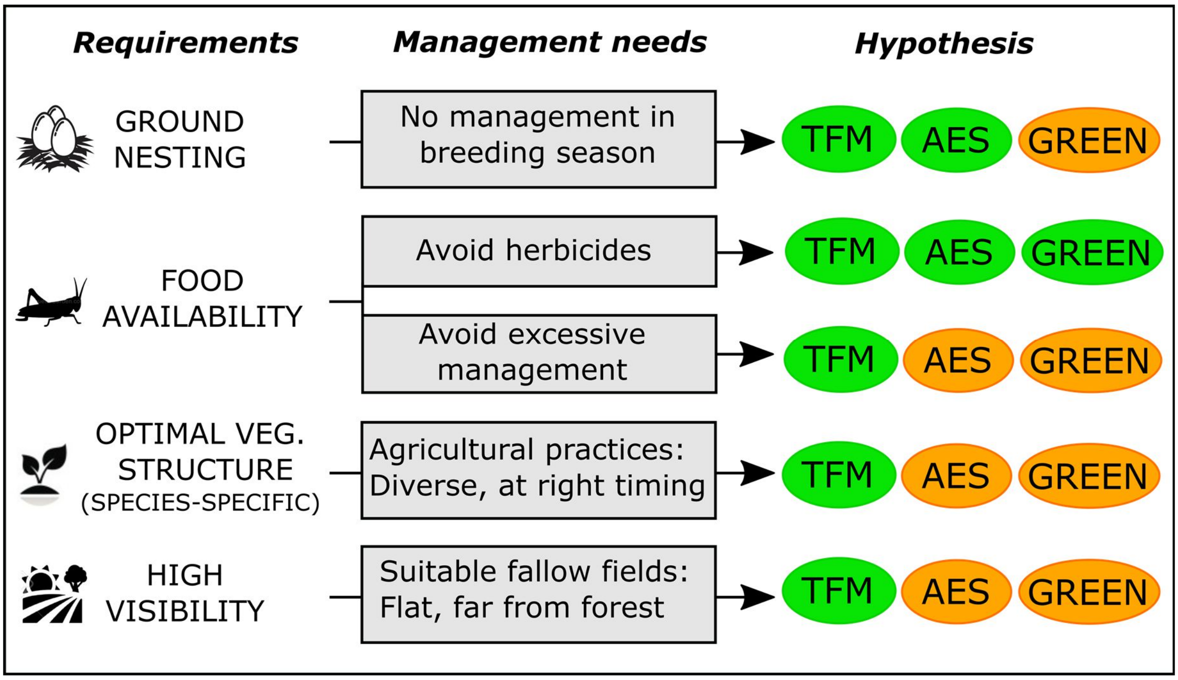


Figure 1. Main ecological requirements of target steppe bird species in an Iberian cereal steppe of north-eastern Spain (Lleida plain), linked to the management needed to meet their requirements, and consequent hypotheses on the success (green) or uncertain outcomes (orange) of the three conservation tools in enhancing bird abundance: Targeted Fallow Management (TFM), Agri-Environmental Schemes (AES) and Greening (GREEN).

MATERIAL AND METHODS

Study area and data collection

The study area was located in the Lleida steppe plain (~3,580 km^2; Catalonia, NE Spain). This semi-arid landscape is characterized by an agricultural mosaic with extensive cultivation of winter cereal crops, woody crops (olive and almond), annual fallow fields and sparse natural shrubland. Extensive grazing is present but generally rare the area.

The study design consisted of 152 transects of 500-m length placed randomly throughout the study area, at a minimum distance of 1,000 m to ensure independence (Buckland et al. 2001). Seventy-five percent of the transects were located within Special Protection Areas designated mainly for steppe bird conservation, belonging to the Natura 2000 European protected areas network. The remaining transects were within steppe-like habitats with similar climatic conditions and landscape characteristics than Special Protection Areas. Transects were sampled annually during the peak breeding season (May) from 2015 to 2019. Bird surveys were performed by 7 professional observers between 6 and 10 a.m. in good weather conditions (i.e., no rain, wind speed < 20km/h, and temperature between 15ºC and 30ºC). Each survey was conducted by a single observer, who walked along the transect and collected data following a distance sampling protocol (Buckland et al. 2001). Birds were recorded on both sides of the transect when first observed either visually or aurally, and observations were assigned to five distance categories (0–25 m; 25–50 m; 50–100 m; 100–200 m; 200–500 m). We limited our analysis to farmland species (i.e., showing general habitat selection patterns for at least one extensive agriculture or dry-land habitat accordying to Estrada, Pedrocchi, Brotons, & Herrando, 2004) that were not migrating during the survey period, and with more than 15 detections throughout the study. This included 26 common species and 11 species of conservation concern at the European and/or regional scale (Table 1). Seven species of the community - including both common and endangered species – were steppe birds constituting the target species from the TFM conservation measure (Table 1; Section 2.3.1).

Hierarchical Distance Sampling (HDS) community model

We fitted a multi-year HDS community model following Sollmann et al. (2016) (see Appendix D for JAGS model code). The process component models local abundance *N* for a given species *s* at a transect *j* and year *t* following a Poisson distribution (1). Variation in expected abundance λ_{sjt} is then modelled on the log scale as a function of an intercept and site-year specific co-variates (2):

$$N_{sjt} \sim Poisson(\lambda_{sjt}) \tag{1}$$

$$\log(\lambda_{sjt}) = \alpha_{st} + sp.site_{sj} + \mathbf{\beta'_s X_{jt}} \tag{2}$$

$$\alpha_{st} \sim Normal(\mu.\alpha, \sigma.\alpha) \tag{3}$$

$$sp.site_{sj} \sim Normal(0, \sigma.sp.site) \tag{4}$$

where the species and year-specific intercept α_{st} is modelled as a random effect with hyperparameters $\mu.\alpha$ and $\sigma.\alpha$ accounting for the dependence of the data within years for each species (3), and $sp.site_{sj}$ is a random site effect that accounts for the dependence of the data within transects for each species (4). The beta coefficients $\boldsymbol{\beta'}$ are related to the site and year-specific habitat co-variates $\boldsymbol{X_{jt}}$. Under the community model approach, the $\boldsymbol{\beta'}$ parameters are species-specific and are modelled with a normally distributed random effect (5):

$$\beta'_s \sim Normal(\mu_{\boldsymbol{\beta}}, \sigma_{\boldsymbol{\beta}}) \tag{5}$$

where $\mu_{\boldsymbol{\beta}}$ and $\sigma_{\boldsymbol{\beta}}$ (the hyperparameters) constitute the community parameters shared by all species.

The observation component of the model links the true abundance of a given species at a site and year N_{sjt} to the raw counts Y_{sjt} through the probability of detection *p* (6):

$$Y_{sjt} \sim Binomial(N_{sjt}, p_{sjt}) \tag{6}$$

In distance sampling, *p* is assumed to be perfect at the transect line and to decrease as a function of perpendicular distance *x* from the transect following a detection function (Buckland et al., 2001). We used a half normal detection function (7):

$$g(x, \sigma) = exp\left(\frac{-x^2}{2\sigma^2}\right) \tag{7}$$

where σ is the scale parameter. With binned distance observations, detection probability for each distance bin *k* can be calculated as the integral of *g(x)* over the break points of *k:*

$$p_k = \frac{\int_{b_k}^{b_{k+1}} g(x)dx}{v_k} \tag{8}$$

where ***b*** are the *K+1* breakpoints of the *K* distance categories and v_k is the width of the k-th distance category. In our study, v_k was 25, 25, 50, 100, and 300 m from the first to the fifth distance category, and the strip width was 500 m. Because individuals are assumed to be uniformly distributed around the transects, the individual probability of occurrence in a distance bin Ψ_k is

$$\Psi_k = \frac{v_k}{strip\ width} \tag{9}$$

Therefore, the cell probability of detection π_k is $p_k \times \Psi_k$, and the overall probability of detection (p_{sjt}, eq. 6) is the sum over all π_k (Kéry & Royle, 2016).

We modelled σ from the half normal detection function (7) on the log scale (10). The intercept constituted a species random effect with hyperparameters $\mu.\sigma$ and $\sigma.\sigma$ (11) and observer was included as random effect following a zero-mean normal distribution with variance $\sigma.obs$ (12).

$$\log(\sigma_{sjt}) = \alpha_s + Observer_{jt} \tag{10}$$

$$\alpha_s \sim Normal(\mu.\sigma, \sigma.\sigma) \tag{11}$$

$$Observer_{jt} \sim Normal\ (0, \sigma.obs) \tag{12}$$

Predictors of bird abundance

We extracted year-specific variables within 500-m buffers around each transect. For the fallow variables, we extracted the area in hectares (ha) of each fallow type (TFM, AES and Greening) within the buffer of each transect and year (Table 2) and log-transformed these areas. The AES fallow type presented the lowest average area per transect (mean (SD) = 2.16 ha (6.03)), corresponding to half of the average TFM fallow area and one-third of the average Greening fallow area (Table 2). We also extracted landscape heterogeneity variables, related to landscape composition (crop richness) and landscape configuration (field size). We scaled all co-variates for analyses, and we modelled all co-variate effects as fixed across years.

Fallow variables

Fallow fields under TFM belonged to a local compensatory conservation measure included in the Environmental Impact Assessment of the Segarra-Garrigues irrigation system. The measure consists in the rental and management of fallow fields by the regional government within Special Protection Areas to promote optimal habitat for seven target species, which where the main steppe bird species found in the study area (Table 1; Mañosa, Bota, Giralt, & Estrada, 2020). TFM targets bird species considered as steppe specialists because they are especially vulnerable to agricultural intensification and most of them are endangered (Table 1).

Table 1. Information on the 37 farmland bird species included in the HDS community model to study the effect of agricultural management on bird abundance in an Iberian cereal steppe of north-eastern Spain (Lleida plain) during 2015 – 2019. Target species of the Targeted Fallow Management conservation measure are marked by a cross.⬇

Common name	Scientific name	Target species[a]	Conservation status		Number of detections	Transects occupied (%)
			EU 27[b]	Catalonia[c]		
Eurasian skylark	*Alauda arvensis*		LC	LC	70	6.17
Red-legged partridge	*Alectoris rufa*		LC	LC	169	19.01
Little owl	*Athene noctua*		LC	VU	32	4.01
Eurasian Stone-curlew	*Burhinus oedicnemus*	X	LC	LC	170	18.8
Greater short-toed lark	*Calandrella brachydactyla*	X	LC	EN	71	4.56
European goldfinch	*Carduelis carduelis*		LC	LC	206	17.54
European greenfinch	*Carduelis chloris*		LC	LC	117	11.36
Lesser short-toed lark	*Alaudala rufescens*		LC	LC	53	2.81
Common linnet	*Linaria cannabina*		LC	LC	138	10.56
Montagu's harrier	*Circus pygargus*		LC	VU	37	4.68
Great spotted cuckoo	*Clamator glandarius*		LC	VU	46	5.25
European roller	*Coracias garrulus*	X	LC	LC	130	14.18
Feral pigeon	*Columba livia var. domestica*		LC	LC	75	8.83
Eurasian jackdaw	*Corvus monedula*		LC	VU	387	32.52
Stock dove	*Columba oenas*		LC	LC	121	13.09
Common wood pigeon	*Columba palumbus*		LC	LC	616	50.07
Common house martin	*Delichon urbicum*		LC	LC	26	3.35
Eurasian hobby	*Falco subbuteo*		LC	LC	26	2.95
Common kestrel	*Falco tinnunculus*		LC	LC	120	15.02
Crested/Thekla's Lark	*Galerida sp.*		LC	LC	2931	92.21
Barn swallow	*Hirundo rustica*		LC	LC	505	44.44
Iberian grey shrike	*Lanius meridionalis*		VU	EN	60	7.09
Woodchat shrike	*Lanius senator*		LC	LC	84	8.56
Woodlark	*Lullula arborea*		LC	LC	157	13.82
European bee-eater	*Merops apiaster*		LC	LC	425	39.61
Calandra lark	*Melanocorypha calandra*	X	VU	LC	2731	68.72
Corn bunting	*Emberiza calandra*		LC	LC	3335	85.08
Eurasian tree sparrow	*Passer montanus*		LC	LC	284	23.31
Rock sparrow	*Petronia petronia*		LC	LC	31	3.48
Eurasian magpie	*Pica pica*		LC	LC	775	60.03
Pin-tailed sandgrouse	*Pterocles alchata*	X	LC	VU	80	6.82
Black-bellied sandgrouse	*Pterocles orientalis*	X	EN	EN	17	1.07
Red-billed chough	*Pyrrhocorax pyrrhocorax*		LC	LC	89	8.96
European serin	*Serinus serinus*		LC	LC	177	13.51
European turtledove	*Streptopelia turtur*		NT	LC	69	8.02
Little bustard	*Tetrax tetrax*	X	VU	EN	282	25.38
Eurasian hoopoe	*Upupa epops*		LC	LC	318	31.92

[a] Target species of the TFM conservation measure (Mañosa et al., 2020)

[b] European conservation status according to the IUCN Red List assessment for the 27 EU Member States (LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; BirdLife International, 2015)

[c] Regional conservation status according to the Catalogue of Endangered Species in Catalonia (pending approval; Generalitat de Catalunya, 2020a) (LC = Least Concern; VU = Vulnerable; EN = Endangered)

TFM has occurred annually since 2014, and consists of specific agricultural practices (Table 2; Sanz - Pérez et al., 2019). The exact timing and type of agricultural practice is adapted to the target species present in each Special Protection Area to meet species-specific requirements during breeding (Giralt et al., 2018; Mañosa et al., 2020).

Fallow fields under AES aim to benefit the whole farmland bird community (Table 2) with special emphasis on steppe birds. Because AES fallow fields were implemented voluntarily by farmers in exchange for subsidies, their location was not always optimal for steppe birds (e.g. next to a road). The AES management prescriptions consist of applying at least one agricultural practice every two years between September-April (Table 2). However, farmers often perform intensive management before the breeding season (Table 2; Giralt et al., 2018) resulting in fallow fields mostly cleared from vegetation.

The fallow fields under Greening were acquired by farmers as a type of EFA (chosen among other EFA types) to receive the basic CAP payments. Greening prescriptions for fallow management are targeted toward biodiversity in general, and therefore are very generic, with no timing or periodicity restrictions regarding management (Table 2).

Some fallow fields were under TFM, AES and/or Greening simultaneously. In those cases, we assigned a fallow field to the category with the most targeted management for steppe and farmland bird conservation (i.e., TFM > AES > Greening).

Landscape heterogeneity variables

We quantified crop richness, defined as the number of different crops within each buffer per year, by using an annual crop land use map from the regional government (Unique Agrarian Statement/DUN; Generalitat de Catalunya, 2019b). We used the same crop classification as regional farmers do to receive Greening payments (Appendix A; Generalitat de Catalunya, 2019a).

We quantified field size by using the regional Geographic Information System of Farming Land (SIGPAC; Generalitat de Catalunya, 2019c). We calculated the yearly average field size for a transect by averaging the total area (ha) of all agricultural fields intersecting with its buffer.

Model implementation

We implemented the model in a Bayesian framework, using the software JAGS version 4.3.0 (Plummer, 2003), accessed through the 'jagsUI' R package version 1.5.0 (Kellner, 2018). The model code is available in the Appendix D. We used normal (0,10) and uniform (0,500) priors for the mean and SD hyperparameters of the species random effects, respectively, and uniform (0,10) priors for the SD of the observer random effect. We ran three parallel Markov chains with 500,000 iterations and a burn-in of 50,000 iterations, thinning chains by 10. We tested for chain convergence by using the Gelman-Rubin statistic (values < 1.1; Gelman et al. 2013). We assessed model fit by calculating Bayesian p-values (Gelman, Meng, & Stern, 1996) based on Freeman-Tukey residuals (Appendix C). We report parameter estimates as the posterior means and standard deviations. We considered coefficients as significant when their 95% Bayesian Credible Interval did not overlap zero. We calculated the posterior probability of a positive effect of a predictor variable as the proportion of all posterior samples of the respective coefficient > 0.

Table 2. Information on fallow field types included in a HDS community model to determine the effect of fallow management on the abundance of a farmland bird community in an Iberian cereal steppe of north-eastern Spain (Lleida plain) during 2015 – 2019.

	TFM[a]	**AES**[b]	**GREEN**[c]
Summary statistics			
Mean (SD)	4.52 (9.77) ha	2.16 (6.03) ha	5.92 (6.07) ha
Range	0 – 90.12 ha	0 - 69.19 ha	0 - 51.06 ha
Total area	4771.22 ha	2282.71 ha	6255.08 ha
% of transect (buffer) area across years	3.85 %	1.63 %	4.82 %
Main features			
Target	Steppe birds (Target species; Table 1)	Farmland bird community	Biodiversity
Who selects fallow fields	Experts conditional on agreement of farmers	Farmers (voluntary measure for extra payment)	Farmers (compulsory measure for basic payment)
Criteria to select fallow fields	Suitable conditions for target species (e.g., location, slope)	Minimum size: 0.5 ha	None
Forbidden management	None (but avoid herbicide when possible)	Herbicide	Herbicide
Most common management applied	- Shredding - Ploughing - Alfalfa sowing - Grazing - No management	Ploughing	Ploughing
Periodicity of management (prescription)	1-3 times per year	Minimum once every two years	None
Most frequent periodicity of management	1-2 times/year	More than 2-3 times/year	More than 2-3 times/year
Criteria to select type and periodicity of management	Suitable vegetation structures for target species requirements (expert's criteria)	Weed control (farmer's criteria)	Weed control (farmer's criteria)
Timing of management	Before breeding season (1st February – 15th April)	Wide period (1st September – 15th April)	All year
Evaluation and adaptation	Yearly	None	None
References	(Giralt et al., 2018) (Sanz - Pérez et al., 2019)	(Generalitat de Catalunya, 2020b)	(Generalitat de Catalunya, 2019a)

[a] Targeted Fallow Management fallow fields

[b] Agri-Environmental Schemes fallow fields

[c] Greening fallow fields

RESULTS

Community response

The only variable showing a significant positive effect on mean community abundance was TFM fallow $(\mu_{\beta}\ (SD) = 0.12\ (0.05))$, in contrast to the negative, but marginally non-significant, community level effect of Greening fallows $(\mu_{\beta}\ (SD) = -0.05\ (0.03))$. AES fallow fields had no significant effect on mean community abundance $(\mu_{\beta}\ (SD) = -0.008\ (0.02))$. The community showed a significant negative response to crop richness and field sizes $(\mu_{\beta}\ (SD) = -0.15\ (0.07);\ \mu_{\beta}\ (SD) = -0.18\ (0.07))$.

Species-specific abundance

The only variable with significantly positive species-specific effects was TFM fallow area, significantly increasing the abundance of four target species (Pin-tailed sandgrouse, Little bustard, European roller, and Eurasian Stone-curlew; see Table 1 for scientific names) and four other species (Fig. 2). The posterior probability of a positive effect was > 70% for 20 species, including five target species (Fig. 2). TFM fallow fields had a significant negative effect on the abundance of two species (Fig. 2). Species-specific effects of AES fallow area were non-significant, and the posterior probability of a positive effect was > 70 % for only one species (Fig. 2). Similarly, the posterior probability of a positive effect of Greening fallow fields was > 70% for only three species, including one target species (Fig. 2). Greening fallow fields did, however, have a significant negative effect on the abundance of three species, including one target species (Greater short－toed lark; Fig. 2).

Other predictors

Crop richness had a significant positive effect on the abundance of four species (including the target species Little bustard; Fig. 3) and a posterior probability of a positive effect > 70 % for 14 species including four target species, but also had significant negative effects on 11 species (including the target species Pin-tailed sandgrouse and Greater short-toed lark; Fig. 3). Field size had a significant positive effect on the abundance of two species (including the target species Black-bellied sandgrouse) and the posterior probability of a positive effect was > 70 % for 6 species, including three target species (Fig. 3). Field size had a significant negative effect on the abundance of 9 species (including the target species Little bustard). Bird populations showed only weak fluctuations over time indicating population stability, according to α_{st} (Table B1, Appendix B).

Model fit

The model presented a good fit (i.e., Bayesian p-value > 0.1 and < 0.9; Table C1, Appendix C) for the abundance component of the community and individual species, and for the detection component of all species except the Calandra lark and Corn bunting, causing a low community-wide Bayesian p-value. Lack of fit for the two problem species was due to very few extreme residuals (for 12 and 9 of the 760 transect-year combinations, respectively). Thus, we considered that the low community Bayesian p-value did not invalidate overall model results, but that estimates for these species-year-transect combinations may be inaccurate.

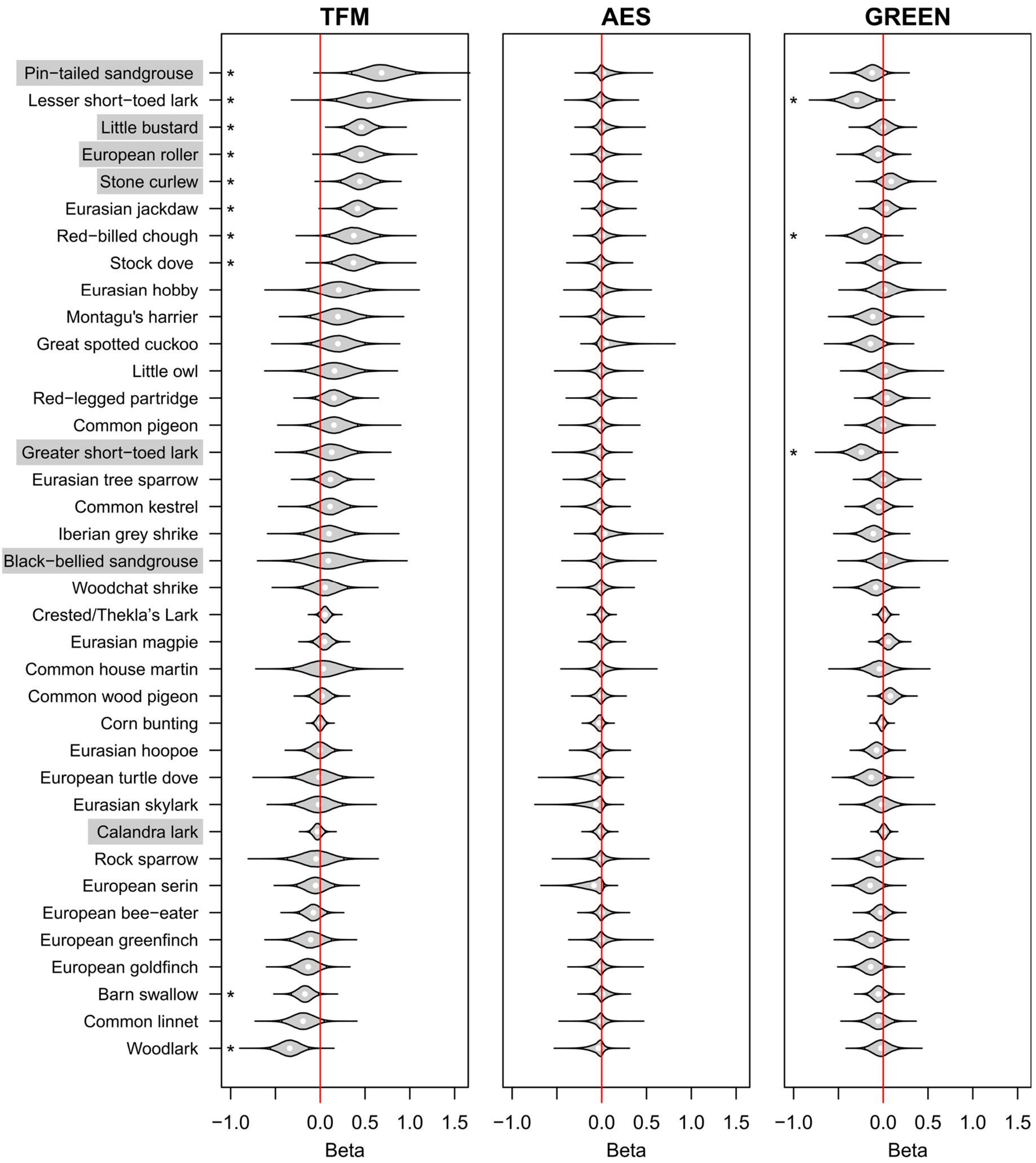


Figure 2. Violin plots showing the posterior distributions (black outline: full posterior; white points: mean; inner grey polygon: 95% credible interval) of the species-specific coefficients β'_s for the variables Targeted Fallow Management (TFM), Agri-Environmental Schemes (AES) and greening (GREEN), estimated within a HDS community model for 37 farmland species sampled during 2015 - 2019 in an Iberian cereal steppe (Lleida Plain, Spain). Species are presented by decreasing values of the Fallow TFM coefficient; target species are highlighted in grey. Significant effects are indicated by an asterisk.

DISCUSSION

Our findings indicate that the efficiency of the principal CAP conservation tools to enhance the abundance of a farmland bird community, including highly specialized and endangered steppe birds, depended to a great extent on the degree of targeted management for specific species. Targeted Fallow Management increased the abundance of most steppe birds (target species) and other farmland birds as expected, yet AES did not benefit the community. Greening fallows showed no or even negative effects on steppe bird abundance, confirming our expectations. Non-fallow Greening measures promoting landscape heterogeneity showed variable effects across the community, being mostly negative or neutral for specialist steppe bird species.

Targeted Fallow Management

We expected TFM to benefit steppe birds because it targets these species both in spatial location (Mañosa et al., 2020) and management prescription (Table 2; Sanz - Pérez et al. 2019). Steppe birds can be highly specialized, thus, specific measures shaping vegetation structure of fallow fields are essential to meet their requirements (Robleño et al., 2017). Our results validate the relationship between TFM and habitat suitability for steppe bird occurrence found by Sanz-Pérez et al. (2019), which is further corroborated by the recent increase in the populations of some of the studied species (e.g., the Pin-tailed sandgrouse; Bota et al., 2020; Mañosa et al., 2020)

Our results also demonstrate the potential of TFM to increase the abundance of the entire farmland bird community. Applying different agricultural practices creates a landscape mosaic of different fallow types that allows niche segregation and benefits not only target species, but also other farmland birds. Indeed, TFM had a high probability of benefitting populations of other common (e.g., Red-billed chough) and endangered farmland species (e.g., Montagu's harrier). These results suggest that steppe species could be considered an umbrella group for the farmland bird assemblage, likely owing to their high co-occurrence and similar sensitivities to disturbance (Fleishman, Murphy, & Brussard, 2000; see also Moreno, Morales, & Traba, 2013). Our results contradict findings by Santana et al (2014) suggesting that flagship steppe bird species conservation within Special Protection Areas does not benefit the broader bird community, which is likely due to different landscape contexts and/or conservation measures (e.g., fallow land has increased by 17% in our study area, in contrast to its declining trend in the study of Santana et. al 2014).

Agri-Environmental Schemes

In contrast to our expectations, AES did not benefit the community or species-specific abundances. AES has previously been shown inefficient to enhance endangered species abundance due to poor targeting (Kleijn et al., 2006), and it is likely that AES management prescriptions still allow for excessive management by farmers. Farmers consider that fallows promote harmful weeds and apply intensive weed control (i.e., ploughing > 2-3 times/year; Giralt et al., 2018), which likely results in structurally simple and similar fallows that could result unsuitable for most species at the start of the breeding season. Alternatively, the presence of TFM (i.e., birds selecting TFM over AES fallow fields) or the low prevalence of AES in the study area may explain its lack of effectiveness (see also Kleijn et al., 2011).

Greening

Greening EFA fallows did not increase community abundance, which is in accordance with the predicted low success of EFAs in enhancing animal populations (Pe'er et al., 2014, 2017). Greening and AES fallows have common regulations, and therefore some of the reasons behind their lack of success are probably shared. Greening fallows further allow agricultural management during the breeding period, which could cause the negative effects observed for

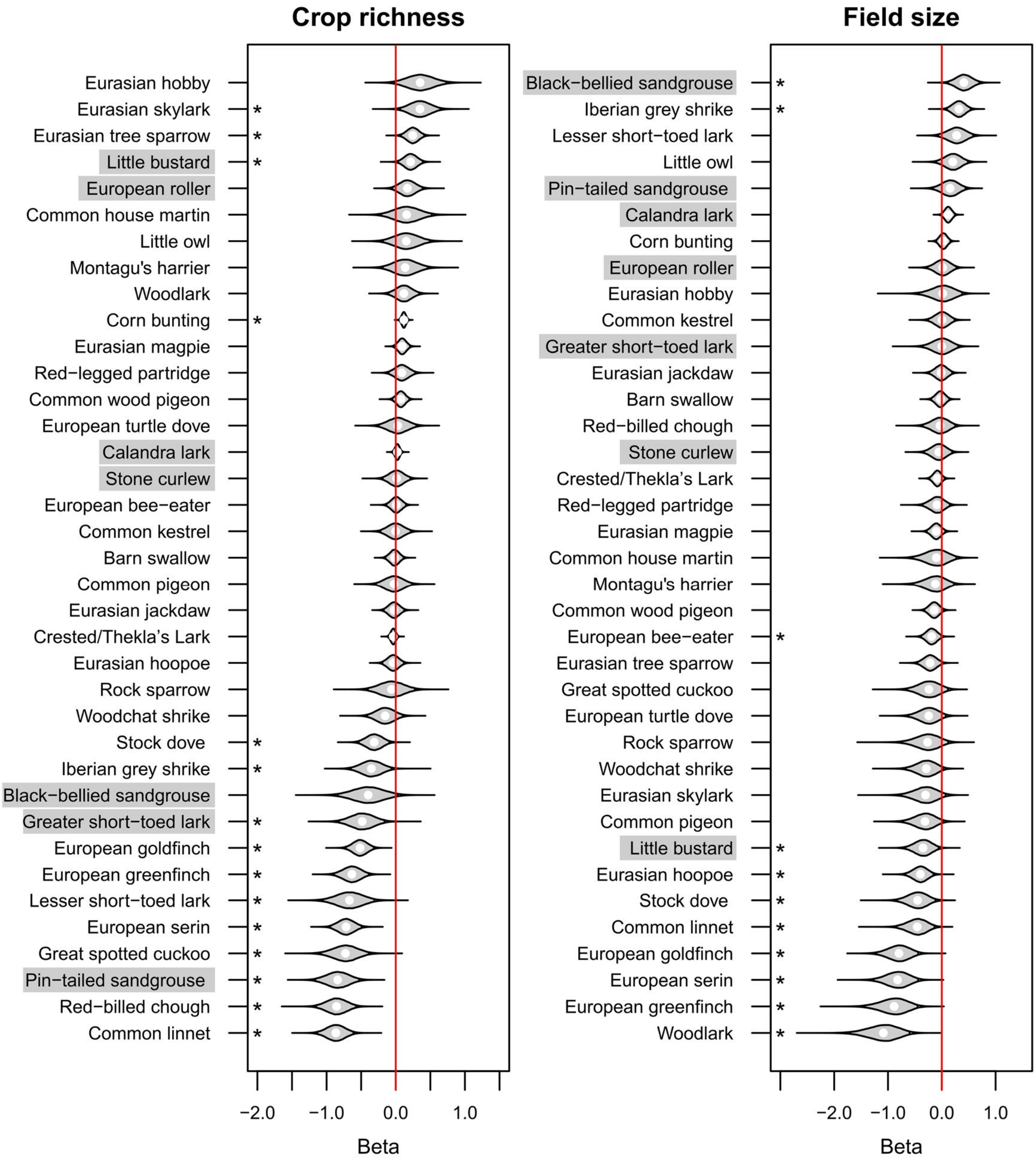


Figure 3. Violin plots showing the posterior distributions (black outline: full posterior; white points: mean; inner grey polygon: 95% credible interval) of the species-specific coefficients β'_s for crop richness (B) and field size (C) (i.e., greening measures), estimated with a HDS community model for 37 farmland species sampled during 2015 - 2019 in an Iberian cereal steppe (Lleida plain, Spain). Species are presented by decreasing values of the crop richness (left panel) and field size (right panel) coefficients; target species are highlighted in grey. Significant effects are indicated by an asterisk.

some species. Greening measures promoting landscape heterogeneity had variable results across the community. Habitat heterogeneity does not generally benefit steppe specialists, which are usually ground-nesting species linked to structurally simple habitats (Filippi-Codaccioni et al., 2010; Pickett & Siriwardena, 2011). Our study supports this notion for most target species except the Little bustard, probably because of its need of habitat complementary to fulfil the requirements of its life cycle (Morales, Traba, Carriles, Delgado, & de la Morena, 2008). Promoting crop structural diversity (i.e., involving crop management and vegetation structure) rather than general crop diversity has already been advocated for the CAP post-2020 (Josefsson, Berg, Hiron, Pärt, & Eggers, 2017), as it could benefit ground-nesting species such as our target species.

Conservation implications

The TFM fallow land evaluated within our study represents exceptional conditions for successful target species conservation (e.g., fallow management in optimal areas, expert criteria to choose timing and type of management, exhaustive monitoring). Although the features of TFM are probably too costly and specific to become a general policy prescription, our results provide a basis for developing guidelines towards conservation of farmland and steppe birds. Here, we translate the characteristics of TFM that make them efficient for conservation into specific recommendations for eco-schemes and AES within the CAP post-2020.

Voluntary eco-schemes are considered simple measures attractive to farmers designed by each Member State. We recommend the inclusion of fallow land as an eco-scheme with two simple requirements essential for its success: 1) no agricultural management during the breeding season and 2) guaranteeing the presence of some vegetation cover at the beginning of the breeding season, avoiding bare soil fields.

AES can be designed and applied at national or regional level (European Commission, 2019), which makes them the perfect policy framework for adjusting conservation measures to local conditions and specialist species (see also Kleijn et al., 2006). We propose adding two requirements to AES regimes: 1) Limiting the number of management actions to 1-3 times/year, outside the breeding season. Vegetation encroachment resulting from fallow land abandonment is as detrimental to steppe bird habitat suitability as excessive management (Sanz - Pérez et al., 2019), and is also despised by farmers, for fear that it will hamper future crop productivity. Promoting moderate fallow management might help changing farmers' attitudes towards fallows and result in a win-win strategy (Tarjuelo et al., 2020). 2) Aligning the type and timing of the agricultural practices applied with the conservation goals of each Special Protection Area, to promote suitable fallows adapted to the species with priority conservation status in each Special Protection Area.

The European cereal steppe system is a globally significant hotspot for steppe bird diversity and conservation, and our findings are thus of high value for EU Member States harboring this system. Beyond that, they have the potential to inform bird conservation in cultivated areas of the Eurasian steppe belt, where fallow management could constitute a tool to combat the ongoing land abandonment and benefit steppe birds (Ioffe, Nefedova, & Kirsten, 2012; Kamp et al., 2011). Moreover, the presence of fallow land and its management has proved positive for sustaining farmland bird populations in central and northern Europe (e.g., Bracken & Bolger, 2006; Doxa et al., 2010), and elsewhere (e.g., Van Buskirk & Willi, 2004). Our findings thus make an important contribution in the global search for efficient pathways to conserve endangered species in agricultural systems where food production and biodiversity need to co-exist.

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subsequent drafts and gave final approval for publication. F.S. - P. and D.G. coordinated fieldwork and G.B. secured funding.

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APPENDIX

Appendix A: Crop classification

In order to receive the greening payment in our study region, farmers are required to have 2-3 different crops (depending on the agricultural area) within their land. We evaluated the greening crop diversification measure by following the same crop classification farmers must apply. In this measure, crops are considered different if they belong to 1) different botanic genus (e.g., oats *Avena sativa*, barley *Hordeum vulgare*, wheat *Triticum spp.*), 2) different species from the genus Brassicae (e.g., rapeseed *Brassica napus*, cabbage *Brassica oleracea*), Solanaceae (tomato *Solanum lycopersicum*, potato *Solanum tuberosum*), and Cucurbitaceae (melon *Cucumis melo*, watermelon *Citrullus lanatus*), 3) fallows, and 4) grass or other herbaceous forages (Generalitat de Catalunya 2019).

Appendix B: Yearly variation in estimates

Yearly variation in abundance

We investigated random fluctuations in abundance over time that were not related to the studied variables to assess the stability of the studied populations. We did this by extracting the intercept of the abundance component (α_{st}, eq. 2,3, main text), which is specific to year and species. The intercept values did not present extreme fluctuations (Table B1)

Yearly variation in the TFM beta coefficient

The prevalence of TFM in our study landscape increased progressively across years, so we ran an additional model in order to test whether there was yearly variation in the effect of TFM due to its increasing prevalence. To account for yearly changes in the effect of TFM, we allowed the respective coefficient to vary across years. Specifically, we modelled the TFM $\boldsymbol{\beta}'$ for a given species as normally distributed across years:

$$\beta.TFM_{st} \sim Normal(\mu_{\beta.TFM_s}, \sigma.t),$$

where $\mu_{\beta.TFM_s}$ is the species-specific mean and $\sigma.t$ is a common standard deviation shared by all species. The results from this model showed no variation in the beta coefficient of the TFM variable across years and thus suggest that the effect of TFM on abundance did not depend on its prevalence (Table B2).

Table B1. Results of the species and year specific intercept of the abundance component obtained in the Hierarchical Distance Sampling community model used determine the effect of fallow management on the abundance of a farmland bird community in an Iberian cereal steppe of north-eastern Spain (Catalonia) during 2015 – 2019

	2015	2016	2017	2018	2019
Eurasian skylark	0.513	0.471	0.438	0.227	0.376
Red-legged partridge	1.175	0.965	1.218	0.941	1.608
Little owl	0.208	0.069	0.136	0.18	0.265
Stone curlew	1.23	0.972	0.778	0.688	0.435
Greater short-toed lark	0.195	0.09	0.189	0.23	0.209
European goldfinch	0.442	0.465	0.512	0.843	1.11
European greenfinch	0.125	0.353	0.487	0.501	0.636
Lesser short-toed lark	0.035	0.06	0.078	0.056	0.049
Common linnet	0.132	0.136	0.221	0.336	0.7
Montagu's harrier	0.092	0.154	0.111	0.083	0.164
Great spotted cuckoo	0.139	0.123	0.044	0.103	0.084
European roller	0.364	0.24	0.343	0.32	0.389
Common pigeon	0.228	0.159	0.181	0.102	0.275
Eurasian jackdaw	0.9	0.773	0.892	0.971	1.393
Stock dove	0.279	0.22	0.343	0.279	0.464
Common wood pigeon	1.782	1.797	2.097	2.517	2.268
Common house martin	0.101	0.164	0.094	0.134	0.109
Eurasian hobby	0.059	0.201	0.122	0.081	0.089
Common kestrel	0.51	0.407	0.595	0.241	0.491
Crested/Thekla’s Lark	11.711	11.707	11.953	11.59	14.134
Barn swallow	1.074	1.832	1.983	1.957	1.941
Iberian grey shrike	0.169	0.124	0.131	0.218	0.285
Woodchat shrike	0.184	0.135	0.334	0.214	0.247
Woodlark	0.279	0.316	0.341	0.281	0.238
European bee-eater	1.271	1.156	1.694	1.427	1.949
Calandra lark	5.831	7.85	6.869	7.051	7.14
Corn bunting	7.996	10.874	13.001	14.44	12.722
Eurasian tree sparrow	0.635	0.825	0.789	0.723	0.726
Rock sparrow	0.062	0.096	0.093	0.054	0.077
Eurasian magpie	2.615	1.893	2.275	2.008	2.447
Pin-tailed sandgrouse	0.073	0.065	0.101	0.082	0.108
Black-bellied sandgrouse	0.013	0.047	0.046	0.022	0.093
Red-billed chough	0.054	0.127	0.12	0.112	0.139
European serin	0.057	0.307	0.26	0.328	0.27
European turtle dove	0.216	0.095	0.231	0.275	0.232
Little bustard	0.646	1.082	0.506	0.629	0.379
Eurasian hoopoe	0.929	1.195	0.946	1.006	0.874

Table B2. Results of the TFM beta coefficient obtained in an additional Hierarchical Distance Sampling community model that tested whether there was a change in the effect of TFM in the abundance of the 37 species across years in an Iberian cereal steppe of north-eastern Spain (Catalonia) during 2015 – 2019

Species	2015	2016	2017	2018	2019
Eurasian skylark	-0.027	-0.02	-0.024	-0.021	-0.022
Red-legged partridge	0.152	0.152	0.149	0.152	0.149
Little owl	0.162	0.16	0.163	0.162	0.163
Stone curlew	0.44	0.453	0.449	0.443	0.445
Greater short-toed lark	0.137	0.133	0.13	0.135	0.136
Goldfinch	-0.138	-0.134	-0.129	-0.132	-0.135
European greenfinch	-0.11	-0.11	-0.106	-0.112	-0.116
Lesser short-toed lark	0.569	0.571	0.571	0.57	0.567
Common linnet	-0.2	-0.193	-0.201	-0.192	-0.185
Montagu's harrier	0.193	0.195	0.198	0.196	0.198
Great spotted cuckoo	0.199	0.199	0.192	0.198	0.199
European roller	0.467	0.467	0.464	0.466	0.465
Common pigeon	0.15	0.15	0.149	0.15	0.155
Eurasian jackdaw	0.415	0.419	0.421	0.422	0.428
Stock dove	0.374	0.381	0.374	0.38	0.386
Common wood pigeon	0.03	0.022	0.018	0.03	0.019
Common house martin	0.026	0.028	0.026	0.027	0.028
Eurasian hobby	0.202	0.205	0.203	0.203	0.2
Common kestrel	0.116	0.113	0.113	0.109	0.117
Crested/Thekla’s Lark	0.063	0.053	0.037	0.064	0.041
Barn swallow	-0.174	-0.162	-0.175	-0.182	-0.166
Iberian Grey Shrike	0.112	0.11	0.108	0.114	0.104
Woodchat shrike	0.053	0.057	0.053	0.057	0.053
Woodlark	-0.346	-0.347	-0.34	-0.345	-0.341
European bee-eater	-0.071	-0.077	-0.077	-0.074	-0.078
Calandra lark	-0.042	-0.018	-0.032	-0.027	-0.031
Corn bunting	-0.002	-0.006	0.006	0.007	-0.011
Eurasian tree sparrow	0.124	0.113	0.125	0.103	0.125
Rock sparrow	-0.04	-0.041	-0.039	-0.043	-0.039
Eurasian magpie	0.047	0.055	0.042	0.046	0.052
Pin-tailed sandgrouse	0.693	0.688	0.692	0.693	0.692
Black-bellied sandgrouse	0.09	0.089	0.09	0.091	0.09
Red-billed chough	0.381	0.387	0.384	0.386	0.377
European serin	-0.051	-0.053	-0.05	-0.051	-0.052
European turtle dove	-0.003	-0.001	-0.002	0.002	0.004
Little bustard	0.451	0.455	0.45	0.458	0.458
Eurasian hoopoe	-0.003	-0.004	-0.013	0.003	-0.004

Appendix C: Model residuals and Bayesian p-values

We assessed model fit by calculating Bayesian p-values based on Freeman-Tukey residuals for both the detection and abundance component. The Freeman-Tukey residuals *R,* take the general form:

$$R(\mathbf{y},\boldsymbol{\theta}) = \sum \left(\sqrt{y} - \sqrt{E(y)}\right)^2$$

where $\mathbf{y}$ is a collection of data, $\boldsymbol{\theta}$ are the parameters of the model describing $\boldsymbol{y}$ and $\mathrm{E}(\boldsymbol{y})$ is the expected value of $\boldsymbol{y}$ under the model of consideration. We calculated Freeman-Tukey residuals for both the observed data and a new data set generated from the model under consideration. We used the calculated residuals to obtain the Bayesian p-value, which is the percentage of times (i.e., MCMC iterations) the residuals from the newly generated data are larger (or smaller) than those of the original data (Hobbs & Hooten 2015).

Detection residuals

For the detection component, we first generated a new number of individuals observed per species *s*, transect *j* and year *t* from the model parameters:

$$Y.new_{sjt} \sim Binomial(N_{sjt}, p_{sjt})$$

We then calculated the Freeman Tukey residuals (*Robs* and *Robs.n*) by comparing the expected total number of individuals detected to both the observed (*Y*) and the generated number of individuals observed (*Y.new*) at each iteration *i* of the Markov chain:

$$Robs_s = \sum_j \sum_t (\sqrt{Y_{sjt}} - \sqrt{p_{sjt} * N_{sjt}})^2$$

$$Robs.n_s = \sum_j \sum_t (\sqrt{Y.new_{sjt}} - \sqrt{p_{sjt} * N_{sjt}})^2$$

We calculated the species-specific Bayesian p-values (*Bp.obs.sp*) as:

$$Bp.obs.sp_s = \frac{\sum_i Robs.n_s > Robs_s}{n_{iter}}$$

We calculated the community Bayesian p-value (*Bp.obs.com*) as:

$$Bp.obs.com = \frac{\sum_i \sum_s Robs.n_s > Robs_s}{n_{iter}}$$

Abundance residuals

For the abundance component, we first generated a new abundance per species *s*, transect *j* and year *t* from the model parameters:

$$N.new_{sjt} \sim Poisson(\lambda_{sjt})$$

We then calculated the Freeman Tukey residuals (*Rab* and *Rab.n*) by comparing the expected abundance λ to both the observed (*N*) and a simulated abundance from the model (*N.new*) at each iteration *i* of the Markov chain:

$$Rab_s = \sum_j \sum_t (\sqrt{N_{sjt}} - \sqrt{\lambda_{sjt}})^2$$

$$Rab.n_s = \sum_j \sum_t (\sqrt{N.new_{sjt}} - \sqrt{\lambda_{sjt}})^2$$

We calculated the species-specific Bayesian p-values (*Bp.ab.sp*) as:

$$Bp.ab.sp_s = \frac{\sum_i Rab.n_s > Rab_s}{n_{iter}}$$

We calculated the community Bayesian p-value (*Bp.ab.com*) as:

$$Bp.ab.com = \frac{\sum_i \sum_s Rab.n_s > Rab_s}{n_{iter}}$$

Results

The species-specific Bayesian p-values indicated good model fit for all species in the abundance component and all species except Calandra lark and Corn bunting in the detection component (i.e., Bayesian p-value > 0.1 or < 0.9; main text, Table C1). The community Bayesian p-value was 0.41 for the abundance component and 0.06 for the detection component. The lack of fit in the detection component was tracked and attributed to very few extreme residuals presented by the species Calandra Lark and Corn Bunting, so we considered that the low community Bayesian p-value did not invalidate the model results (main text).

Table C1. Species-specific Bayesian p-values for the observation (Bp.obs) and abundance (Bp.ab) component of the Hierarchical Distance Sampling community model analysing the abundance of 37 farmland species in an Iberian cereal steppe of north-eastern Spain (Catalonia) during 2015 – 2019.

Species	Bp.obs	Bp.ab
Eurasian skylark	0.60	0.58
Red-legged partridge	0.68	0.47
Little owl	0.54	0.52
Stone curlew	0.66	0.49
Greater short-toed lark	0.40	0.49
Goldfinch	0.41	0.56
European greenfinch	0.49	0.53
Lesser short-toed lark	0.74	0.40
Common linnet	0.52	0.52
Montagu's harrier	0.63	0.58
Great spotted cuckoo	0.71	0.61
European roller	0.58	0.56
Common pigeon	0.39	0.43
Eurasian jackdaw	0.20	0.44
Stock dove	0.57	0.56
Common wood pigeon	0.60	0.47
Common house martin	0.64	0.62
Eurasian hobby	0.72	0.60
Common kestrel	0.43	0.49
Lark sp.	0.14	0.42
Barn swallow	0.58	0.48
Iberian Grey Shrike	0.59	0.56
Woodchat shrike	0.47	0.50
Woodlark	0.14	0.37
European bee-eater	0.15	0.40
Calandra lark	0.99	0.89
Corn bunting	0.99	0.77
Eurasian tree sparrow	0.78	0.66
Rock sparrow	0.75	0.56
Eurasian magpie	0.11	0.26
Pin-tailed sandgrouse	0.58	0.37
Black-bellied sandgrouse	0.70	0.31
Red-billed chough	0.60	0.38
European serin	0.79	0.62
European turtle dove	0.61	0.53
Little bustard	0.39	0.45
Eurasian hoopoe	0.40	0.42

Appendix D: JAGS model code

```
cat("model{

    # PRIORS
    # SPECIES SPECIFIC PARAMETERS (random effects)
    for (s in 1:nSpecies){              # Random intercept for sigma (different detection per species)
    asig[s] ~ dnorm(mu_s, tau_s)
    b.a1[s] ~ dnorm(mu_a1, tau_a1)
    b.a2[s] ~ dnorm(mu_a2, tau_a2)
    b.a3[s] ~ dnorm(mu_a3, tau_a3)
    bCropdiv[s] ~ dnorm(mu_cd, tau_cd)
    bFieldsize[s] ~ dnorm(mu_fs, tau_fs)
    }
    for(s in 1:nSpecies){               # Random intercept for lambda (different abundance per species and year)
    for(t in 1:nyrs){
    alam[s,t] ~ dnorm(mu_l,tau_l)}}

    for (s in 1:nSpecies){              # Random effect for lambda (different abundance per species and site)
    for (i in 1:max.sites){
    spsite[s,i] ~ dnorm(0, tau_spsite) }}

    # Hyperparameters of species level random effects
    mu_s ~ dnorm(0,0.01) # Hyperparameters for sigma intercept
    tau_s <- 1/(sig_s*sig_s)
    sig_s ~ dunif(0,500)

    mu_l ~ dnorm(0,0.01) # Hyperparameters for lambda intercept
    tau_l <- 1/(sig_l*sig_l)
    sig_l ~ dunif(0,500)

    mu_a1 ~ dnorm(0,0.01) # Hyperparameters for beta coefficient area1
    tau_a1 <- 1/(sig_a1*sig_a1)
    sig_a1 ~ dunif(0,500)

    mu_a2 ~ dnorm(0,0.01) # Hyperparameters for beta coefficient area2
    tau_a2 <- 1/(sig_a2*sig_a2)
    sig_a2 ~ dunif(0,500)

    mu_a3 ~ dnorm(0,0.01) # Hyperparameters for beta coefficient area3
    tau_a3 <- 1/(sig_a3*sig_a3)
    sig_a3 ~ dunif(0,500)

    mu_cd ~ dnorm(0,0.01) # Hyperparameters for beta coefficient crop diversity
    tau_cd <- 1/(sig_cd*sig_cd)
    sig_cd ~ dunif(0,500)

    mu_fs ~ dnorm(0,0.01) # Hyperparameters for beta coefficient field size
    tau_fs <- 1/(sig_fs*sig_fs)
    sig_fs ~ dunif(0,500)

    tau_spsite <- 1/(sig_spsite*sig_spsite) # Hyperparameter for site random effect in lambda
    sig_spsite ~ dunif(0,500)


    # PRIORS FOR SIGMA
    sig.sig.ob ~ dunif(0, 10) # Random effects for sigma per observer
    tau.sig.ob <- 1/(sig.sig.ob*sig.sig.ob)

    #Random observer effect for sigma
    for (o in 1:nobs){
    sig.obs[o] ~ dnorm(0, tau.sig.ob)}

    for(i in 1:nind){
    dclass[i] ~ dcat(fct[sp.dclass[i],siteYear.dclass[i], 1:nG])}
```

```
for (s in 1:nSpecies){
for(j in 1:n.allSiteYear){
sigma[s,j] <- exp(asig[s] + sig.obs[ob[j]])
f.0[s,j] <- 2 * dnorm(0,0, 1/sigma[s,j]^2)
# Construct cell probabilities for nG multinomial cells (distance categories) PER SITE
for(k in 1:nG){
up[s,j,k]<-pnorm(db[k+1], 0, 1/sigma[s,j]^2) ##db are distance bin limits
low[s,j,k]<-pnorm(db[k], 0, 1/sigma[s,j]^2)
p[s,j,k]<- 2 * (up[s,j,k] - low[s,j,k])
pi[s,j,k] <- int.w[k] / strip.width
f[s,j,k]<- p[s,j,k]/f.0[s,j]/int.w[k]                 ## detection prob. in distance category k
fc[s,j,k]<- f[s,j,k] * pi[s,j,k]               ## pi=percent area of k; drops out if constant
fct[s,j,k]<-fc[s,j,k]/pcap[s,j]
}
pcap[s,j] <- sum(fc[s,j,1:nG]) # Different per site and year (sum over all bins)

y[j,s] ~ dbin(pcap[s,j], N[j,s])
N[j,s] ~ dpois(lambda.eff[j,s])
lambda[j,s] <- exp(alam[s,allyears[j]] + spsite[s,sitesYears[j]]
+ b.a1[s]*area1[j] + b.a2[s]*area2[j] + b.a3[s]*area3[j] + bCropdiv[s]*cdiv[j] + bFieldsize[s]*fsiz[j] )

lambda.eff[j,s] <- lambda[j,s] * restrict.sp[j,s]

# FOR BP.OBS
# Create a new Y (detections)
y.new[j,s]~ dbin(pcap[s,j], N[j,s])
# Calculate residuals residuals: look at the total number of individuals detected instead
Tobsp[j,s] <- pow(  sqrt(y[j,s]) - sqrt(pcap[s,j] * N[j,s]) ,2)
Tobsnewp[j,s] <- pow(  sqrt(y.new[j,s]) - sqrt(pcap[s,j] * N[j,s]) ,2)

# FOR BP.N
# Create replicate abundances (new observations) for Bayesian p-value on abundance component
Nnew[j,s]~dpois(lambda.eff[j,s])
# Residuals for 'observed' and new abundances: species and site specific residuals
FT1[j,s] <- pow(sqrt(N[j,s]) - sqrt(lambda.eff[j,s]),2)
FT1new[j,s] <- pow(sqrt(Nnew[j,s]) - sqrt(lambda.eff[j,s]),2)
}

# FOR BP.OBS:
# Sum residuals over sites and years to get sp-specific bp.obs.values
T1obsp[s]<-sum(Tobsp[1:n.allSiteYear,s])
T1obsnewp[s]<-sum(Tobsnewp[1:n.allSiteYear,s])
# SP-SPECIFIC BP.OBS
Bp.Obs.sp[s] <-  T1obsp[s] > T1obsnewp[s]

# FOR BP.N
# Sum residuals over sites and years to get sp-specific bp.N.values
T1p[s]<-sum(FT1[1:n.allSiteYear,s])
T1newp[s]<-sum(FT1new[1:n.allSiteYear,s])
# SP-SPECIFIC BP.N
Bp.N.sp[s] <- T1p[s] > T1newp[s]
}
# COMMUNITY BP.OBS
Bp.Obs <- sum(T1obsnewp[1:nSpecies]) > sum(T1obsp[1:nSpecies])

# COMMUNITY BP.N
Bp.N <- sum(T1newp[1:nSpecies]) > sum(T1p[1:nSpecies])

for (s in 1:nSpecies){
for (i in 1:nyears){
Ntotal[i,s] <- sum(N[,s]*indexYears[,i]) }}

}"
```

Chapter III:

Fallow management increases habitat suitability for endangered steppe bird species through changes in vegetation structure

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Fallow management increases habitat suitability for endangered steppe bird species through changes in vegetation structure

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ABSTRACT.

1. In the face of the dramatic worldwide decline of farmland bird populations, the preservation of fallow fields is a conservation measure encouraged through subsidies (e.g. agri-environmental schemes, AES). Beyond the general benefits of increasing fallow availability for endangered steppe bird populations, there is a lack of knowledge on how fallow management can contribute to meeting speciesspecific habitat requirements.

2. We used occurrence data from three steppe bird species protected at the EU level (Stone Curlew *Burhinus oedicnemus*, Little Bustard *Tetrax tetrax* and Calandra Lark *Melanocorypha calandra*), framed in a quasi-experimental approach covering an unprecedented spatio-temporal scale that included 612 fallow fields over a 3-year study period in an agricultural Mediterranean landscape (Spain). We used path analysis to explore the mechanisms by which common agricultural practices affected species-specific occurrence. We examined partial effects of agricultural practices on vegetation structure and food availability, and the partial effect of these variables on bird occurrence compared to control fields (no agricultural practices applied).

3. Agricultural practices had a significant effect on the presence of the three studied species. Through changes in the vegetation structure, Shredding + Herbicide and Tillage increased the occurrence of the Stone Curlew and Shredding increased the occurrence of the Little Bustard. The occurrence of Calandra Lark was mostly affected by landscape variables.

4. *Synthesis and applications.* Our study highlights that, in addition to the acknowledged positive role of fallow availability, applying a limited number of specific agricultural practices before the breeding season can further increase bird occurrence by changing the vegetation structure. Using path analysis, we explored the mechanisms driving the occurrence of three steppe bird species under different agricultural practices. Such information is key to providing specific recommendations for future conservation management of endangered species within agri-environmental schemes.

Keywords: agricultural practices, agri-environmental schemes, bird occurrence, conservation, fallow management, path analysis, steppe birds, vegetation structure.

INTRODUCTION

Agricultural lands have become a major conservation focus due to the large proportion of global biodiversity which rely on them for persistence (Flynn et al., 2008). The severe decline in biodiversity and farmland bird populations across Europe (Donald, Sanderson, Burfield, & van Bommel, 2006) and the Iberian Peninsula (Santos & Suárez,) has been attributed to the intensification of agriculture since the 1970s, which has compromised the quality of habitats, food supplies, and nesting sites (Wretenberg, Pärt, & Berg, 2010).

In agricultural landscapes, the presence of key features such as cereal, ploughed fields or non - cropped lands (i.e. fallow fields, hereafter FFs) plays an important role in the persistence of farmland bird populations (Henderson, Cooper, Fuller, & Vickery, 2000). FFs are particularly important, since they enhance feeding opportunities by supporting a greater abundance of invertebrates (Moreby & Aebischer, 1992) and weeds and seeds (Henderson et al., 2000), optimize foraging efficiency, and reduce the predation risk by reducing vegetation cover and height (Whittingham, Devereux, Evans, & Bradbury, 2006).

Fallow fields are essential for steppe birds (McMahon, Giralt, Raurell, Brotons, & Bota, 2010; Morales, Traba, Carriles, Delgado, & de la Morena, 2008; Moreira, 1999), which reinforces their conservation value (i.e. given unfavourable conservation status of steppe birds at the European level; Burfield, 2005). Steppe birds' strong dependence on FF stems from their narrow niche requirements (Robleño, Bota, Giralt, & Recasens, 2017; Traba, Morales, Carmona, & Delgado, 2015), which are exclusively met within these landscapes as they resemble the original steppes in which these species evolved (Santos & Suárez, 2005). This explains the increasing impact of global change and agricultural intensification on steppe bird populations, since these processes act as ecological filters against specialist species (Gámez - Virués et al., 2015).

Habitat selection in farmland bird species, which is driven by the minimization of predation risk and the maximization of foraging efficiency and reproductive success (Green, Tyler, & Bowden, 2000; Traba et al., 2015), has been shown to be influenced by fallow vegetation structure (Whittingham et al., 2006). FFs are usually managed seasonally by farmers for agronomic purposes (i.e. to control weeds and prepare the soil for subsequent crops), which results in vegetation structures that may not always meet the narrow habitat requirements of steppe birds during the breeding season. Consequently, using agricultural practices a limited number of times before the breeding season can manage the vegetation structure of FF (Fried, Kazakou, & Gaba, 2012) and benefit farmland bird conservation. Although extensive information on species - specific requirements is available (Morales & Traba, 2016), comprehensive evaluations on the effect of agricultural practices on the habitat requirements of farmland and specifically steppe - land bird species are rare (but see Barré, Le Viol, Julliard, & Kerbiriou, 2018).

Such knowledge is crucial to promote FF management and improve conservation action effectiveness (e.g. within agri - environmental schemes (AES), where farmers are subsidized to promote FF; Kleijn & Sutherland, 2003). For example, the cost - efficiency of AES has been questioned (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011; Kleijn & Sutherland, 2003), partly because benefits of FF strongly depend on the vegetation structure (Henderson et al., 2000).

Within a quasi - experimental context, we evaluated the effect of different agricultural practices (commonly used by farmers in our study area and Spain; ESYRCE, 2017) applied to FF compared to control FF (no agricultural practices), on the occurrence of three steppe bird species having different niche requirements in northeastern Spain. Using path analysis, we built a causal network to disentangle the indirect effects (i.e. through vegetation structure and food availability) of agricultural practices on the presence of Stone Curlew *Burhinus oedicnemus* (SC), male Little Bustard *Tetrax tetrax* (LB) and Calandra Lark *Melanocorypha calandra* (CL) (see Supporting Information S1 for details).

MATERIAL AND METHODS

Study area

The study area was an agricultural mosaic landscape in the Lleida steppe plains (Catalonia, NE Spain; Supporting Information S2: Figure S5), covering approximately 3,580 km2 of semi - arid habitat. This area was dominated by extensive cultivation of winter cereal crops interspersed with woody crops, small patches of sparse shrub land and annual FFs. The latter are mainly promoted (for among others, steppe - land bird conservation purposes) by regional AES (Cantero - Martínez & Moncunill, 2012) and a local conservation measure occurring in Special Protection Areas (SPA), which purpose is to compensate the construction of the irrigation project Segarra - Garrigues.

We conducted our research in 612 FFs (average size ± *SD* = 3.11 ± 2.87 ha) from 2015 to 2017, covering 1,925.74 ha (Supporting Information S2: Tables S4 and S5). All FFs were funded through the local compensatory conservation measure and were located within six SPA (Supporting Information S2: Figure S5).

Agricultural practices

Fallow fields were managed in a quasi - experimental manner by applying one agricultural practice (Cantero - Martínez & Moncunill, 2012; Supporting Information S2: Table S4) from February to early April (before breeding season). These were: chisel ploughing to a minimum tillage of 10 cm (hereafter Tillage), cutting the vegetation at 5–10 cm height (hereafter Shredding), Shredding with subsequent application of a glyphosate herbicide spray at a rate of 2–4 L/ha, depending on vegetation density (hereafter Shredding + Herbicide), or sowing alfalfa (*Victoria R1* variety) at 20 kg/ha dose (hereafter Alfalfa).

Apart from this experiment, farmers in our study area regularly implement these practices in FF one to three times per year (Cantero - Martínez & Moncunill, 2012) to control for weeds on future and surrounding crops. Alfalfa is also a common crop on irrigated land, but in this study, it was never harvested as it had conservation purposes (e.g. Bretagnolle et al., 2011). FFs with no agricultural practices from February to early April were considered as control fields (hereafter Control). Agricultural practices were assigned randomly to the FFs, with a certain dependence on each farmer's context (e.g. capability in terms of machinery; Supporting Information S2: Figures S6–S8).

We sought a similar vegetation structure in all FFs (i.e. a yearly reset of the system) by applying a shredding treatment in September - November in FF with >50% cover and >30 cm height, before the application of the agricultural treatments described above. This preparatory resetting protocol was applied based on previous knowledge of the response of vegetation to the different agricultural practices.

Bird occurrence

We chose three steppe bird species protected at the EU level (Stone Curlew (SC), Little Bustard (LB) and Calandra Lark (CL); Annex I of the EU Birds Directive: Directive 2009/147/EC 2009), with different intrinsic characteristics and habitat requirements (Supporting Information S3). Bird censuses were performed by trained observers during May, the peak of the target species' breeding season. Censuses took place from after dawn until 10:00 a.m. in good weather conditions. We used two sampling methods for each field (Bibby, Burguess, Hill, & Mustoe, 2000), namely: (a) A point count sampling, where visual and auditory observations of all detected target species were recorded during 10 min. (b) A variation of the line transect method (Bibby et al., 2000), which consisted of walking in a zigzag pattern through the FF to detect elusive species (e.g. SC and LB). The presence/absence of individuals of each species in either of the two methods was used as species occurrence per FF. Due to the low detectability of LB females (Morales, Traba, Delgado, & Morena, 2013), we only analysed male presence.

Environmental variables

We used three groups of variables, namely: vegetation structure, food availability and landscape, to explain bird occurrence (Supporting Information S2: Table S6). We also included the size of the FF (m2) as a covariate when modelling species occurrence (McMahon et al., 2010).

Vegetation structure

We measured vegetation structure using 3–6 (i.e. proportional to the field size) 2 × 2 m plots in each FF. In each plot, one measure of vegetation height (cm) and the proportion of dead and live vegetation cover were visually estimated by approximating the measure to the nearest 5 cm and 5% value, respectively. Each variable was averaged among plots to obtain a unique field measure (Supporting Information S2: Table S6). We also calculated a Simpson Diversity Index derived from the cover of each dominant plant species (i.e. >20% cover within the plot). We considered this value as a pseudo plant diversity index (only dominant species were used for the index) for each FF.

We characterized within - field heterogeneity in the FF by visually estimating the proportion of the FF area covered by 10 different categories of vegetation structure (i.e. vegetation cover and height combinations) (Supporting Information S2: Table S6). This proportion was approximated to the nearest 5% value. We estimated field heterogeneity in each FF with the Levin's index of niche breath, by substituting species with FF ID and dietary items with vegetation structure categories.

Food availability

We estimated orthopteran biomass using the regression equations derived by Hódar (1996), from orthopteran counts performed in two transects of 20 m long × 2 m wide per FF.

We calculated leaf and seed availability indexes by combining information about functional traits and the cover of dominant plant species identified in the plots (see Robleño et al., 2017; Supporting Information S2: Table S6). The Leaf Availability Index was estimated as [vegetation cover × height × Specific Leaf Area (SLA, mm^2/mg)], and Seed Availability Index was estimated as [vegetation cover × height × seed mass (the average individual weight of 1,000 seeds)], weighted by flowering period (Robleño et al., 2017).

Landscape variables

To control for landscape heterogeneity (i.e. configuration and composition), we extracted landscape characteristics within an average circular home range size of each target species (i.e. buffer of 500 m-radius for LB and SC and 200 m - radius for CL; Caccamo, Pollonara, Emilio Baldaccini, & Giunchi, 2011; Ponjoan, Bota, & Mañosa, 2012; Suárez - Seoane et al., 2002).

Configuration: Using the regional Geographic Information System of Farming Land (SIGPAC; Supporting Information S2: Table S6), we calculated Total Border Length (TBL) as the sum of the field perimeters. We also calculated the Mean Perimeter - Area Ratio (MPAR) as indicator of field regularity (Supporting Information S2: Table S6), by calculating the Perimeter - Area Ratio of each field as the ratio of the field perimeter to the perimeter of a circular field of the same area (Donald, Evans, Buckingham, Muirhead, & Wilson, 2001), and then averaging the field values within each buffer.

Composition: Using a crop - land use map annually updated by the regional government (Unique Agrarian Statement/DUN; Supporting Information S2: Table S6), we calculated the proportion of fallow land and crop diversity using the Shannon Diversity index on relevant cover categories for the target species (see Supporting Information S2: Table S6 for a description of the land cover categories).

Statistical analyses

We performed a confirmatory - exploratory path analysis (Supporting Information S1; Grace, 2006) using piecewise Structural Equation Modelling (SEM) to investigate how the effect of different agricultural practices on bird occurrence was mediated by the changes in vegetation structure and/or food availability. Piecewise SEM links information of multiple component models for different response variables and allows rigorous estimation of indirect effects in a single causal network (Shipley, 2009). We constructed this network based on previous knowledge of the system for each target species and agricultural practice, that represented our partial hypotheses (Supporting Information S1; Grace et al., 2012). We only included variables with a Pearson correlation coefficient <0.5. We then used Shipley's (2009) directional separation approach (D - sep), which consists of the following two main steps.

The first step consisted of constructing the path model as a set of hierarchical linear mixed models. Regressions related to the first part of the path (i.e. linking agricultural practice with vegetation and food variables; Supporting Information S1) were modelled with an identity link function using the 'lme' function (nlme r package; Pinheiro, Bates, DebRoy, & Sarkar, 2018), and regressions related to the second part (i.e. linking all explanatory variables with bird presence/ absence; Supporting Information S1) were fitted with a logit link function using the 'glmmPQL' function (MASS R package; Venables & Ripley, 2002). We included year as random intercept and a Gaussian correlation structure (corGaus(form = ~Lon_x + Lat_y)) in all models to account for the spatial clustering of the fields (Lefcheck, 2016; Supporting Information S2: Figures S6–S8). We created a path model for each of the agricultural practices and used Control as a reference by including the agricultural practice as dummy variable (1— Agricultural practice; 0—Control). All variables were standardized (mean ± *SD* = 0 ± 1) in order to compare their effect size.

The second step consisted of fitting the overall path model using the r package *piecewiseSEM* (Lefcheck, 2016). This approach applies the D - sep test to estimate the overall goodness - of -

fit by combining the significance of missing paths and correlated errors into a single chi-squared distributed Fisher's *C*-statistic (Shipley, 2009).

Once the best path model validated, we estimated the standardized model parameters of causal effects. Parameter estimates are given in the link function scale and expressed as mean ± *SE*. All analyses were conducted using r v. 3.3.3 (R Core Team, 2017).

RESULTS

The proportion of species presence per agricultural practice was highest in Alfalfa fields for LB (31.25%, Supporting Information S2: Table S8), and in Shredding + Herbicide fields for CL (65%, Supporting Information S2: Table S8) and SC (40%, Supporting Information S2: Table S8). The lowest proportion of species presence was found in Alfalfa fields for SC (7.5%), in Control fields for CL (25.64%), and in Shredding + Herbicide fields for LB (10%).

Stone curlew

The presence of SC was affected by the vegetation variables in all paths, but was not affected by the food variables (Supporting Information S1: Table S2). Across all agricultural practices, SC benefited from a decrease in cover and height (Figure 1a; Table 1). It was the only species positively affected by plant diversity (Supporting Information S1: Table S2). Shredding + Herbicide had the strongest positive effect on the presence of SC compared to Control (OESH = 2.22, Table 1). This positive effect occurred because of the decrease in cover and height (Supporting Information S1: Figure S3, Table S2). Tillage was the second-best agricultural practice for SC (OET = 0.63, Table 1), due to its negative effect on cover and height (Figure 1a; Supporting Information S1: Table S2). Shredding and Alfalfa had a lower positive effect (Table 1) on SC presence. SC presence was not affected by any of the landscape variables (Table 2).

Little bustard males

Little bustard occurrence was not affected by food variables, but did increase with lower vegetation heights in half of the agricultural treatments (Supporting Information S1: Table S2; Figure 1b). Shredding resulted in the highest LB occurrence, due to the reduction in vegetation height (OES = 0.21, Table 1; Figure 1b). Shredding + Herbicide had no overall effect on LB occurrence as compared to Control (Table 1). Tillage had a negative effect on LB occurrence (OET = −0.05, Table 1), because the benefit of decreased vegetation height was countered by the decrease in vegetation cover (Table 1; Supporting Information S1: Table S2). Alfalfa had a direct negative effect on LB presence that was not explained by any of the included variables. From the landscape variables, the presence of LB was hindered by the compositional variables (i.e. fallow land proportion and crop diversity) and field regularity (MPAR) (Table 2).

Calandra lark

Calandra lark (CL) was generally not affected by any of the vegetation or food variables (Table 1). Shredding + Herbicide and Shredding had a direct positive effect, and Alfalfa had a direct negative effect in CL presence that was not mediated by any of the included variables (Table 1). CL was the species most affected by the landscape variables. Its presence was positively affected by TBL and negatively affected by field regularity (MPAR), fallow land proportion and crop diversity (Table 2).

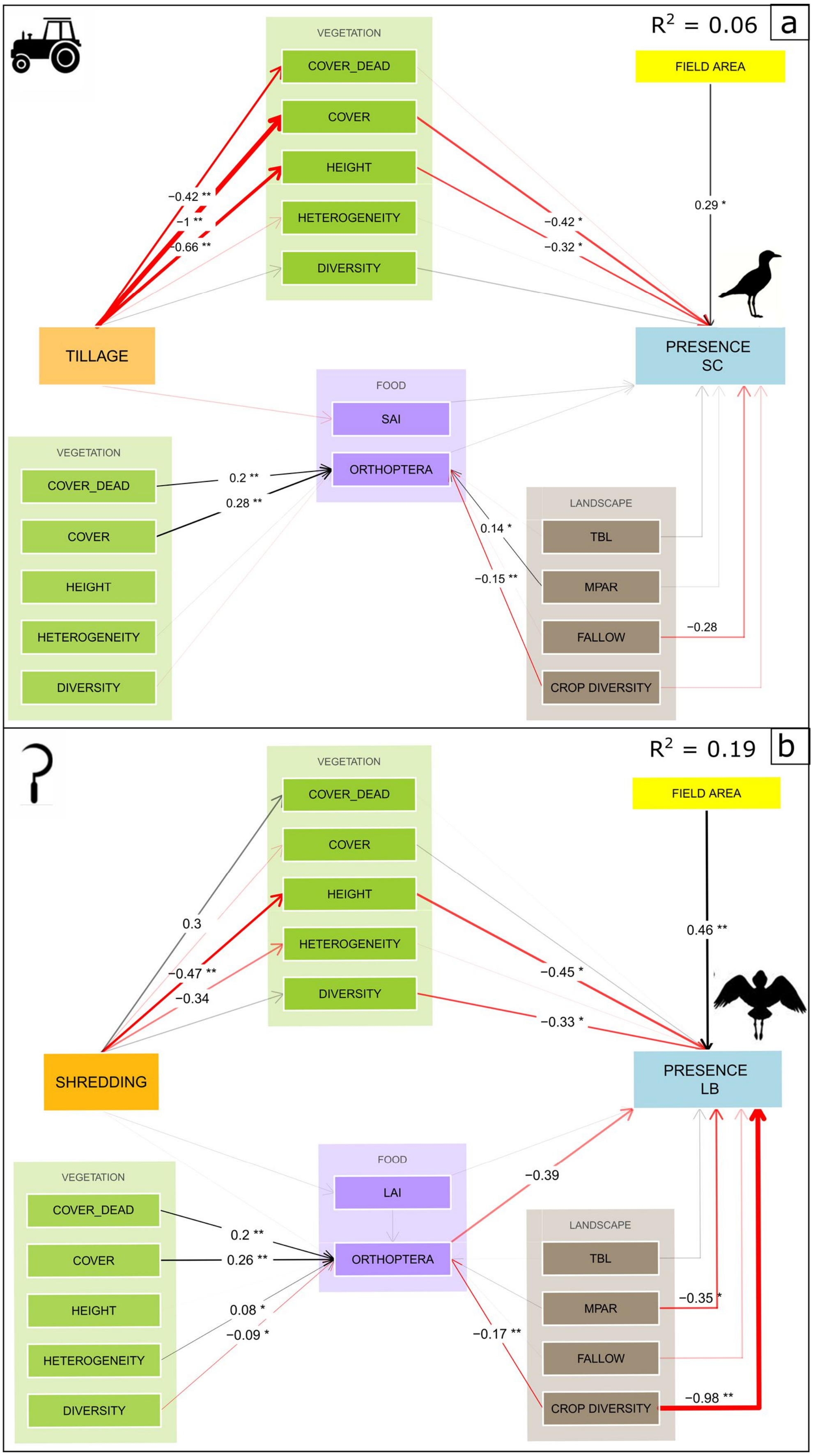

Figure 1. Results of path analyses for agricultural practices highlighted as relevant for conservation implications on the studied species (see discussion section), exploring (a) the effect of Tillage on the Stone Curlew (SC) presence and (b) the effect of Shredding on the Little Bustard (LB) presence. Conditional R^2 is shown in the top‐right corner of each path. Thickness of black (positive) and red (negative) paths is proportional to standardized path coefficients. Path transparency is proportional to the *p*‐value significance level. Standardized path coefficients with $p < 0.10$ are shown according to the criteria: $p < 0.01$**;$0.01 < p < 0.05$*;$0.05 < p < 0.10$

Table 1. Standardized effects of the significant paths between the agricultural practices Shredding + Herbicide, Shredding, Tillage and Alfalfa, predicted for the Stone Curlew (SC), Little Bustard (LB) and Calandra Lark (CL)

Species	Agricultural practice	Path (Agricultural practice → Variable → Species)	Indirect Effect	Overall Effect
SC 	Shredding + Herbicide (S+H)	S+H → Cover → SC	1.27	**2.22**
		S+H → Height → SC	0.95	
	Shredding (S)	S → Height → SC	0.22	0.22
	Tillage (T)	T → Cover → SC	0.42	0.63
		T → Height → SC	0.21	
	Alfalfa (A)	A → Diversity → SC	-0.29	0.28
LB 	Shredding (S)	S → Height → LB	0.21	**0.21**
	Tillage (T)	T → Cover →LB	-0.39	-0.05
		T → Height → LB	0.34	
	Alfalfa (A)	A → LB	-0.83	-0.83
CL 	Shredding + Herbicide (S+H)	S+H → CL	1.5	**1.5**
	Shredding (S)	S → Height → CL	0.08	1.08
		S → CL	1	
	Alfalfa (A)	A → CL	-0.93	-0.93

The indirect effects are the coefficients of the significant agricultural practices on each species mediated by the vegetation/food variables, obtained by multiplying the partial standardized path coefficients. The overall effects are the total effect of the agricultural practices on each species, obtained by summing all indirect effects. The strongest positive effects are shown in bold.

DISCUSSION

Despite the number of studies showing positive effects of fallow availability on steppe and farmland birds (e.g. Henderson et al., 2000; Van Buskirk & Willi, 2004), managing field vegetation structure is considered as key to improving habitat quality and halting, or even reversing, the farmland bird populations decline (McMahon et al., 2010; Morales et al., 2008; Wilson, Whittingham, & Bradbury, 2005). We used a unique quasi - experimental setup, covering an unprecedented spatio - temporal scale, to evaluate how the use of common agricultural practices applied in FFs can increase the occurrence of three steppe bird species with different ecological requirements (Supporting Information S3). Our study does not only emphasize the role of vegetation structure for steppe birds within FFs (e.g. Moreira, 1999), but also highlights the benefits of applying common agricultural practices at a specific timing (i.e. before the breeding season) and frequency (two times per year), to meet the habitat requirements of different bird species. Specifically, our comprehensive analysis highlights that the use of Shredding + Herbicide and Shredding increased the occurrence of the three studied species, in

Table 2. Standardized path coefficients and 95% confidence intervals shown for the 12 path analyses for each species (from left to right: Stone Curlew, Little Bustard and Calandra Lark) and each agricultural practice (from top to bottom Shredding + Herbicide, Shredding, Tillage, Alfalfa)

						
	β	**95 % CI**	***β***	**95 % CI**	***β***	**95 % CI**
TBL	-0.03	[-0.47 – 0.41]	0.23	[-0.74 – 1.2]	0.31	[-0.13 – 0.75]
MPAR	0.20	[-0.29 – 0.70]	-0.02	[-1.37 – 1.32]	**-0.67***	[-1.08 – (-0.08)]
Fallow	-0.35	[-0.91 – 0.21]	-0.49	[-1.93 – 0.96]	-0.08	[-0.77 – 0.61]
Crop diversity	-0.50	[-1.11 – 0.11]	0.41	[-2.40 – 1.59	**-0.90****	[-1.53 – (-0.26)]
Field area	**0.84****	[0.33 – 1.34]	-0.34	[-1.78 – 1.10]	**1.03****	[0.44 – 1.61]
TBL	-0.05	[-0.43 – 0.32]	0.14	[-0.20 – 0.49]	**0.3**	[-0.02 – 0.61]
MPAR	0.32	[-0.08 – 0.73]	**-0.35***	[-0.70 – 0.009]	**-0.76****	[-1.14 – (-0.38)]
Fallow	-0.13	[-0.54 – 0.28]	-0.27	[-0.63 – 0.08]	**-0.48****	[-0.84 – (-0.11)]
Crop diversity	-0.21	[-0.62 – 0.21]	**-0.98****	[-1.39– (-0.57)]	**-0.46****	[-0.79 – (-0.12)]
Field area	**0.35***	[0.06 – 0.63]	**0.46****	[0.16 – 0.76]	**0.73****	[0.46 – 0.99]
TBL	0.15	[-0.16 – 0.42]	**0.32***	[0.01– 0.62]	0.21	[-0.06 – 0.48]
MPAR	0.06	[-0.26 – 0.37]	**-0.50****	[-0.82 – (-0.17)]	**-0.82****	[-1.16 – (-0.47)]
Fallow	**-0.28**	[-0.61 – 0.06]	**-0.39****	[-0.70 – (-0.09)]	**-0.29***	[-0.58 – (-0.01)]
Crop diversity	-0.17	[-0.48 – 0.14]	**-0.84****	[-1.17 – 0.52]	**-0.40****	[-0.67 – (-0.14)]
Field area	**0.29****	[0.05 – 0.54]	**0.41****	[0.14 – 0.68]	**0.58****	[0.34 – 0.83]
TBL	0.06	[-0.37 – 0.49]	0.28	[-0.07 – 0.61]	**0.62****	[0.22 – 1.02]
MPAR	0.33	[-0.16 – 0.81]	**-0.61****	[-1 – (-0.21)]	**-0.55***	[-1.01 – (-0.07)]
Fallow	-0.24	[-0.70 – 0.23]	**-0.35**	[-0.72 – 0.01]	**-0.57***	[-1.04– (-0.11)]
Crop diversity	-0.18	[-0.68 – 0.30]	**-0.68****	[-1.04 – (-0.31)]	-0.16	[-0.53 – 0.20]
Field area	0.04	[-0.32 – 0.39]	**0.65****	[0.29 – 1]	**0.43****	[0.13 – 0.73]

Path coefficients are presented for partial paths between the landscape variables total border length (TBL), Mean of the Perimeter - Area Ratio (MPAR), Fallow, Crop diversity and Field area, and the presence of target species. Standardized path coefficients with $p < 0.10$ are shown according to the criteria: $p < 0.01$**; $0.01 < p < 0.05$*; $0.05 < p < 0.10$.

two of them (i.e. SC and LB males) through a change in the vegetation structure, and in the case of CL for causes unexplained by either of the included variables. The use of Tillage also increased SC through a change in the vegetation structure rather than a change in food availability.

Our study shows species‐specific responses to different vegetation structure. Vegetation structure may either protect or expose an individual to predators (Whittingham et al., 2006), extreme weather conditions (Walsberg, 1985) or influence its feeding behaviour (Wilson et al., 2005). Therefore, these specific responses are likely caused by different evolutionary strategies developed by species to deal with environmental pressures (Wilson et al., 2005). Unmanaged FFs usually develop important vegetation growth (Supporting Information S2: Table S7), which does not meet the habitat requirements of steppe birds (Whittingham et al., 2006). The production of excess vegetation in Control (unmanaged) FFs is likely due to the long‐term over‐fertilization and lack of livestock which characterize these farmlands.

We did not detect any effect of plant‐food variables on species occurrence, possibly because leaf and seed availability was not limiting, and/or because it was not the main driver of microhabitat selection for the studied species. Indeed, Traba et al. (2015) found that these species tend to minimize predation risks by selecting a particular vegetation structure, even when this choice limits their access to food. We did not have access to direct measures of food availability, and had to rely on indexes that may have only partially captured plant‐food availability within each FF. We did not find an effect of orthopteran biomass in the studied species' occurrence, although orthopterans represent a part of the diet of the SC (Amat, 1986; Green et al.., 2000) and the LB (Jiguet, 2002; but see Bretagnolle et al., 2011). However, it is possible that our measure did not capture the whole effect of invertebrate availability, as bird's diet can also include other taxa such as coleopterans.

Our study design was partially conditioned by each farmer's limitations to apply certain agricultural practices (Supporting Information S2: Figures S6–S8). We attempted to overcome this limitation by including a spatial correlation structure in all path models. Likewise, we dealt with the potential bias produced by the different management histories of FF by establishing a vegetation resetting protocol (see Section 22). Despite using a combination of point count sampling and zigzag line transects to ensure detection of birds possibly hidden in the vegetation, our data collected using a single survey method did not allow us to explicitly account for imperfect detection, which is another possible source of bias of our study. We encourage further research on this topic to improve upon these shortcomings.

Stone Curlew was the species with the strongest requirements in terms of vegetation structure (low vegetation cover and height). This preference has been previously documented (Green et al., 2000), and attributed to an anti‐predator behaviour linked to its lack of vision above eye level (Martin & Katzir, 1994). Its downward visual orientation optimizes foraging (Aebischer, Green, & Evans, 2000), but requires a wide visual field at ground level to detect predators and prey. Our results indicate that Shredding + Herbicide creates optimal habitats for SC presence due to the sparse and heterogeneous vegetation structure produced by the combination of both practices. However, given the detrimental impact of herbicides on biodiversity and the environment (Boatman et al., 2004), we do not recommend the use of herbicide‐related practices. Based on our results, Tillage may be the best alternative because it also promotes sparse vegetation (Wilson et al., 2005), facilitates camouflage by exposing the substrate colour

(Green et al., 2000), and increases food accessibility by unearthing invertebrates (Ponce, Bravo, & Alonso, 2014).

Little Bustard males benefited from the restrictions in vegetation height but not in vegetation cover provided by Shredding, probably due to their conflicting needs of visibility for displaying and courtship, and significant cover of short green plants for feeding (Morales et al., 2008). Agricultural practices did not affect LB male occurrence through food availability despite its known preferences for food - rich territories to afford the costs of mating activities (Faria, Rabaça, & Morales, 2012; Traba, Morales, García dela Morena, Delgado, & Krištín, 2008). This finding may be reasonable for this species, because unploughed FFs and moderate management (e.g. moderate grazing; Faria et al., 2012) have been shown to provide an equitable balance between food and conspicuousness for LB (Morales et al., 2008). Alfalfa had a negative effect on LB, despite this species being generally benefited by legume fields (Bretagnolle et al., 2011; Ponce et al., 2014). Drought conditions after the sowing date in some years of the study period may have undermined the competitive capacity of alfalfa, leading other weeds to dominate and produce a similar structure to control fields (see also Robleño et al., 2017). We therefore encourage the use of a drought - adapted alfalfa ecotype, or other leguminous species, in future studies testing leguminous crops as a fallow management treatment. While fallows are important nesting and foraging areas (Morales et al., 2013; Tarjuelo et al., 2013), cereal stubbles are also a key foraging habitat for LB females and their chicks (Tarjuelo et al., 2013). Therefore, the positive response of LB males to Shredding may not necessarily lead to increased breeding success, and different vegetation structures might be needed to meet the requirements of each sex (Morales et al., 2008).

Calandra Lark occurrence was not affected by the vegetation structure (see also CL abundance response; Supporting Information S1.2). This could be related to its generalist behaviour at the microhabitat scale (McMahon et al., 2010; Morgado et al., 2010), which allows CL to breed within different types of vegetation structure (Delgado & Moreira, 2002). The direct effects from Shredding and Shredding + Herbicide that were not mediated by the vegetation and food variables encourages further research on the effect of agricultural practices on this species (but see Supporting Information S1.2 for CL abundance response).

The occurrence of CL and LB tended to decrease when fallow land availability surrounding the FF was higher. This could be caused by the scattering of individuals when the availability of suitable habitat is higher (i.e. dilution effect; see also McMahon et al., 2010). Moreover, the negative effect of crop diversity could be expected for grassland specialists favoured by homogeneous landscapes (Moreira et al., 2012; Morgado et al., 2010). The presence of CL was mainly driven by the landscape context, which further reinforces the importance of considering landscape effects in field - scale analyses (Kleijn et al., 2011).

Conservation implications

Our study provides an evaluation of the effectiveness of common agricultural practices for the conservation of three steppe bird species. Although the importance of FFs is recognized, to our knowledge, this is the first study showing how different agricultural practices applied on FFs, when targeted towards specific - species requirements, could increase steppe bird occurrence. Indeed, the best management solution for these species points to a mosaic of fallows managed by Tillage or Shredding with a limited number of applications (one or two times per year), before the breeding season. This might be a good incentive to involve farmers in steppe bird conservation, because they usually prefer to avoid the excess of weeds and support agricultural management.

Moreover, our results suggest that increasing the availability of FFs as promoted by generic AES, might not be sufficient to protect the entire steppe - land bird community. A substantial amount of money is allocated to steppe bird conservation in AES (e.g. 3,526,147 € in Catalonia from 2010 to 2016; Gencat, 2018), and therefore improving cost - efficiency of AES by applying species - specific management measures should be prioritized (Kleijn & Sutherland, 2003).

This study not only reinforces the idea that agricultural practices can be used as a conservation tool for farmland birds (Barré et al., 2018) and biodiversity (Conover, Dinsmore, & Burger, 2014), but also highlights the important aspects of endangered steppe bird species ecology that can be directly applied to improve conservation actions in farmland areas. Understanding the mechanisms (e.g. shelter, visibility, food availability) by which agricultural practices determine species occurrence may prove useful when inferring conclusions about other systems, where these and other agricultural practices (e.g. livestock grazing) may be needed to meet the species requirements. Our methodological approach may prove useful for future research which evaluates how agricultural practices affect steppe bird species, and also in terms of demographic parameters such as reproduction and survival.

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Author's contributions: D.G., F.S. - P., G.B., I.R. and A.S. - P. conceived and designed the study with C.M. and S.M.'s suggestions. A.S. - P. and C.M. implemented the analysis. A.S. - P. wrote the manuscript with the help of D.G. and F.S. - P. All the authors contributed to subsequent drafts and gave final approval for publication. F.S. - P., D.G. and G.B. coordinated fieldwork and secured funding.

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APPENDIX

Supporting information S1 – Partial hypotheses and path analysis

Path construction

The presence of the studied species (Stone Curlew *Burhinus oedicnemus*, Little Bustard *Tetrax tetrax*, and Calandra Lark *Melanocorypha calandra*) and other farmland species has been previously related to vegetation structure, food availability and landscape characteristics (Benton, Vickery, & Wilson, 2003; Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011; M. Whittingham & Markland, 2002). Therefore, a specific understanding of how a given agricultural practice may change the vegetation structure and food availability, and ultimately affect bird occurrence, is a key factor for developing sound conservation plans. In this study, we address this question by using path analyses based on structural equation models (SEM). Despite the confirmatory character of our path analysis, we also used its exploratory potential (Grace, 2006), given the general lack of information on specific parts of the path model for the studied species. We followed the recommendations of Grace et al. (2012) and the procedure of Lefcheck and Duffy (2015) to construct and validate a path diagram for each studied species and agricultural practice (see Material and Methods chapter in main text).

Firstly, we generated a conceptual 'meta-model' (Figure S1) (Grace et al., 2012). This meta-model was based on our general predictions (see Introduction in the main text), that can be summarized in a three-part path as the best descriptor of our system. The first part of the path describes the hypothesized influence of the different agricultural practices (tillage, shredding, shredding + herbicide application, alfalfa sowing and control) on vegetation structure and food availability (Robleño, Bota, Giralt, & Recasens, 2017). The second part of the path describes the potential causal effect of vegetation structure and landscape on food availability. The third part of the path, describes the hypothesized influence of vegetation structure, food availability and landscape characteristics on the studied bird species occurrence (Benton et al., 2003; Kleijn et al., 2011; M. Whittingham & Markland, 2002). A direct effect of the agricultural practices on bird occurrence was not included because we expected that all important mediators would be represented by the analysed variables. However, the D-sep test (Statistical analyses section, main text) revealed a relevant direct link between the agricultural practices and the species in some of the path models.

We completed this meta-model to obtain a hypothesized causal network (Figure S2), by adding relevant variables describing vegetation structure, food availability and landscape characteristics (i.e., selecting those that could be used for inferring useful conclusions for management and conservation purposes of the studied species). Given the high number of variables, we performed a pearson correlation matrix (Table S3) to exclude correlated variables. Figure S2 shows the basic path for all analyses, and results from completing the variable groups of Figure S1. Below, we describe the supporting theory and rationale behind each part of the path.

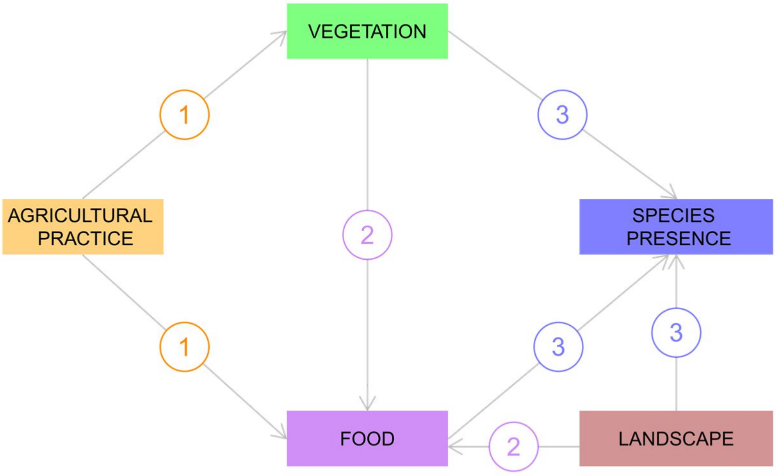


Figure S1. Conceptual 'meta-model' corresponding to the hypothesized three-parts path model: (**1**) describes the influence of the different agricultural practices on vegetation and food, (**2**) describes the influence of vegetation and landscape on food availability, and (**3**) describes the influence of vegetation, food and landscape context on bird presence. Vegetation, Food and Landscape correspond with the three variable groups described in the methods section.

1) Influence of the agricultural practices on vegetation and food

The different agricultural practices used in this study are likely to shape the vegetation structure. For instance, Shredding and Shredding + Herbicide should result in a higher dead vegetation cover compared to the control fields, and all agricultural practices, except Alfalfa, are likely to have lower green vegetation cover and height than control fields. Likewise, we expected an effect of agricultural practices on food availability as compared to control fields. These effects could be negative, if herbicide application would be detrimental for orthopteran species. A given agricultural practice could cause a direct effect in terms of food availability by favouring or restricting plant species producing large amount of leaves and seeds. For instance, the alfalfa agricultural practice could have a positive influence in the leaf availability by producing high values of Specific Leaf Area (Fig. S1, S2).

2) Effects of vegetation structure and landscape on food availability

Food availability is generally directly determined by vegetation structure (Henderson, Cooper, Fuller, & Vickery, 2000; M. J. Whittingham, Devereux, Evans, & Bradbury, 2006). The Seed and Leaf Availability Indexes were calculated by combining information of dominant plant species cover and functional traits (see methods section in main text). Therefore, variable vegetation cover at a given FF may have an influence on the food availability index obtained at that field. Also, a high vegetation height and cover (Bonari et al., 2017) or a high leaf availability (Joern, 1979) may benefit orthopteran species. Landscape structure may also play a role in the abundance and distribution of orthopteran populations (Batáry et al., 2007; Jordán, Báldi, Orci, Rácz, & Varga, 2003).

3) Influence of explanatory variables on bird occurrence

Vegetation structure may influence perceived predation risk and energy gain (Lima & Dill, 1990; M. J. Whittingham et al., 2006), and is therefore determinant for species predominantly terrestrial in their lifestyle, such as the studied species (see SI 3). For instance, dead vegetation cover may constrain food accessibility (M. J. Whittingham et al., 2006) and/or movement ability. Vegetation cover may play an important role in providing food-rich patches (e.g., for the Little Bustard; Morales, Traba, Carriles, Delgado, & de la Morena, 2008), while low vegetation height might be needed to better detect predators (e.g., for the Stone Curlew; Wilson, Whittingham, & Bradbury, 2005). Regarding the influence of food availability on bird occurrence, orthopteran are considered as a relevant arthropod food component for chick survival and adult performance during the breeding period (e.g., for the SC; Green, Tyler, & Bowden, 2000; for the LB; Jiguet, 2002). Because the Seed Availability Index (SAI) and Leaf Availability Index (LAI) variables were slightly correlated (Pearson's correlation > 0.5), we chose the most relevant one for each species ecology, including LAI for the Little Bustard (Bravo, Cuscó, Morales, & Mañosa, 2017), and SAI for Calandra Lark and Stone Curlew (Cramp & Simmons, 2004).

The landscape characteristics (i.e. configuration and composition) and the size of the field, have been also considered important for farmland species (Kleijn et al., 2011; e.g., Sanza, Traba, Morales, Rivera, & Delgado, 2012), so we controlled for the effects of these variables in the occurrence of the studied species

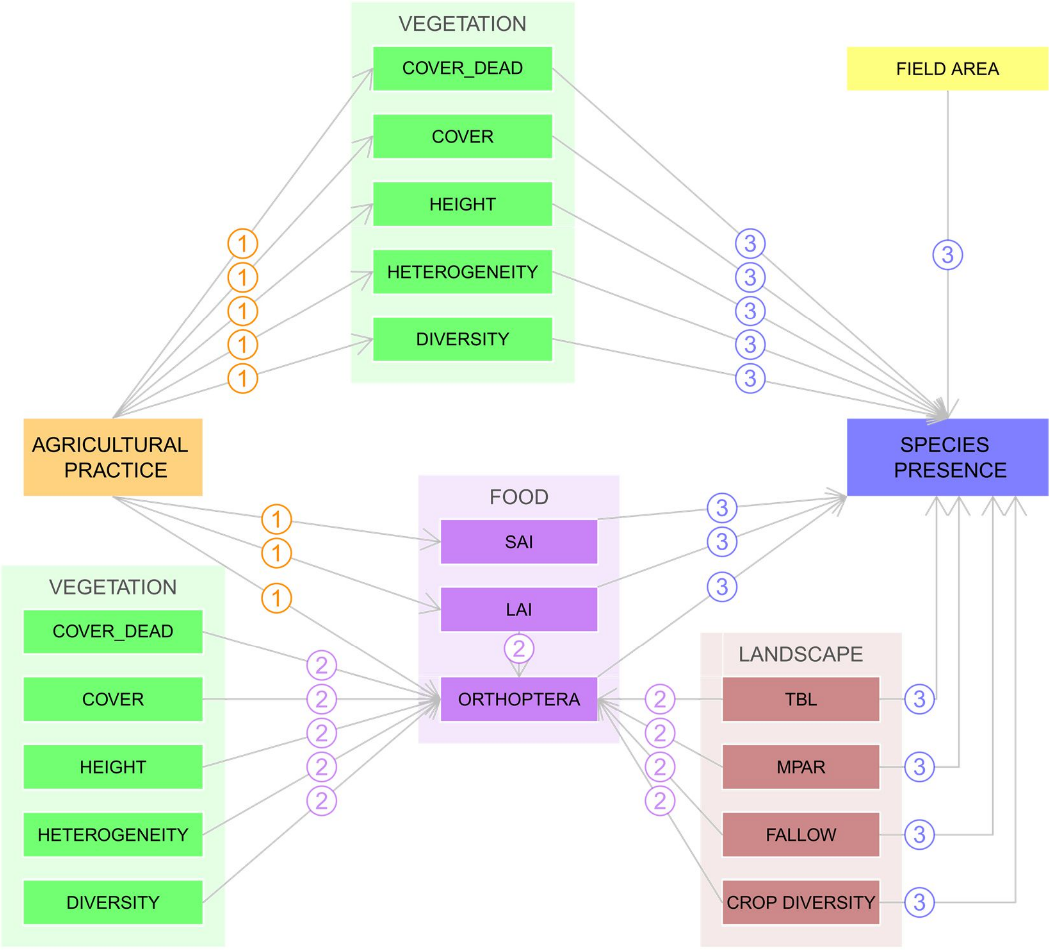
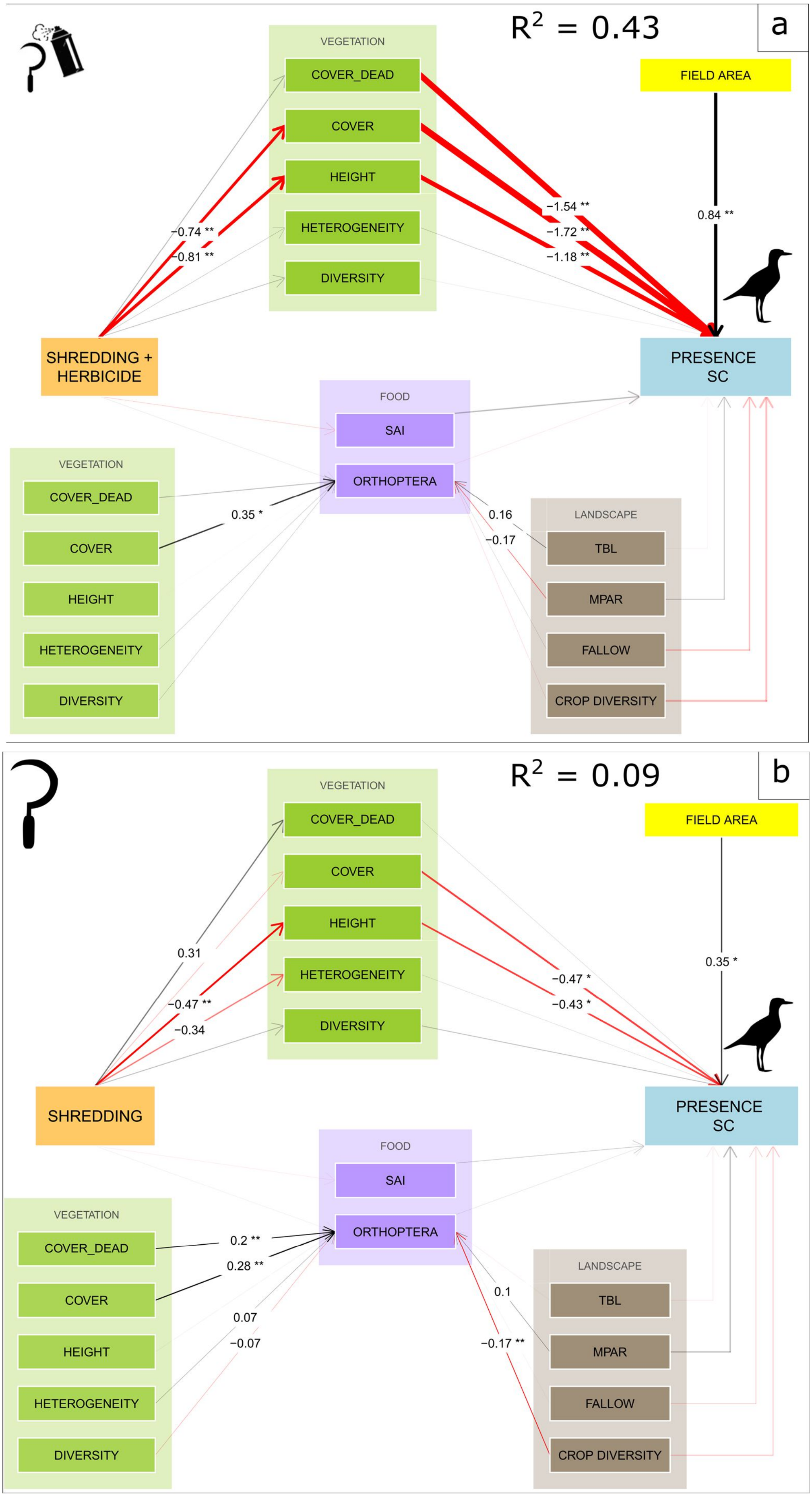
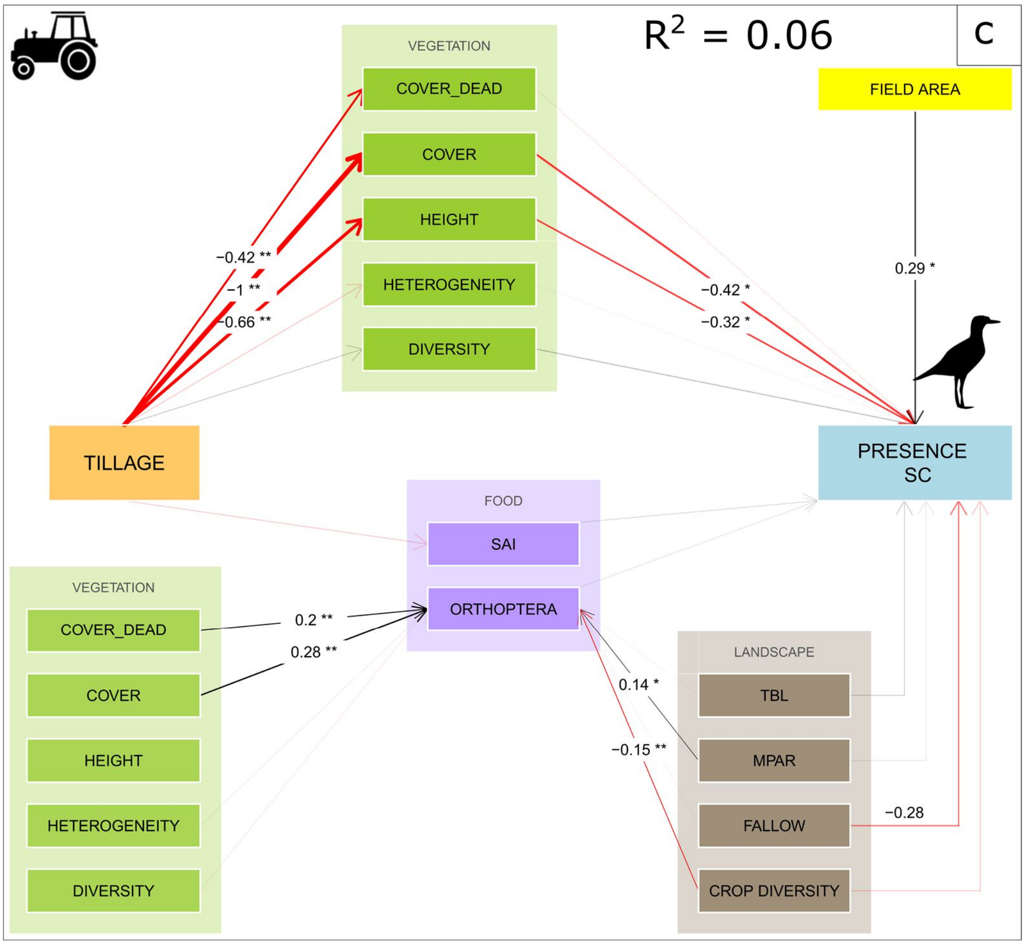


Figure S2. Hypothesized causal network describing causal links between variables, obtained by completing the initial meta-model (Figure S1) with relevant variables describing vegetation structure, food availability, and landscape characteristics. Numbers in circles correspond to each of the three parts of the initial meta-model described in Figure S1.

Results of the path analyses

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HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
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−0.66 **
−0.42 *
−0.32 *
0.29 *
TILLAGE
PRESENCE SC
FOOD
SAI
ORTHOPTERA
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
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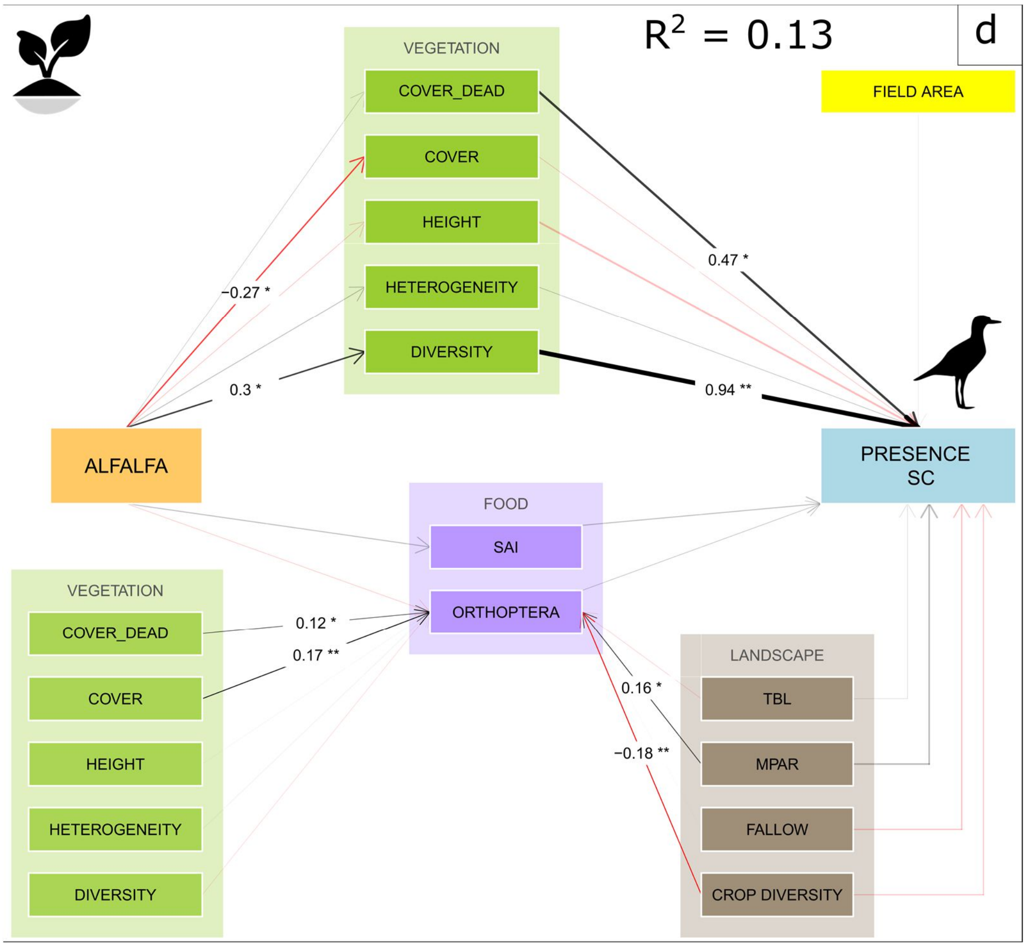
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
−0.28


$R^2 = 0.13$
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DIVERSITY
FIELD AREA
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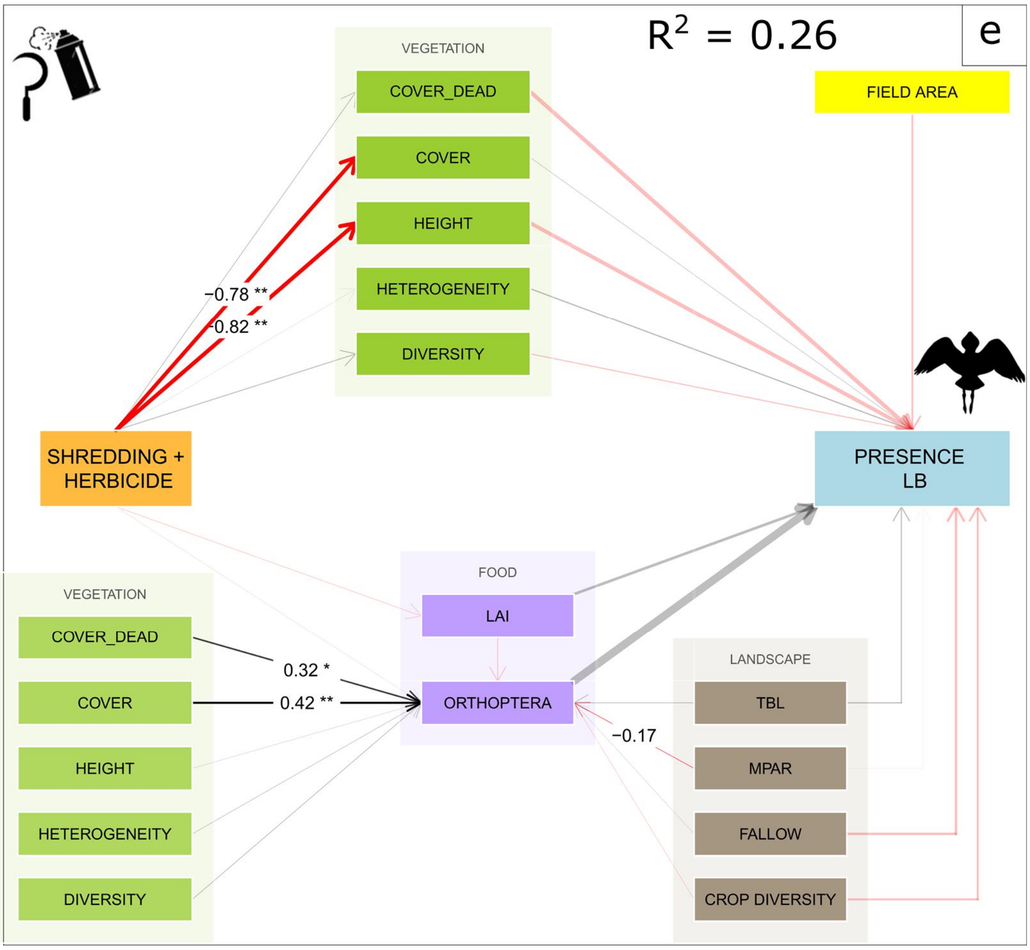
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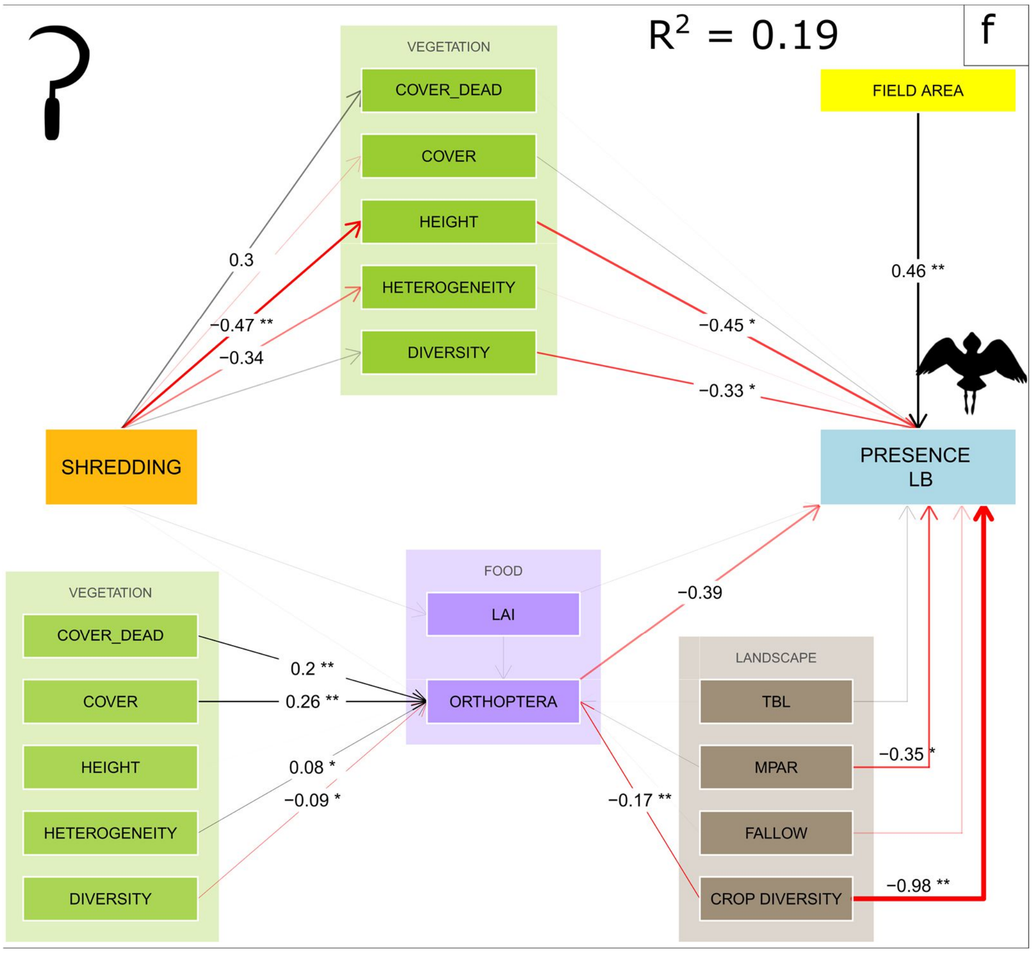
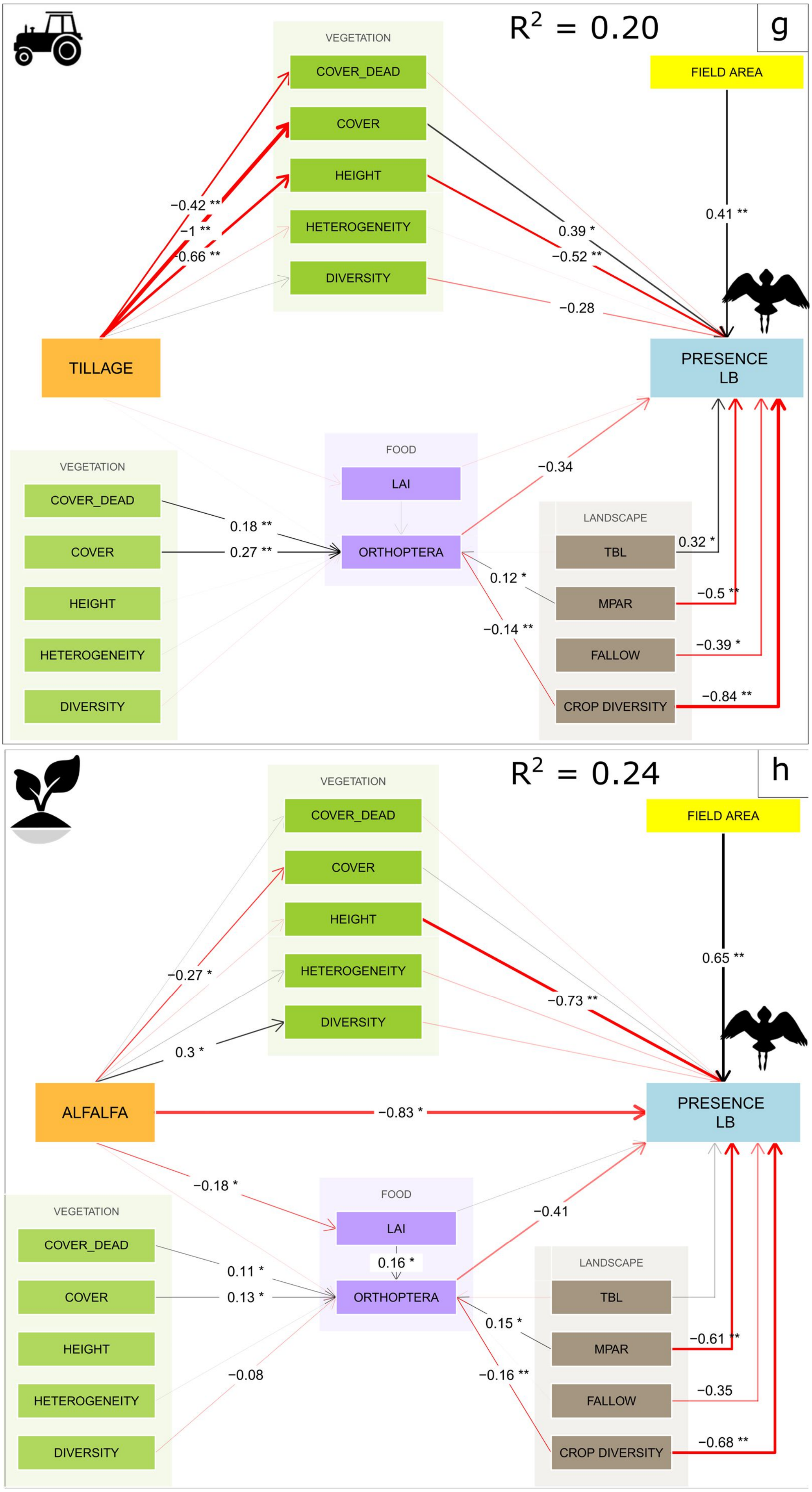
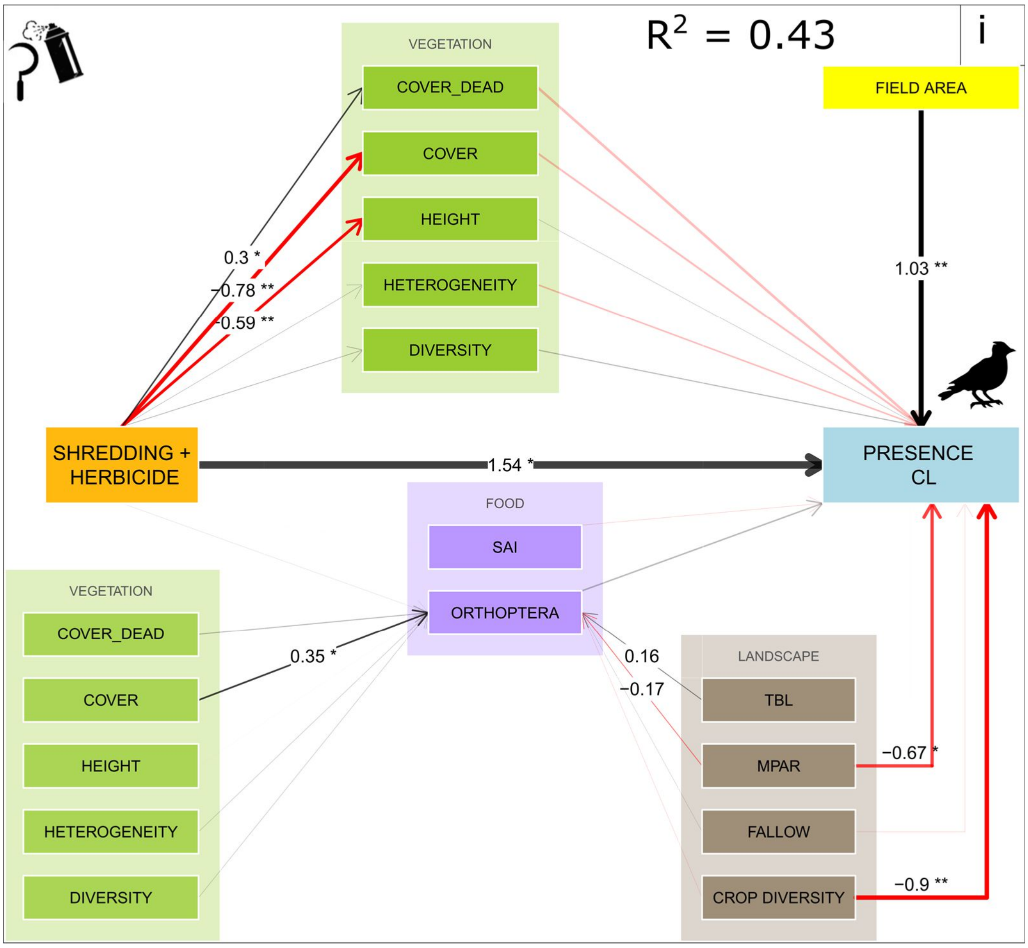
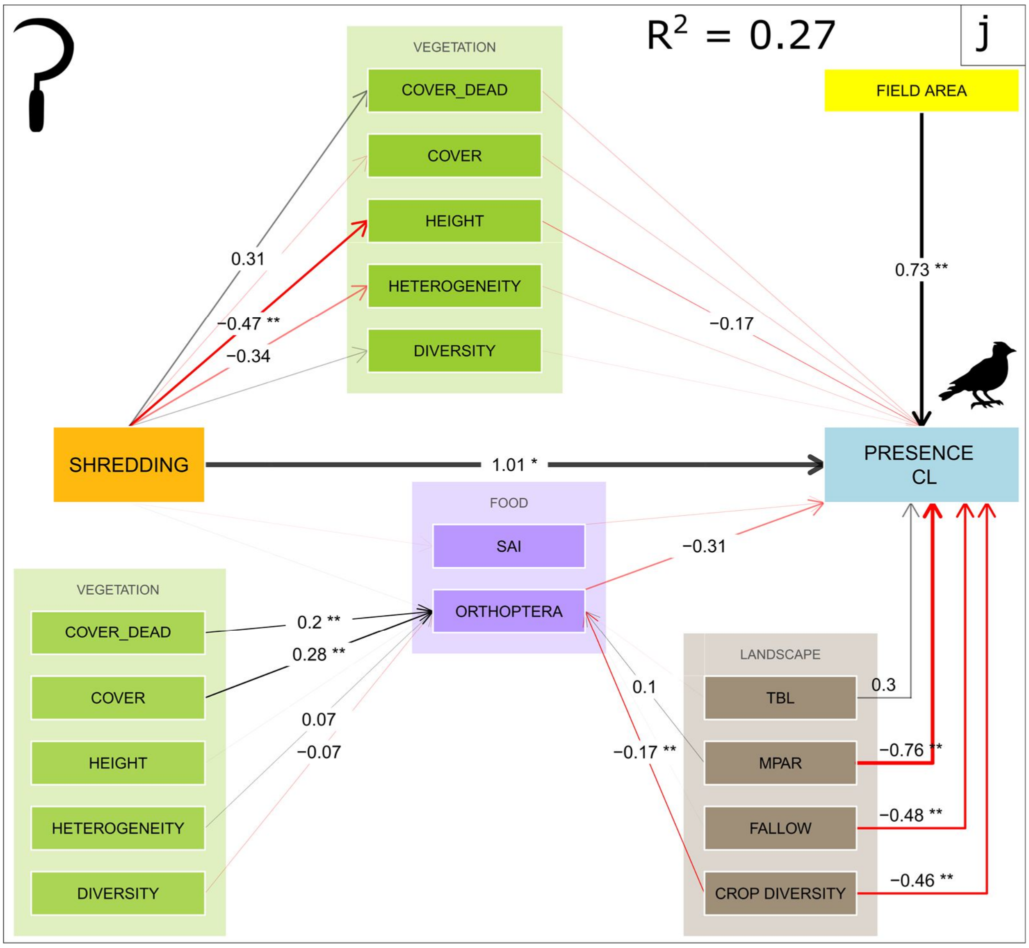
PRESENCE LB
FOOD
LAI
ORTHOPTERA
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.32 *
0.42 **
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
−0.17


R2 = 0.19
f
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
0.46 **
0.3
−0.47 **
−0.34
−0.45 *
−0.33 *
SHREDDING
PRESENCE LB
−0.39
FOOD
LAI
ORTHOPTERA
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.2 **
0.26 **
0.08 *
−0.09 *
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
−0.17 **
−0.35 *
−0.98 **


$R^2 = 0.20$
g
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
−0.42 **
−1 **
−0.66 **
0.39 *
−0.52 **
0.41 **
−0.28
TILLAGE
PRESENCE LB
FOOD
LAI
ORTHOPTERA
−0.34
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.18 **
0.27 **
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
0.32 *
0.12 *
−0.14 **
−0.5 **
−0.39 *
−0.84 **
$R^2 = 0.24$
h
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
0.65 **
−0.27 *
−0.73 **
0.3 *
ALFALFA
−0.83 *
PRESENCE LB
−0.18 *
FOOD
LAI
0.16 *
ORTHOPTERA
−0.41
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.11 *
0.13 *
−0.08
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
0.15 *
−0.16 **
−0.61 **
−0.35
−0.68 **


$R^2 = 0.43$
i
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
1.03 **
0.3 *
−0.78 **
−0.59 **
SHREDDING + HERBICIDE
1.54 *
PRESENCE CL
FOOD
SAI
ORTHOPTERA
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.35 *
0.16
−0.17
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
−0.67 *
−0.9 **


$R^2 = 0.27$
j
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
0.73 **
0.31
−0.47 **
−0.34
−0.17
SHREDDING
1.01 *
PRESENCE CL
FOOD
SAI
ORTHOPTERA
−0.31
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.2 **
0.28 **
0.07
−0.07
0.1
−0.17 **
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
0.3
−0.76 **
−0.48 **
−0.46 **

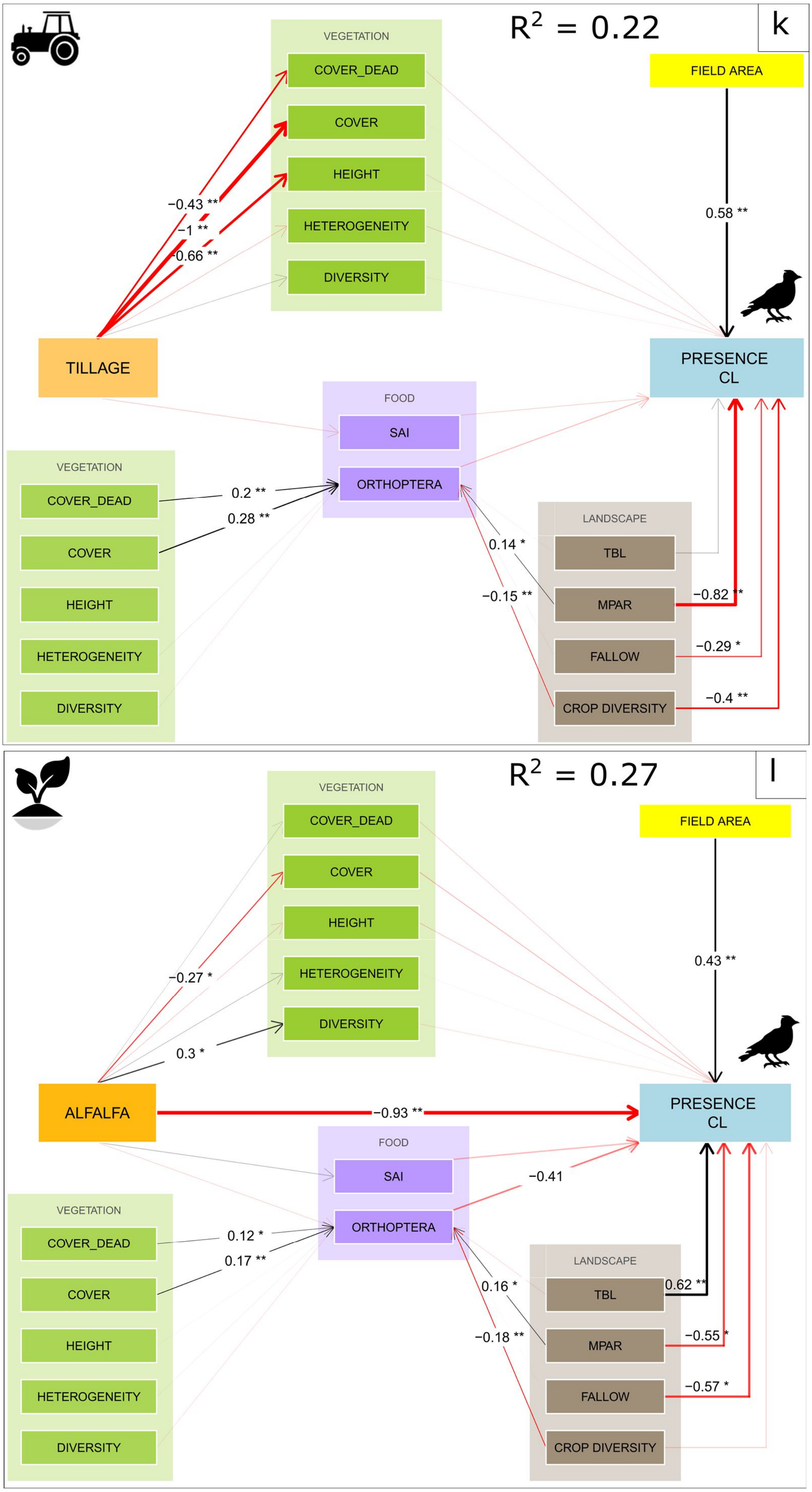

$R^2 = 0.22$
k
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
0.58 **
−0.43 **
−1 **
−0.66 **
TILLAGE
PRESENCE CL
FOOD
SAI
ORTHOPTERA
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.2 **
0.28 **
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
0.14 *
−0.15 **
−0.82 **
−0.29 *
−0.4 **
$R^2 = 0.27$
l
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
0.43 **
−0.27 *
0.3 *
ALFALFA
−0.93 **
PRESENCE CL
FOOD
SAI
ORTHOPTERA
−0.41
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.12 *
0.17 **
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
0.16 *
−0.18 **
0.62 **
−0.55 *
−0.57 *

Figure S3. Path analyses exploring the effect of Shredding + Herbicide, Shredding, Tillage and Alfalfa in Stone Curlew (SC) presence (a-d), in Little Bustard (LB) presence (e-h), and in Calandra Lark (CL) presence (i-l). R-squared (R^2) is shown in the top-right corner of each path. Thickness of black (positive) and red (negative) paths is proportional to standardised path coefficients. Path transparency is proportional to the p-value significance level. Standardised path coefficients with $p < 0.10$ are shown according to the criteria: $p < 0.01$**/ $0.01 < p < 0.05$ */ $0.05 < p < 0.10$.

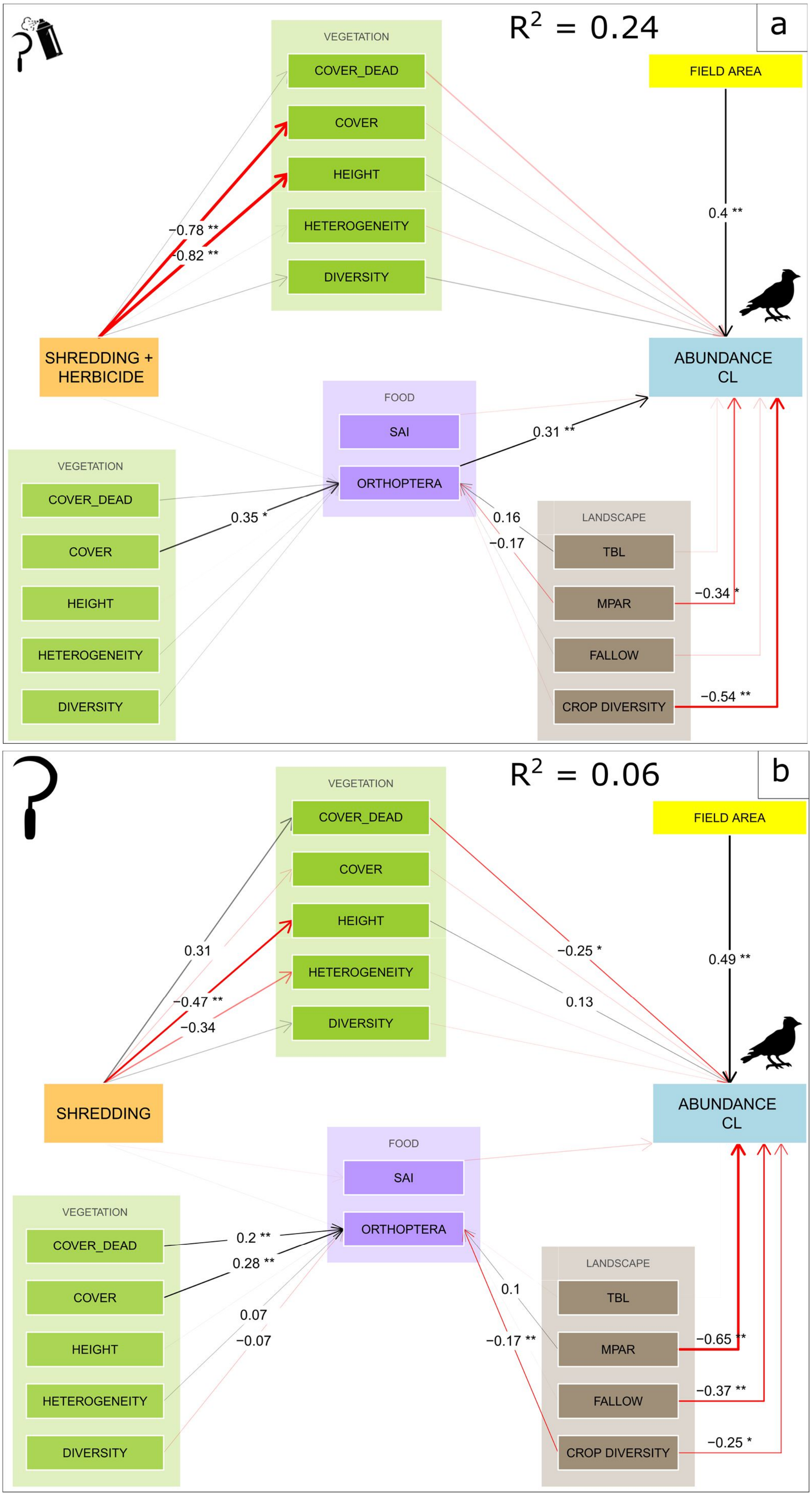
Results of the path analyses on Calandra Lark abundance

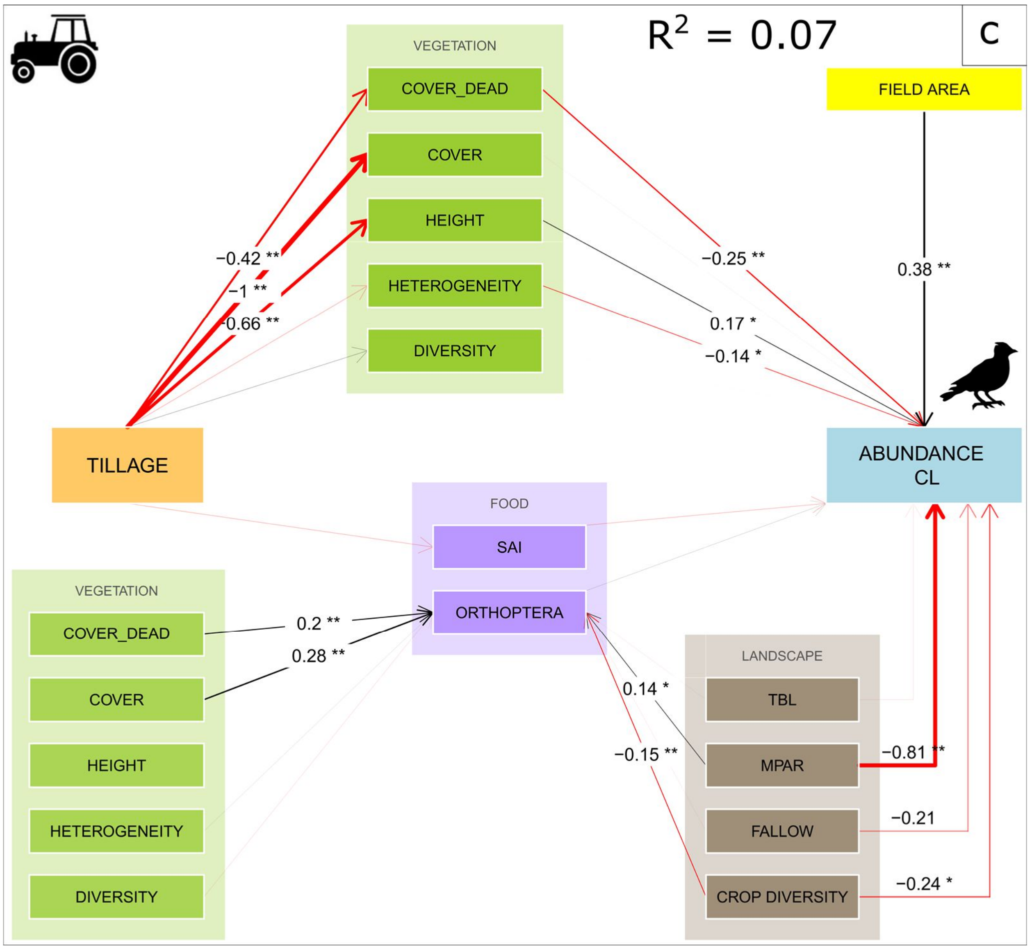
Because Calandra Lark is a species that presents conspecific attraction (Morgado et al., 2010), we examined whether CL abundance would respond in a different manner to the same agricultural practices. Therefore, we performed path analyses with the same network and model structure (see methods section; SI 1.1), using CL abundance as response variable following a quasi-Poisson distribution. As in the analysis with occurrence, these results show essentially no effect of the agricultural practices on CL abundance mediated by vegetation structure (Fig. S4, Table S1). Nevertheless, these results show no direct effect of the agricultural practices on CL abundance as compared with occurrence. The landscape context also seems to play an important role in CL abundance (Fig. S4).

Table S1. Standardized effects of the significant paths between the agricultural practices Shredding + Herbicide, Shredding, Tillage and Alfalfa, predicted for the abundance of Calandra Lark (CL). The Indirect Effects (IE) are the coefficients of the significant agricultural practices on each species mediated by the vegetation/food variables ($p < 0.05$), obtained by multiplying the partial standardised path coefficients. The Overall Effects (OE) are the total effect of the agricultural practices on each species, obtained by summing of all indirect effects.

Species	**Agricultural practice**	**Path (Agricultural practice → Variable → Species)**	**Indirect Effect**	**Overall Effect (OE)**
CL 	Tillage (T)	T → Cover dead → CL	0.11	0
		T → Height → CL	-0.11	

Figure S4. Path analyses exploring the effect of Shredding + Herbicide (a), Shredding (b), Tillage (c) and Alfalfa (d) in Calandra Lark (CL) abundance. R-squared (R2) is shown in the top-right corner of each path. Thickness of black (positive) and red (negative) paths is proportional to standardised path coefficients. Path transparency is proportional to the p-value significance level. Standardised path coefficients with $p < 0.10$ are shown according to the criteria: $p < 0.01$**/ $0.01 < p < 0.05$ */ $0.05 < p < 0.10$.➡


R^2 = 0.24
a
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
0.4 **
−0.78 **
−0.82 **
SHREDDING + HERBICIDE
ABUNDANCE CL
FOOD
SAI
ORTHOPTERA
0.31 **
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.35 *
0.16
−0.17
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
−0.34 *
−0.54 **
R^2 = 0.06
b
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
0.31
−0.47 **
−0.34
−0.25 *
0.13
0.49 **
SHREDDING
ABUNDANCE CL
FOOD
SAI
ORTHOPTERA
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.2 **
0.28 **
0.07
−0.07
0.1
−0.17 **
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
−0.65 **
−0.37 **
−0.25 *


$R^2 = 0.07$
c
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
−0.42 **
−1 **
0.66 **
−0.25 **
0.38 **
0.17 *
−0.14 *
TILLAGE
ABUNDANCE CL
FOOD
SAI
ORTHOPTERA
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.2 **
0.28 **
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
0.14 *
−0.15 **
−0.81 **
−0.21
−0.24 *

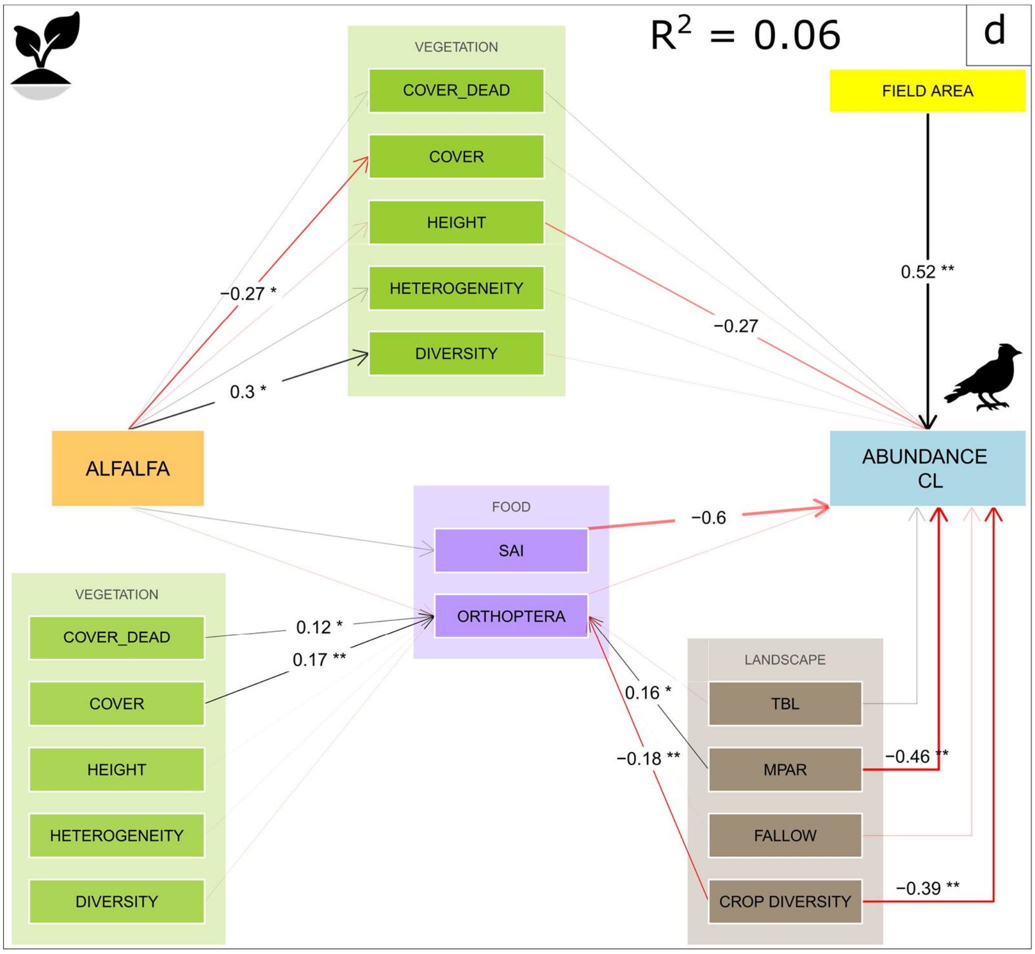

$R^2 = 0.06$
d
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
FIELD AREA
−0.27 *
0.3 *
−0.27
0.52 **
ALFALFA
ABUNDANCE CL
FOOD
SAI
ORTHOPTERA
−0.6
VEGETATION
COVER_DEAD
COVER
HEIGHT
HETEROGENEITY
DIVERSITY
0.12 *
0.17 **
LANDSCAPE
TBL
MPAR
FALLOW
CROP DIVERSITY
0.16 *
−0.18 **
−0.46 **
−0.39 **

Table S2. Standardized path coefficients and 95 % Confidence Intervals (CI) for the 12 path analyses made for each species (symbols from left to right: Stone curlew, Little Bustard and Calandra Lark) and each practice (symbols from up to down: Shredding plus herbicide, Shredding, Tillage and Alfalfa). Path coefficients are presented for partial paths between 1) each agricultural practice and the vegetation/food variables in shaded grey, and 2) each vegetation/food variable and the studied species in white. The variables are: dead cover (Cov.dead), cover, height, field heterogeneity (Heter.), plant diversity, Seed and Leaf Availability Index (SAI/LAI), and Orthopteran (Orthop.). Standardised path coefficients with $p < 0.10$ are shown according to the criteria: __$p < 0.01$ **__ / __$0.01 < p < 0.05$__ */ __$0.05 < p < 0.1$__

	Agricultural practice influence		**Species response**		**Agricultural practice influence**		**Species response**		**Agricultural practice influence**		**Species response**	
	β	95 % CI	*β*	95 % CI	*β*	95 % CI	*β*	95 % CI	*β*	95 % CI	*β*	95 % CI
Cov. dead	0.24	[-0.07 / 0.56]	__-1.53**__	[-2.48 / -0.58]	0.8	[0.13 / 0.42]	-0.80	[-3.72 / 0.02]	__0.30*__	[-0.001 / 0.60]	-0.51	[-1.26 / 0.23]
Cover	__-0.74**__	[-1.13 / -0.35]	__-1.72**__	[-2.76 / -0.68]	__-0.78**__	[-1.11 / -0.45]	0.09	[-2.42 / 2.61]	__-0.78**__	[-1.11 / -0.45]	-0.40	[-1.16 / 0.37]
Height	__-0.81**__	[-1.17 / -0.45]	__-1.18**__	[-1.94 / -0.42]	__-0.82**__	[-1.19 / -0.44]	-0.77	[-2.07 / 0.54]	__-0.59**__	[-1 / -0.19]	0.09	[-0.49 / 0.67]
Heter.	0.11	[-0.27 / 0.48]	0.11	[-0.42 / 0.64]	0.04	[-0.35 / 0.42]	0.26	[-0.84 / 1.36]	0.11	[-0.24 / 0.46]	-0.32	[-0.72 / 0.08]
Diversity	0.16	[-0.19 / 0.52]	0.03	[-0.52 / 0.58]	0.19	[-0.17 / 0.55]	-0.20	[-1.44 / 1.04]	0.16	[-0.19 / 0.51]	0.23	[-0.28 / 0.75]
SAI/LAI	-0.10	[-0.56 / 0.36]	0.37	[-0.14 / 0.87]	-0.10	[-0.41 / 0.21]	0.55	[-1.25 / 2.35]	-0.002	[-0.45 / 0.45]	-0.08	[-0.46 / 0.31]
Orthop	0.03	[-0.45 / 0.52]	-0.0	[-0.57 / 0.49]	0.03	[-0.45 / 0.52]	1.61	[-0.38 / 3.59]	0.03	[-0.45 / 0.52]	0.31	[-0.13 / 0.75]
Cov. dead	__0.31__	[-0.01 / 0.63]	0.06	[-0.31 / 0.44]	__0.30__	[-0.03 / 0.62]	0.009	[-0.36 / 0.38]	__0.31__	[-0.01 / 063]	-0.16	[-0.42 / 0.10]
Cover	-0.17	[-0.53 / 0.19]	__-0.47*__	[-0.86 / 0.07]	-0.16	[-0.52 / 0.19]	0.15	[-0.23 / 0.53]	-0.17	[-0.54 / 0.19]	-0.15	[-0.44 / 0.13]
Height	__-0.47**__	[-0.83 / -0.12]	__-0.42*__	[-0.77 / - 0.08]	__-0.47**__	[-0.84 / -0.11]	__-0.45*__	[-0.83 / -0.07]	__-0.47**__	[-0.84 / -0.11]	__-0.17__	[-0.35 / 0.02]
Heter.	__-0.34__	[-0.70 / 0.02]	0.05	[-0.24 / 0.35]	__-0.34__	[-0.70 / 0.02)]	-0.04	[-0.34 / 0.25]	__-0.34__	[-0.70 / 0.02]	-0.11	[-0.29 / 0.07]
Diversity	0.21	[-0.12 / 0.55]	0.19	[-0.08 / 0.16]	0.21	[-0.12 / 0.55]	__-0.33*__	[-0.65 / 0.02]	0.21	[-0.12 / 0.55]	-0.05	[-0.21 / 0.11]
SAI/LAI	-0.04	[-0.51 / 0.44]	0.13	[-0.16 / 0.41]	0.05	[-0.23 / 0.34]	0.04	[-0.39 / 0.48]	-0.04	[-0.51 / 0.44]	-0.11	[-0.38 / 0.15]
Orthop.	0.02	[-0.32 / 0.37]	0.04	[-0.32 / 0.41]	0.02	[-0.32 / 0.36]	-0.39	[-0.82 / 0.05]	0.02	[-0.32 / 0.37]	-0.31	[-0.68 / 0.06]
Cov. dead	__-0.42**__	[-0.67 / -0.17]	-0.06	[-0.37 / 0.24]	__-0.42**__	[-0.67 / -0.17]	-0.16	[-0.48 / 0.14]	__-0.43**__	[-0.68 / -0.18]	-0.10	[-0.35 / 0.14]
Cover	__-1**__	[-1.21 / -0.79]	__-0.42*__	[-0.75 / -0.09]	__-1**__	[-1.20 / -0.79]	__0.39*__	[0.03 / 0.75]	__-1**__	[-1.20 / -0.79]	0.009	[-0.28 / 0.30]
Height	__-0.66**__	[-0.88 / -0.44]	__-0.32*__	[-0.63 / 0.02]	__-0.66**__	[-0.88 / -0.44]	__-0.52*__	[-0.87 / -0.17]	__-0.66**__	[-0.88 / -0.44]	-0.09	[-0.30 / 0.12]
Heter.	-0.15	[-0.40 / 0.09]	0.01	[-0.24 / 0.27]	0.15	[-0.40 / 0.09]	-0.03	[-0.29/ 0.23]	0.15	[-0.39 / 0.09]	-0.15	[-0.40 / 0.09]
Diversity	0.14	[-0.08 / 0.36]	0.17	[-0.48 / 0.14]	0.14	[-0.08 / 0.36]	__-0.28__	[-0.57 / 0.01]	0.14	[-0.08 / 0.36]	0.14	[-0.08 / 0.36]
SAI/LAI	-0.14	[-0.40 / 0.11]	0.09	[-0.18 / 0.36]	-0.06	[-0.24 / 0.13]	-0.07	[-0.50/ 0.35]	-0.14	[-0.40 / 0.12]	-0.13	[-0.38 / 0.12]
Orthop.	__-0.005__	[-0.26 / 0.25]	0.06	[-0.25 / 0.36]	-0.01	[-0.24 / 0.26]	-0.34	[-0.73 / 0.05]	-0.005	[-0.26 / 0.25]	0.25	[-0.59 / 0.08]
Cov. dead	0.08	[-0.16 / 0.33]	__0.47*__	[-0.004 / 0.95]	-0.08	[-0.16 / 0.33]	-0.08	[-0.46 / 0.29]	0.08	[-0.16 / 0.33]	-0.11	[-0.41 / 0.18]
Cover	__-0.27**__	[-0.51 / -0.03]	-0.11	[-0.61 / 0.39]	__-0.27*__	[-0.51 / -0.04]	0.16	[-0.23 / 0.56]	__-0.27*__	[-0.51 / (-0.04)]	-0.24	[-0.60 / 0.13]
Height	-0.12	[-0.42 / 0.17]	-0.38	[-0.86 / 0.10]	-0.12	[-0.41 / 0.17]	__-0.73**__	[-1.14/ -0.32]	-0.12	[-0.41 / 0.17]	-0.16	[-0.37 / 0.05]
Heter.	-0.15	[-0.10 / 0.42]	0.12	[-0.32 / 0.56]	0.15	[-0.1 / 0.42]	-0.23	[-0.54 / 0.08]	-0.16	[-0.10 / 0.42]	0.02	[-0.21 / 0.24]
Diversity	__0.30*__	[0.04 / -0.56]	-0.19	[0.68 / 0.30]	__0.30*__	[0.04 / 0.56]	-0.24	[-0.58 / 0.1]	__0.30*__	[0.04 / 0.56]	-0.08	[-0.29 / 0.13]
SAI/LAI	0.20	[-0.07 / 0.46]	0.20	[-0.14 / 0.53]	__-0.18*__	[-0.35 / -0.01]	0.1	[-0.42 / 0.62]	-0.19	[-0.07 / 0.46]	-0.37	[-0.87 / 0.12]
Orthop.	-0.10	[-0.34 / 0.13]	0.11	[-0.34 / 0.57]	-0.07	[-0.31 / 0.16]	__-0.41__	[-0.86 / 0.03]	-0.10	[-0.34 / 0.13]	0.41	[-0.86 / 0.04]

Table S3. Pearson correlation matrix showing the correlation between the variables included in all path models. We set the Pearson correlation threshold as 0.5, and excluded one of the variables when the pairwise comparison was above this value (showed in bold in the table). Under this criteria, we excluded LAI_sd in the case of the Stone Curlew and Calandra Lark, and SAI_sd in the case of the Little Bustard.

	Cover	Cover_dead	Height	Diversity	Heter	area	tbl	mpar	fallow	biom	LAI_sd	SAI_sd	crop_diversity
Cover	1.00												
Cover_dead	-0.23	1.00											
Height	0.32	0.06	1.00										
Diversity	0.33	-0.25	0.12	1.00									
Heter	0.07	-0.13	-0.11	0.07	1.00								
area	0.05	-0.10	-0.08	0.20	0.02	1.00							
tbl	0.23	-0.05	0.01	0.02	0.20	-0.07	1.00						
mpar	0.30	-0.21	-0.01	0.19	0.14	-0.01	0.18	1.00					
fallow	-0.11	-0.12	-0.18	0.08	0.03	0.23	0.00	0.08	1.00				
biom	0.30	0.22	0.08	0.08	0.13	0.05	0.12	0.18	-0.07	1.00			
LAI_sd	0.46	-0.02	0.50	0.46	-0.07	0.25	-0.07	0.19	-0.06	0.19	1.00		
SAI_sd	0.21	-0.07	0.36	0.24	-0.01	0.15	-0.06	0.11	-0.08	0.11	**0.54**	1.00	
crop_diversity	-0.10	-0.08	-0.11	-0.01	-0.12	0.12	-0.24	-0.09	0.09	-0.22	-0.09	-0.04	1.00

Supporting information S2

Table S4. Number of fallow fields sampled every year grouped by the different agricultural practices.

Year	**Control**	**Shredding + Herbicide**	**Shredding**	**Tillage**	**Alfalfa**	Total
2015	151	30	6	25	10	222
2016	133	12	21	21	28	215
2017	28	18	4	83	42	175
Total	316	60	32	129	82	**612**

Table S5. Total and annual surface (ha) covered by the studied fallow fields managed with different agricultural practices. The percentage of Special Protection Areas (coloured polygons in Figure S5) occupied by the fallow fields is presented annually.

Year	**Area of Fallow (ha)**	**% of SPA covered**
2015	684.85	1.89
2016	675.95	1.86
2017	564.94	1.55
Total	1925.74	-

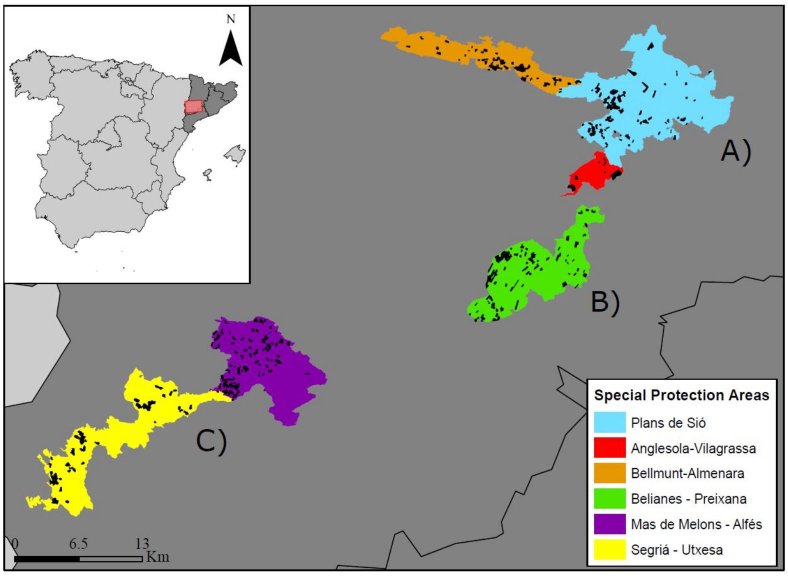


Figure S5. Study area representing the fallow fields sampled (black polygons) in the western and eastern part of the Lleida steppe plain of Catalonia (Spain) during 2015 - 2017. The SPA to which fallow fields belong are showed in different colours. The letters A), B) and C) correspond to the different maps shown in Figure S6, S7 and S8, showing the spatial distribution of the agricultural practices during the 3 years of the study period.

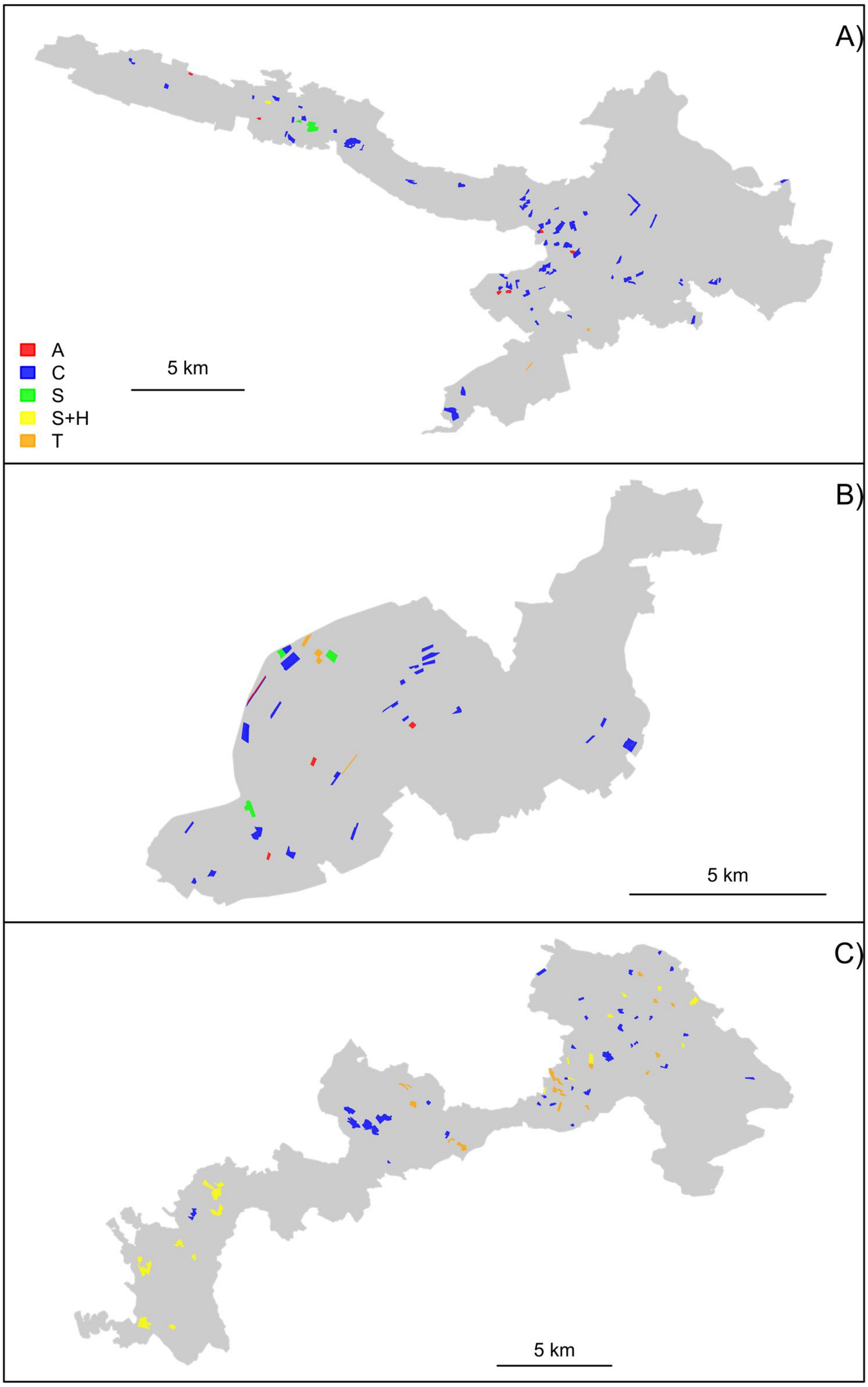


Figure S6. Spatial distribution of the agricultural practices applied in 2015. The agricultural practices are shown in different colours (A: Alfalfa, C: Control, S: Shredding, S+H: Shredding + Herbicide, T: Tillage). For visual purposes, the map has been divided in three parts corresponding to the zones A), B), and C) represented in the Figure S5. The area covered by the Special Protection Areas (SPA) is shown in light shaded grey.

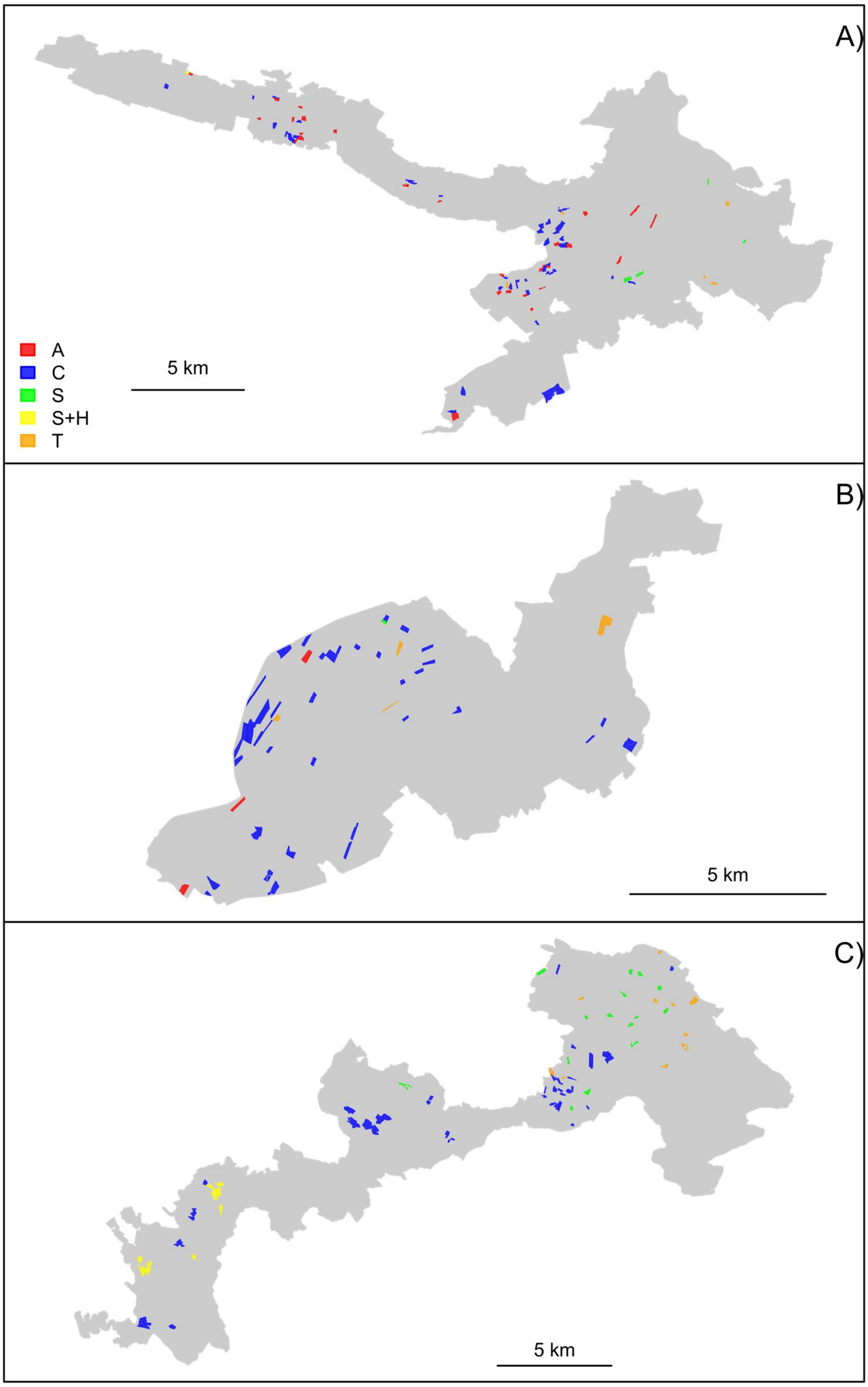


Figure S7. Spatial distribution of the agricultural practices applied in 2016. The agricultural practices are shown in different colours (A: Alfalfa, C: Control, S: Shredding, S+H: Shredding + Herbicide, T: Tillage). For visual purposes, the map has been divided in three parts corresponding to the zones A), B), and C) represented in the Figure S5. The area covered by the Special Protection Areas (SPA) is shown in light shaded grey.

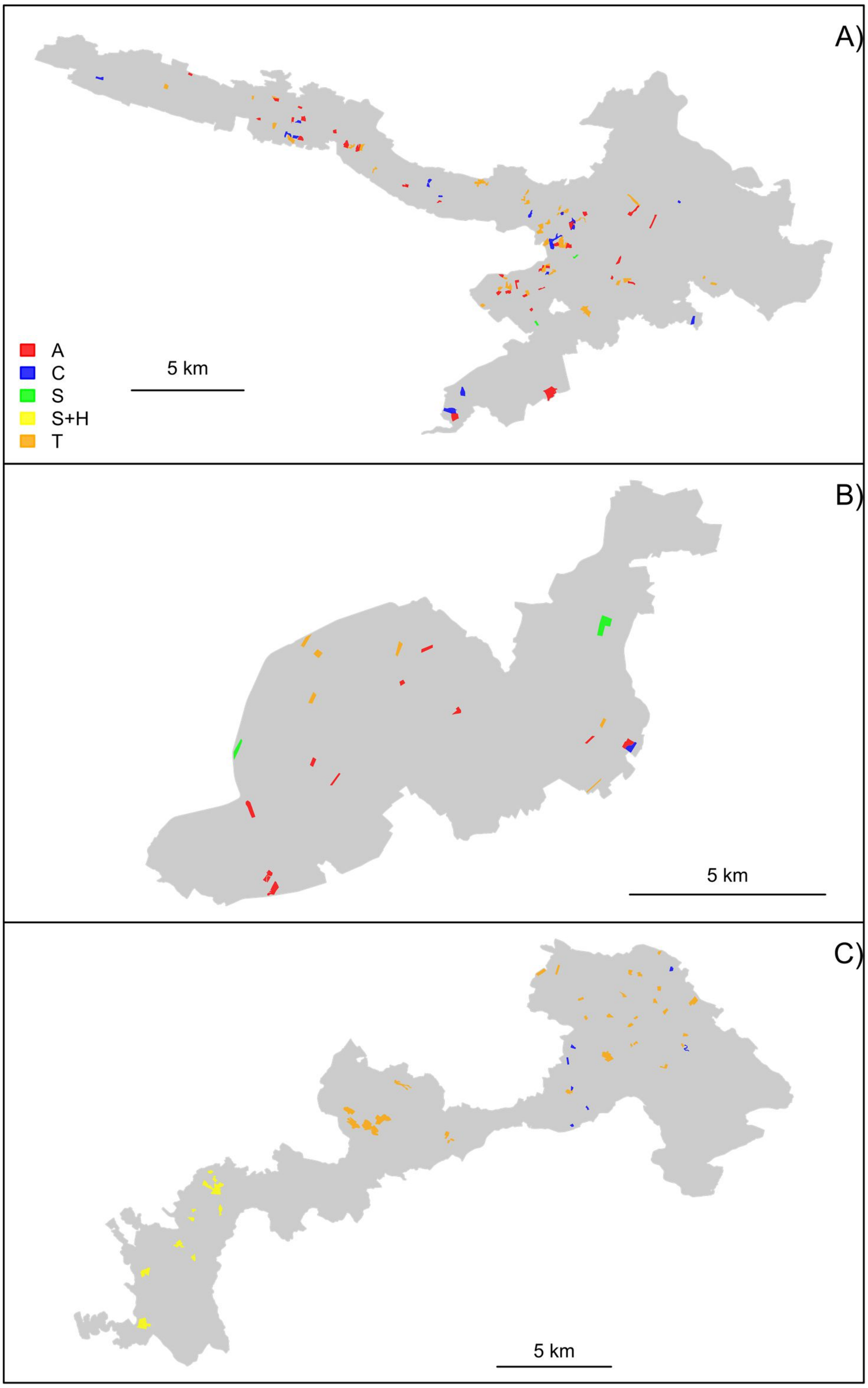


Figure S8. Spatial distribution of the agricultural practices applied in 2017. The agricultural practices are shown in different colours (A: Alfalfa, C: Control, S: Shredding, S+H: Shredding + Herbicide, T: Tillage). For visual purposes, the map has been divided in three parts corresponding to the zones A), B), and C) represented in the Figure S5. The area covered by the Special Protection Areas (SPA) is shown in light shaded grey.

Table S6. Summary, description, and sources of information of the variables used to analyse effects of agricultural practices on species occurrence. Landscape composition variables were stored in a raster of 50 m x 50 m resolution.

Variables	Description	Source
Field size	Area of the fallow field (m^2)	SIGPAC: http://agricultura.gencat.cat
Vegetation		
Live vegetation cover	Average percentage per fallow field	Field data; plot scale
Dead vegetation cover	Average percentage per fallow field	Field data; plot scale
Vegetation height	Average height per fallow field in cm	Field data; plot scale
Plant diversity	Pseudo Simpson Diversity Index derived from the cover of the dominant plant species	Field data; plot scale
Fallow heterogeneity	Levin's Index over the percentage of the vegetation structure categories: Cat. 1 Bare ground (0-5% cover) Cat. 2 (5-25% cover, 0-20 cm height) Cat. 3 (5-25% cover, 20-40 cm height) Cat. 4 (5-25% cover, >40cm height) Cat. 5 (25-50% cover, 0-20 cm height) Cat. 6 (25-50% cover, 20-40cm height) Cat. 7 (25-50% cover, >40cm height) Cat. 8 (>50% cover, 0-20 cm height) Cat. 9 (>50% cover, 20-40 cm height) Cat. 10 (>50 % cover, >40 cm height)	Field data; field scale
Food availability		
Orthopteran biomass	Weight in mg of the orthopterans detected in 2 20m x2m transects within the fallow field	Field data; Weight derived from length (cm) and counts from the regression equation of Hódar (1996)
Leaf Availability Index (LAI)	Leaf availability derived from vegetation cover, vegetation height and Specific Leaf Area of the dominant plant species in field plots	(Robleño et al., 2017); (de Bolòs, Vigo, Masalles, & Ninot, 1993) (Kattge et al., 2011); Field data
Seed Availability Index (SAI)	Seed availability derived from vegetation cover, vegetation height and seed mass of the dominant plant species in field plots	(Robleño et al., 2017); (de Bolòs et al., 1993) (Kattge et al., 2011); Field data
Landscape		
Configuration		
Total Border Length	Sum of field border lengths in m extracted from 500 and 200 radius buffers	SIGPAC: http://agricultura.gencat.cat
Mean of the Perimeter-Area Ratio[1]	Average the perimeter-area ratio of fields extracted from 500 and 200 radius buffers	SIGPAC: http://agricultura.gencat.cat; Donald et al. (2001)
Composition		
Fallow	Percentage of fallow land extracted from 500 and 200 radius buffers	DUN: http://agricultura.gencat.cat 50 x 50 m.
Crop diversity	Shannon Diversity Index of a simplified land cover classification[2] extracted from buffers.	

[1] Equation MPAR from Donald et.al 2001: $MPAR = \frac{Perimeter}{2\pi\sqrt{a}/\pi}$

[2] Land cover categories included: Alfalfa, Cereal, Almond trees, Fallow, Olive grove, Fruit trees, Corn, Colza, Peas, Vineyard, Other

Table S7. Summary of the vegetation variables Cover (%), Cover dead (%) and Height (cm) for the agricultural practices Control (C), Shredding + Herbicide (S+H), Shredding (S), Tillage (T) and Alfalfa (A). The mean with the associated standard deviation of all FF are shown for each vegetation variable and agricultural practice.

Agricultural practice	**Cover (%)**	**Cover dead (%)**	**Height (cm)**
C	51.06 ± 21.17	29.59 ± 26.74	38.15 ± 15.62
S+H	26.92 ± 24.03	37.55 ± 28.11	25.75 ± 14.09
S	48.86 ± 21.99	32.91 ± 24.55	30.16 ± 11.12
T	29.47 ± 25.16	20.21 ± 14.49	25.36 ± 11.92
A	65.67 ± 18.54	24.43 ± 24.5	43.94 ± 17.38

Table S8. Summary table of the proportion of Stone Curlew (SC), Little Bustard (LB), and Calandra Lark (CL) presence for each agricultural practice applied to FF.

Agricultural practice	**SC** 	**LB** 	**CL** 
Control	16.34	18.91	25.64
Shredding + Herbicide	40	10	65
Shredding	25.8	29.03	51.61
Tillage	24.03	20.93	34.11
Alfalfa	7.5	31.25	33.75

Supporting information S3 – Model bird species

We investigated the effect of different agricultural practices on the occurrence of the Stone Curlew *Burhinus oedicnemus* (SC), the male Little Bustard *Tetrax tetrax* (LB), and the Calandra Lark *Melanocorypha calandra* (CL). We selected these species to cover a wide range of diets, microhabitat selection requirements and body sizes. All three species use FF as nesting, displaying and foraging areas during breeding season (Green et al., 2000; Morales et al., 2008; Morgado et al., 2010). From the diet perspective, these species feed on a broad spectrum of food items, ranging from plants, invertebrates, and occasionally small vertebrates for SC (Giannangeli, de Sanctis, Manginelli, & Medina, 2004; Green et al., 2000), to seeds and invertebrates for CL (Suárez, Hervás, & Herranz, 2009), and mainly green plants for LB (Bravo et al., 2017; Jiguet, 2002). Regarding microhabitat selection requirements, they also present a wide gradient in the selected vegetation structure characteristics, that ranges from lower to higher vegetation cover and height values in the case of the SC and CL, respectively (Robleño et al., 2017). As for the body size, our model species range from a small passerine bird like CL (weight 44 - 66 grams; de Juana & Suarez, 2018) to a large non-passerine like LB (weight 794 - 975 grams; Collar, Garcia, & de Juana, 2018).

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Chapter IV:

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

Manuscript in preparation

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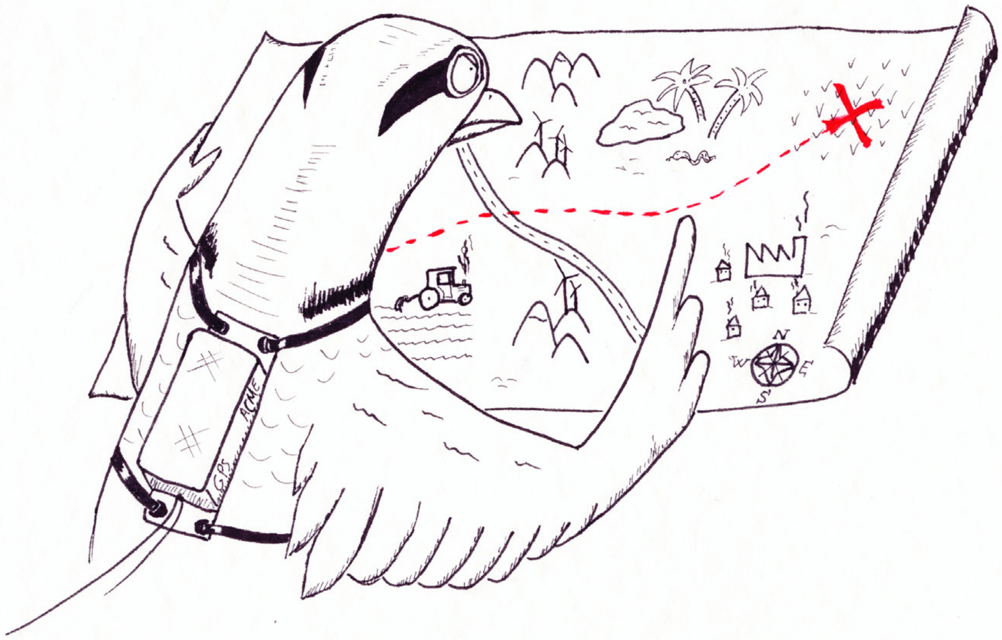

High-resolution tracking data reveals the importance of fallow land during a seasonal habitat bottleneck for a steppe-land specialist

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ABSTRACT

Farmland ecosystems are dynamic habitats shaped by crop cycles and rotations. In the face of agriculture intensification and the steady loss of natural and semi-natural habitats, farmland birds may be seasonally constrained with limited foraging and breeding resources. During spring, the growth of cereal crops makes a large proportion of arable land no longer suitable for some steppe bird species with narrow vegetation structure requirements. We investigated limitations in suitable habitat for the Pin-tailed sandgrouse (*Pterocles alchata*), a steppe bird species with declining populations whose European strongholds are found in Spain. During three years, we studied habitat selection of Pin-tailed sandgrouse throughout the cereal crop cycle in a cereal steppe of north-eastern Spain (Lleida plain), by tracking sandgrouse for the first-time with lightweight GPS tags. Cereal crops were avoided when cereal height increased until harvest (March-May), resulting in a 30% reduction of suitable habitat surface within individual home ranges at the start of the breeding season. We proved the existence of a habitat bottleneck, during which Pin-tailed sandgrouse only selected natural habitats and fallow land. Increased travelled distances during the bottleneck suggests increased search for resources in the face of scarce suitable habitat, which could be energetically costly. Conservation measures promoting optimal vegetation structures in fallows for steppe birds during the breeding season (Targeted Fallow Management, TFM) could alleviate seasonal habitat bottlenecks. Pin-tailed sandgrouse strongly selected fallows, yet habitat selection was not stronger towards TFM fallows during and after the bottleneck. TFM might yield a similar vegetation structure than that of conventionally managed fallows in the study area, that together with the low availability of alternative suitable habitats may result in similar habitat selection. This might not translate into similar effects of TFM and conventional management at the population level, as conventional management presents conservation drawbacks such as agricultural management during the breeding season. Our findings highlight the importance of conservation efforts to halt the ongoing loss of fallow land in optimal locations, as they constitute a key refuge for steppe birds to buffer the impacts of seasonal habitat bottlenecks.

Keywords: Habitat bottleneck, Pin-tailed sandgrouse, cereal steppe, GPS-tracking, vegetation structure, movement patterns, steppe birds

INTRODUCTION

Agricultural ecosystems have been profoundly intensified since the 20th century, which has resulted in a severe biodiversity loss (Kleijn et al., 2011) and dramatic declines of farmland bird populations (Voříšek et al., 2010). A major reason of these declines has been the rapid land use change occurring in farmland across years and the loss of natural and semi-natural habitats that provide key resources for biodiversity (e.g., fallow land; Traba and Morales, 2019; Van Buskirk and Willi, 2004). Moreover, farmland is characterized by seasonal land use changes caused by crop rotations, agricultural management, and crop cycles (Cardador et al., 2014), which turns it into a highly dynamic landscape. Understanding how farmland biodiversity copes with yearly and seasonally dynamic landscapes is key to promote farmland conservation and requires considering habitat selection as a dynamic process (Catry et al., 2012; Johst et al., 2001).

Specialist farmland species are more prone to suffer from temporal reductions or lack of key resources (i.e., seasonal habitat bottlenecks), being therefore more vulnerable to agriculture intensification (Clavel et al., 2011; Gámez-Virués et al., 2015). The specialist guild with worst conservation status in farmland ecosystems are the so-called steppe birds (Burfield, 2005), characterized by narrow niche requirements (e.g., require low vegetation height and cover; Robleño et al., 2017; Sanz - Pérez et al., 2019). Steppe birds have their European strongholds in the Iberian Peninsula where arid and extensive cereal cropland (also called cereal steppes or pseudo-steppes; Sainz Ollero, 2013) creates a landscape mosaic dominated by cereal, pastures and fallows (Benton et al., 2003). Fallow land is one of the most important habitats for steppe birds in agriculture ecosystems (Traba and Morales, 2019), as it usually presents cleared vegetation structures providing a good balance between predation risk and foraging opportunities (McMahon et al., 2010), as well as undisturbed habitats for nesting (e.g., Morales et al., 2013).

Cereal steppes are subject to strong seasonal dynamics, where the spring prompts the development of tall and dense vegetation (Cardador et al., 2014). Vegetation encroachment within cereal crops during spring restricts the amount of suitable habitat available for some of the steppe bird species, that can only occupy habitats with relatively stable vegetation structure throughout the year (i.e., natural vegetation and fallow land; Martín et al., 2010a; Tarjuelo et al., 2020a). The existence of potential bottlenecks in the amount of suitable habitat available has been suggested (e.g., Tarjuelo et al., 2020a) but has yet to be demonstrated and quantified, especially in a context where fallow land is declining at an unprecedented rate (Tarjuelo et al., 2020b), which has been linked with steppe bird populations declines (Traba and Morales, 2019).

The abundance of food resources and suitable vegetation structures for steppe birds on fallows can be jeopardized by conventional management practices applied by farmers, which can occur during the bird breeding season and are usually excessive, as they fear that weeds would hamper future crop productivity (Giralt et al., 2018). However, fallow abandonment is as detrimental as an intensive management, as long-term over-fertilization of arable fields can result in an excessive growth of vegetation in fallow fields, also unsuitable for steppe birds. Applying different agricultural practices in fallows in a moderate intensity can benefit steppe bird species. Indeed, Targeted Fallow Management (TFM), is a successful conservation measure in in north-eastern Spain (see Sanz-Pérez et al., 2021 for abundance; Sanz - Pérez et al., 2019 for occurrence), where fallows in optimal locations for steppe birds are specifically managed outside the sensitive season to meet their vegetation structure requirements during breeding season (Sanz - Pérez et al., 2019)

The Pin-tailed sandgrouse (*Pterocles alchata*) is a medium-sized steppe bird with narrow habitat requirements in terms of vegetation structure (Benítez-López, 2014; Benítez-López et al., 2017; Robleño et al., 2017), which are related to its ground nesting nature and foraging needs (Martín et al., 2010a). Spain currently holds 92% of the European population of Pin-tailed sandgrouse (Mougeot et al., 2021), where its populations have declined by 19% since 2005 and its breeding range is increasingly fragmented (Mougeot et al., 2020). Loss of non-cropped habitat due to agricultural intensification (Tarjuelo et al., 2020a), agrochemical use (e.g. the extended use of pesticide-coated seeds; Lopez-Antia et al., 2018), or human disturbances (see Benítez-López et al., 2017 for habitat selection; Mougeot et al., 2014 for reproduction) are likely drivers of sandgrouse population declines. Pin-tailed sandgrouse selects different substrates of cereal steppes depending on the season (fallows, extensive pastures, cereal stubbles, and ploughed fields; Martín et al., 2010a; Suárez et al., 1997, 1999; Tarjuelo et al., 2020a), but always conditional on low vegetation cover and/or height (Benítez-López et al., 2017). The specialist nature of this species could make it especially vulnerable to potential habitat bottlenecks occurring on cereal steppes at the beginning of the breeding season, when meeting habitat and energetic requirements is key for reproductive success. Thus, Pin-tailed sandgrouse could be particularly dependent on fallow land and natural vegetation during bottleneck periods (Tarjuelo et al., 2020a).

Habitat selection patterns of Pin-tailed sandgrouse have been studied based on discrete observations from field counts (e.g., Benítez-López et al., 2017) and radio-tracking (Martín et al., 2010a; Tarjuelo et al., 2020a). These methods have provided essential ecological insights, yet present high costs, imperfect detectability, and low spatial precision (Martin et al., 2009). Moreover, discrete observations constitute a mere snapshot of 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 (Martin et al., 2009; Recio et al., 2011). Latest developments have allowed using GPS advantages in light-weight birds (Recio et al., 2011), enabling the expansion of habitat selection studies for secretive species such as the Pin-tailed sandgrouse.

Here, we used GPS data from 12 Pin-tailed sandgrouse individuals during 2017 - 2019 to link habitat selection within the home range with changes in habitat suitability in a cereal steppe from north-eastern Spain (Catalonia). Specifically, we aimed to 1) identify and quantify a bottleneck in suitable habitat, 2) explore movement patterns as indicators of potential energetic costs during the bottleneck period, and 3) analyze the effect of Targeted Fallow Management (TFM) – ongoing conservation measure in our study area – as compared to conventional fallow management applied by farmers on sandgrouse habitat selection. We built our habitat bottleneck hypothesis upon three different time periods (Fig. 1): Short cereal, Tall cereal, and Stubble. We hypothesized that Pin-tailed sandgrouse will switch from selection to avoidance of cereal crops between the Short and Tall-cereal periods when their structural characteristics become unsuitable, and habitat selection towards cereal will be reinstated after harvesting in early June (Stubble period). We expected that fallows and natural vegetation would be the major habitat selected, acting as buffers during the Tall-cereal period.

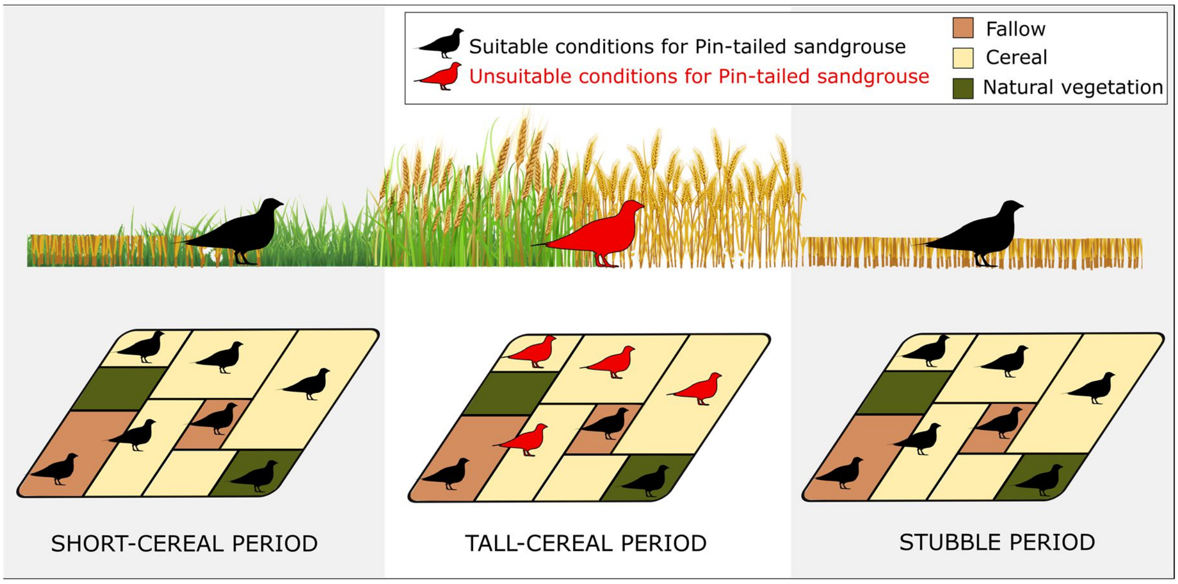


Figure 1. Graphic representation of the hypothesis on the habitat bottleneck for Pin-tailed sandgrouse in extensive cereal steppes, where fallow (brown), natural vegetation (green), and cereal (yellow) are the dominant and most used substrates by the species. Black birds represent suitable conditions for this species, occurring in the three substrates 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).

MATERIAL AND METHODS

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-Alfés' (0°40'E, 41°31'N; 6856.44 ha). This SPA holds an average population of ~ 167 (95% Confidence Interval = 77 – 327) breeding Pin-tailed sandgrouse individuals (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). The agricultural mosaic is dominated by natural vegetation (i.e., shrubland or sparse shrubland; 25%), winter cereal crops (24%), and fallows (15%), interspersed with olive groves (9%), almond (8%) and irrigation crops (6%) (Fig. 2). Land use surrounding the SPA is dominated by irrigated annual and permanent crops. Rainfalls and warmer weather in spring trigger the development of vegetation in cereal crops until it dries around May. Cereal is harvested 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 irrigation Mañosa et al., 2020) and is aimed to benefit vulnerable steppe bird species. This conservation measure named Targeted Fallow Management (TFM; Sanz - Pérez et al., 2019), represents 60 % of the fallow land in the study area, that would otherwise be allocated to rainfed cereal crops. TFM emerged as a compensatory measure for the construction of the Segarra-Garrigues irrigation project around SPAs (Mañosa et al., 2020), and consists of 1) the leasing of fallow fields and 2) applying common agricultural practices (e.g., shredding, tillage; Cantero-Martínez and Moncunill, 2012) once or twice per year from February to early April (before breeding season), in a subset of the leased fallow fields. The main goals of this conservation measure are to increase the fallow surface and obtain a suitable vegetation structure that meets the specific requirements of different steppe bird species, specifically the Pin-tailed sandgrouse in our study area (Giralt et al., 2018; Sanz - Pérez et al., 2019). The study area also presents fallow land conventionally managed by farmers (Conventional Fallow Management, CFM), who plough and/or herbicide > two times per year, sometimes during the breeding season, and mainly maintain fallows completely cleared from vegetation to avoid weeds.

Data collection

We captured and marked 12 Pin-tailed sandgrouse individuals between 2017 – 2019 with GPS-UHF loggers (PICA Ecotone, Gdynia, Poland). Birds were captured at night with a thermal camera and a large hand-held net (Benítez-López et al., 2011). Handling time was < 20 minutes and GPS weights represented < 3% of the birds weight, which fits in the recommended values for sandgrouse species (Casas et al., 2015). Data was downloaded from fixed antennas permanently located next to water holes, which avoided human disturbances. We used GPS locations from December 1st to August 31st in each of the three study years (2017 - 2019; Table A1, Appendix A). We excluded GPS locations during September – November because the population moves to a different region. The GPS locations were obtained at high-frequency (i.e., 60 min intervals) between 5:00 am – 7:00 pm UTC, the active hours for Pin-tailed sandgrouse.

We selected important habitat variables for Pin-tailed sandgrouse habitat selection based on previous knowledge (Table 1; Benítez-López et al., 2017; Tarjuelo et al., 2020a). Land-use variables were extracted from crop land-use maps (DUN; Generalitat de Catalunya, 2019a, SIGPAC; 2019b). Land uses were categorized as fallow, natural vegetation, olive, almond, irrigated woody crops, cereal, other dry or irrigated herbaceous crops, and forest (Table 1). We used distance to roads and dirt roads (m) as human-related variables, which were calculated in the log scale from a 1:50,000 topographic map of Catalonia (ICGC, 2017a)(ICGC, 2017a). We also calculated slope in degrees from the Digital Elevation Model at a 25 m resolution (ICGC, 2017b). To test the effectiveness of TFM as compared to CFM, we calculated the area of CFM from the crop land use map (Generalitat de Catalunya, 2019c) and TFM from a digitalized land use map from the conservation measure (Sardà-Palomera et al., 2015) (Table 1).

Study period division

In In order to study differences in the habitat selection of Pin-tailed sandgrouse in relation to the cereal annual cycle, we defined three periods in accordance with our hypothesis on the existence of a habitat bottleneck. The selection of dates delimiting each period was done according to expert criteria based on knowledge of the species breeding phenology and 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, we supported the expert criteria with 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).

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 2017-2019. The analysis column indicates whether the variable was used for analyses aimed at identifying the habitat bottleneck (1) or the analyses on 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	
Habitat				
Crop land use	1	Presence/absence of fallow, cereal, olive, almond, irrigated woody crops (Fruit.irri), dry or irrigated herbaceous crops (Herb.irri).	Dummy	DUN crop land use map of 2017, 2018 and 2019 (Unique Agrarian Statement) (Generalitat de Catalunya, 2019c)
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, 2019b)
Fallow management land use	2	Presence/absence of TFM and CFM	Dummy	DUN (Generalitat de Catalunya, 2019c) and map of managed fallow fields (Sardà-Palomera et al., 2020)
Slope	1, 2	Slope in degrees	Continuous	DEM 25x25m (ICGC, 2017b)

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 the threshold between the Short-cereal and Tall-cereal periods (See Appendix B for details on NDVI calculation and results). For each NDVI image, we used a 3x3 moving window and extracted the average NDVI from a 10 m-inner buffer drawn within cereal fields (Appendix B). We extracted the NDVI from cereal fields falling within the polygon of all individual home ranges (i.e., Minimum Convex Polygon, MCP), as this represents the area available for the studied individuals. The time threshold between the Tall-cereal and Stubble periods was defined based upon expert criteria on common harvesting dates in the study area, which are highly synchronized within a short time-span (Cantero-Martínez and Moncunill, 2012).

The periods were thus defined as follows: the Short-cereal period lasts from 1st December to 25th February and encloses the wintering time frame, when cereal fields have been recently sown (November) and have low vegetation height and cover, matching with the tillering agronomic growth stage (Large, 1954); the Tall-cereal period lasts from 8th March to 31st May, and includes the pre-breeding and start of breeding season, constituting the moment when the vegetation structure of cereal crops is high and dense (i.e., matching the stem extension, heading and ripening growth stages; Large, 1954); the Stubble period last from 10th June – 31st August and occurs during the core of the Pin-tailed sandgrouse breeding season, when cereal fields become stubbles after harvest. We excluded all GPS locations obtained during 5 days before and after the decided threshold dates to avoid confounding effects due to inter-annual variation in cereal phenology.

Habitat selection analyses

We performed two habitat selection analyses: the first analysis aimed at identifying and quantifying a potential habitat bottleneck by studying general habitat selection patterns, and the second one focused on determining the effect of fallow management (CFM vs. TFM) on Pin-tailed sandgrouse habitat selection.

Identify and quantify the habitat bottleneck.

First, we determined individual home ranges to define habitat availability by creating 99% MCP from the GPS locations of each individual obtained across the three study periods (Table A2, Appendix A). We then sampled the same number of random locations than the number of bird locations in each study period (Table A1) within the total MCP of each individual. We extracted the habitat characteristics of used and available locations using land use and human co-variates indicated in Table 1.

We quantified habitat selection patterns by using Resource Selection Probability Function (RSPF) built with the R package “ResourceSelection” (Lele et al., 2019). RSPF 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):

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

where β_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 RSPF’ reference category. We added an ID-Year structure that limited the comparison among used and available locations within individuals and years to account for the potential dependence of the data. 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, we performed 100 RSPF per period and computed the average standard error and p-values for each explanatory variable (see also Tarjuelo et al., 2020a).

We used the sign of the beta coefficients obtained in the RSPF to quantify the habitat bottleneck by calculating the land surface (ha) under selection (land-uses with significant positive coefficients) or avoidance (land-uses with significant negative coefficients) for each year and study period. We studied individual variability in the habitat bottleneck by calculating the proportion of selected and avoided land-use surface within each individual MCP. We also calculated the proportion of used and available habitats for each year and study period (Fig. 2).

Role of Targeted Fallow Management

Our second goal was to evaluate the importance of TFM for Pin-tailed sandgrouse habitat selection. Thus, we built one RSPF for each study period by using only GPS locations falling within fallow (both categories, TFM and CFM) and natural vegetation areas. We constrained the definition of habitat availability (i.e., random locations) to these land uses, and we extracted their habitat characteristics of used and available locations (Table 1). We used natural vegetation as the RSPF reference category because habitat selection towards this land use should remain positive in time (i.e., for feeding and nesting, as well as fallow fields; Tarjuelo et al., 2020a). This allowed us to better discern selection patterns towards TFM and CFM through time. We included all continuous variables (standardized) from the first RSPF analyses to control for their potential effects (Table 1), and we followed the same approach for bootstrapping, standard error, and p-value calculation.

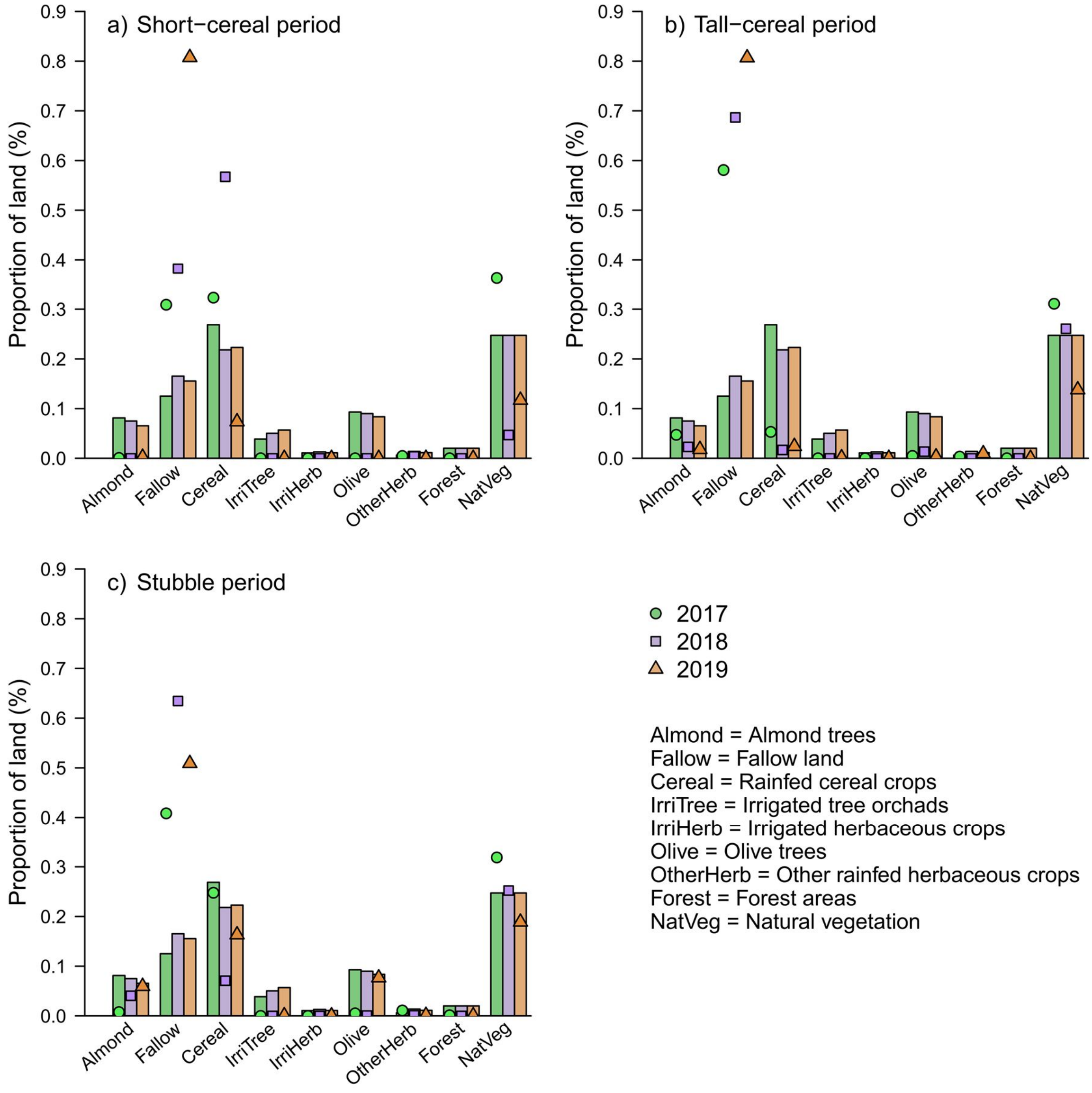


Figure 2. Proportion of habitat available for each land use (vertical bars) and habitat selected (symbols) during the study years 2017 – 2019 (colours) in the MCP of all studied Pin-tailed sandgrouse in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain). Proportions are shown for the Short-cereal (a), Tall-cereal (b), and Stubble (c) period.

Movement patterns

Movement parameters were calculated for each individual and period. We determined for each position whether the individual was flying by using instantaneous speed and a threshold of 1.5 knots (n = 737; Appendix A). We also determined whether each observation was in a different field than the previous observation and calculated the field change rate as the percentage of observations changing field. We also calculated the home range size (ha) from the individuals' MCP 99%, and the Euclidean distance between consecutive locations (m). We performed linear mixed models, using individual ID as random intercept and year as random effect, and determined whether movement variables differed significantly among periods by using ANOVA. We log-transformed the Euclidean distance variable to meet model assumptions. When models showed significant differences among periods, we used the "emmeans" function (Lenth, 2021) to discern differences among group means through the post-hoc Tukey test.

RESULTS

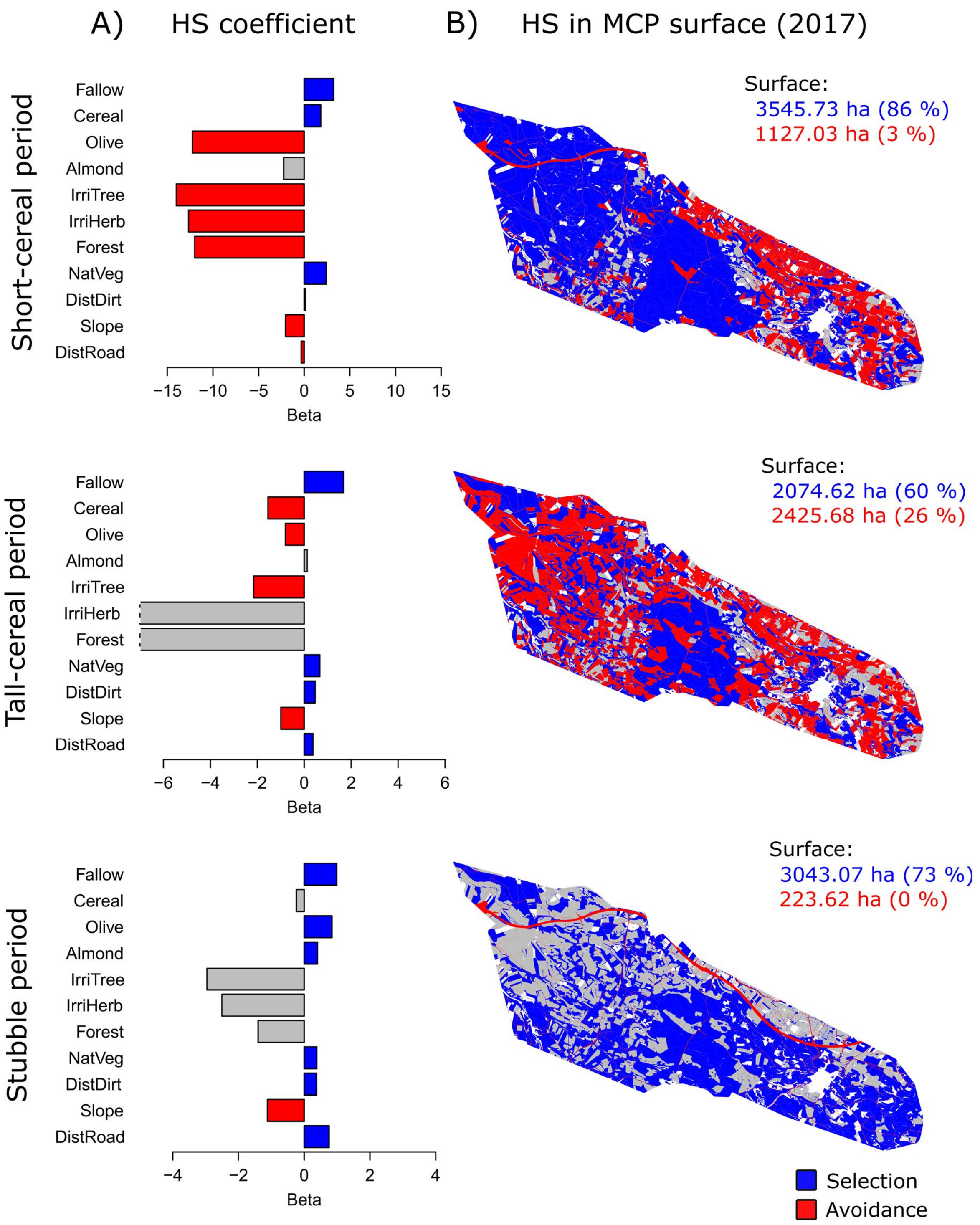
We used 20,212 GPS locations to investigate habitat selection (excluding 737 flying locations, Appendix A) and movement patterns, from which 13% belonged to the Short-cereal, 48% to the Tall-cereal, and 39% to the Stubble period (Table A1, Appendix A). Average home range size of Pin-tailed sandgrouse was 1,108.16 ha (SD = 646.21), which ranged from 775.81 (SD = 265.7) in the Short-cereal, to 1,362.26 (SD = 805.49) in the Tall-cereal, and 969.95 (SD = 618.8) in the Stubble period (Table A2, Appendix A).

Identify and quantify the habitat bottleneck

Pin-tailed sandgrouse consistently selected fallow and natural vegetation during the whole study period (Fig. 3a; see Table C1 for standard errors), which were also present in a relatively high proportion during the three study years (Fig. 2; Table 2). Individuals showed a positive selection towards winter cereal fields during the Short-cereal period, switching to a negative selection towards cereal fields during the Tall-cereal period (Fig. 2,3a). This negative selection towards cereal fields was no longer significant during the Stubble period (Fig. 2,3a). Sandgrouse avoided herbaceous and woody irrigated crops, as well as forest, presenting significant effects of these variables during the Short and Tall-cereal periods (Fig. 3a, Table C1). Pin-tailed sandgrouse also avoided olive crops during the Short and Tall-cereal periods (Fig. 3a), while switched to selecting olive and almond crops during the Stubble period (Fig. 3a). Pin-tailed sandgrouse preferred flat terrain across all periods, as well as locations far from roads and dirt roads, except in the Short-cereal period (Fig. 3a). Beta coefficients of the distance to roads and dirt roads (DistDirt and DistRoad; Fig. 3a) increased throughout the three study periods.

The percentage of selected habitat area within individual MCPs was on average 30% lower during the Tall than during the Short-cereal period (when it consisted solely of fallow land and natural vegetation), and was 21.7% higher during the Stubble than the Tall-cereal period (Table 2). By contrast, the percentage of avoided habitat area within individual MCPs increased from 3 to 26% between the Short and the Tall-cereal period and decreased to zero in the Stubble period (Table 2; see Fig. 3a and Fig. C1 for changes in the total MCP surface).

Figure 3. Habitat Selection (HS) results during the Short-cereal (upper panels), Tall-cereal (central panels) and Stubble (bottom panels) study periods used to identify and quantify a habitat bottleneck for Pin-tailed sandgrouse during 2017-2019 in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain). HS beta coefficients obtained from the RSPF of the three study periods are shown in the left panels (A; see Fig. 2 for variable acronyms). Right panels (B) show the land-use maps covered by habitat selected (blue), avoided (red), or used proportionate to their availability (grey) during each study period, using data from 2017 as an example (see Supplementary Material for 2018 and 2019). Maps cover the MCP 99% built from bird locations during 2017-2019. The surface in hectares covered by selected and avoided habitats is shown on top of each map. Percentages of avoided and selected land-uses within MCP (i.e., excluding continuous variables; see Table 2) are shown in brackets.➡



Role of Targeted Fallow Management

TFM enhanced the semi-natural habitat within home ranges (containing 25 % of natural vegetation and 6 % of conventionally managed fallows), increasing the fallow surface by 60%. The effect size of Pin-tailed sandgrouse habitat selection towards TFM and CFM fallows was positive and similar throughout the three study periods (Table 3). Positive selection of TFM was stronger than CFM in the Short-cereal period. During the Tall-cereal and Stubble periods, sandgrouse apparently preferred CFM over TFM. However, the effect of the two fallow types on the absolute probabilities of bird presence is notably lower than during the Short-cereal period due to the large negative intercepts (Table 3). In accordance with the previous analysis, Pin-tailed sandgrouse preferred flat terrain throughout the three study periods, as well as locations far from roads and dirt roads (Table 3).

Table 2. Relative importance (% of average Pin-tailed sandgrouse home range area) of each land use under selection (blue) and avoidance (red) of Pin-tailed sandgrouse along the Short-cereal, Tall-cereal, and Stubble study periods in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain). The table shows the mean and Standard Deviation (in brackets) of the percentages calculated within individual MCPs (see Table C2, Appendix C for results on each individual MCP). The total percentage of selected and avoided habitat obtained by summing percentages of land uses is also provided.

	Short-cereal period	Tall-cereal period	Stubble period
Almond	0.03 (0.02)	0.06 (0.02)	0.06 (0.04)
Fallow	0.19 (0.06)	0.27 (0.11)	0.27 (0.12)
Cereal	0.38 (0.13)	0.24 (0.13)	0.2 (0.13)
IrriTree	0.01 (0.01)	0.01 (0.01)	0.02 (0.02)
IrriHerb	0 (0)	0.01 (0)	0.01 (0)
Olive	0.02 (0.02)	0.04 (0.02)	0.06 (0.04)
Herb.sec	0.02 (0)	0.01 (0.01)	0 (0)
Forest	0.01 (0)	0.01 (0.01)	0.01 (0.01)
NatVeg	0.29 (0.06)	0.33 (0.07)	0.34 (0.07)
Total Selected	**0.86 (0.01)**	**0.6 (0.18)**	**0.73 (0.15)**
Total Avoided	**0.03 (0.02)**	**0.26 (0.14)**	**0 (0)**

Table 3. Habitat selection results from the RSPF analysis studying the role of Targeted Fallow Management (TFM) and Conventional Fallow Management (CFM) on Pin-tailed sandgrouse habitat selection during 2017 – 2019 in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain). Averaged beta coefficients (β 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.

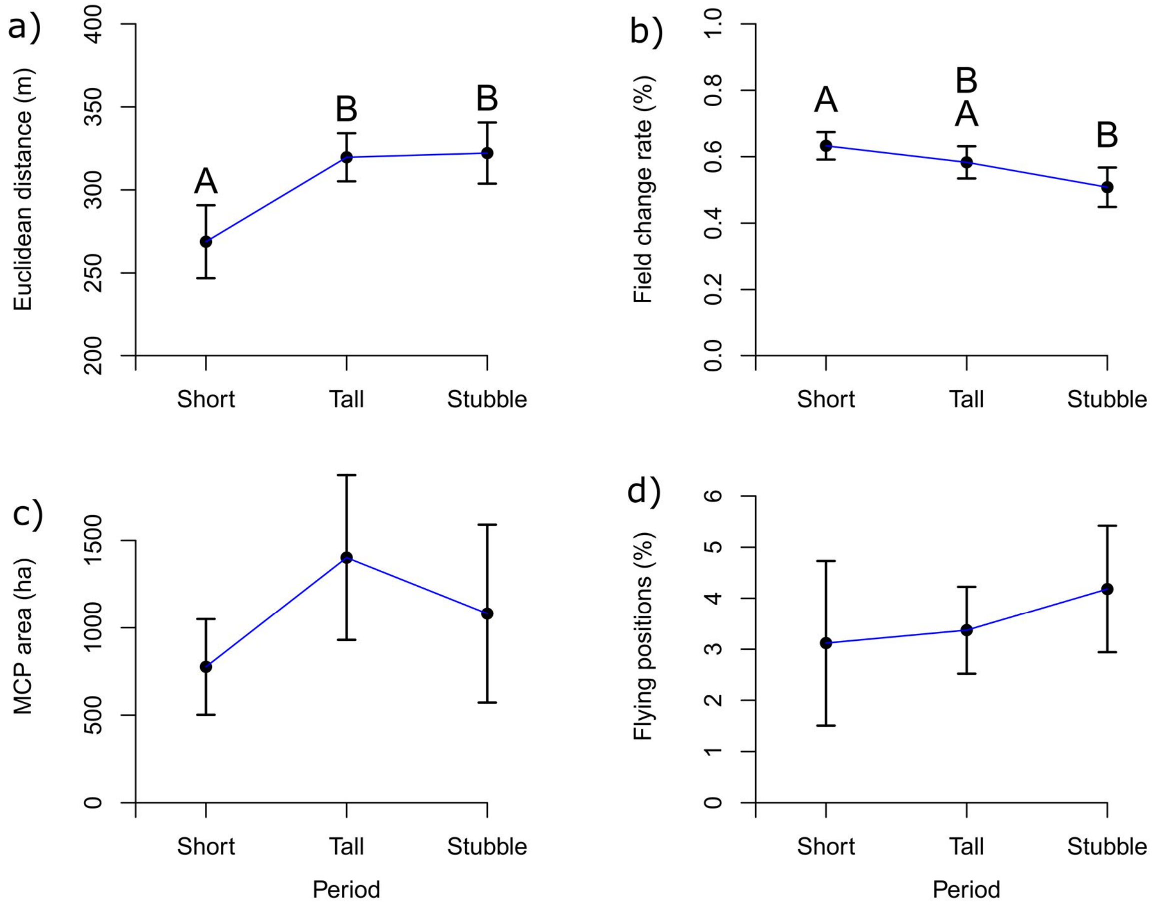
	Short-cereal period			**Tall-cereal period**			**Stubble period**		
	β coef.	**SE**	**p-value**	**β coef.**	**SE**	**p-value**	**β coef.**	**SE**	**p-value**
Intercept	-2.70	2.22	0.22	-13.25	0.16	< 0.01*	-10.07	0.47	< 0.01*
CFM	0.88	0.15	< 0.01*	1.34	0.04	< 0.01*	0.67	0.04	< 0.01*
TFM	1.02	0.26	< 0.01*	0.92	0.03	< 0.01*	0.52	0.03	< 0.01*
DistDirt[a]	0.24	0.05	< 0.01*	0.40	0.02	< 0.01*	0.34	0.02	< 0.01*
Slope	-2.09	0.32	< 0.01*	-1.03	0.03	< 0.01*	-1.03	0.05	< 0.01*
DistRoad[b]	-0.10	0.07	0.20	0.27	0.01	< 0.01*	0.33	0.01	< 0.01*

[a] Distance to dirt roads
[b] Distance to roads

Movement patterns

There were statistically significant differences among periods for Euclidean distances ($F_{(2,\ 19429)} = 5.69$, $p < 0.01$). The post-hoc Tukey test showed that Euclidean distances were significantly lower during the Short-cereal period than during the Tall-cereal and Stubble periods (Fig. 4; Table D1, Appendix D). There were statistically significant differences on field change rate among the three study periods ($F_{(2,10)} = 8.99$, $p < 0.01$), which decreased between Short-cereal and Stubble periods (Fig. 4; Table D1). Finally, there were not statistically significant differences among periods for neither the MCP area ($F_{(2,10)} = 2.79$, $p = 0.11$) nor the percentage of flying positions ($F_{(2,10)} = 0.73$, $p = 0.51$; Fig. 4).

Figure 4 Results on movement patterns of Pin-tailed sandgrouse studied during 2017 – 2019 in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain). 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, b) Field change rate, c) MCP area, and d) % of flying positions. Periods presenting with significant differences in movement patterns as determined by Tukey tests are indicated by different capital letters (see also Table D1, Appendix D).



DISCUSSION

The underlying effects of seasonal fluctuations of cereal steppes on the habitat selection of specialist steppe-land birds have been claimed across literature (Benítez-López et al., 2017; Martín et al., 2010a; Tarjuelo et al., 2020a), and accurate GPS data can improve the state-of-the-art on this question, most particularly on 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 quantify a decrease in suitable habitat from 86 to 60% when cereal vegetation became tall, and habitat was restricted to fallow land and natural vegetation. Sandgrouse responded to the bottleneck by increasing their movement patterns in terms of travelled distances, but not their home range size, flying time, or field change rate. Optimal vegetation structures within fallows should be critical for steppe birds (Sanz - Pérez et al., 2019) – especially during the bottleneck – yet fallows under target-conservation management were only preferred over fallows conventionally managed before the bottleneck.

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

Pin-tailed sandgrouse switched from selection to avoidance of cereal crops between the Short-cereal and Tall-cereal periods, supporting our 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; Martín et al., 2010a; Tarjuelo et al., 2020a). Likewise, cereals after harvest did not enhance Pin-tailed sandgrouse habitat selection, probably because stubbles are not optimal in reducing predation risk (Martín et al., 2010b). Cereal is prevalent on cereal steppes such as our study area (Fig. 2), so large habitat fluctuations for steppe birds (i.e., > 20 % in our study) are reasonable when cereal vegetation develops. Detecting such habitat fluctuations 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).

Preferred habitats for sandgrouse during the Tall-cereal period consisted of fallows and natural vegetation. They covered 60% of bird home ranges on average, though individual variability was high (36-93%). These land uses were also prevalent (Fig. 2), owing to the particular character of our study area hosting the ‘Secans de Mas de Melons-Alfés’ SPA and local conservation efforts increasing the fallow surface at a vast spatiotemporal scale (i.e., TFM, constituting a 60% of the fallows; Sanz - Pérez et al., 2019). Suitable semi-natural habitats such as fallows are becoming scant in many cereal-steppe regions (Tarjuelo et al., 2020b), which has been already linked to steppe-bird populations declines (Traba and Morales, 2019). Fallow loss is alarming not only during bottlenecks, but also throughout the year as confirmed by our results showing strong fallow selection during the whole study period, and other studies on seasonal habitat selection (Martín et al., 2010a; Tarjuelo et al., 2020a).

Human disturbance and general habitat selection patterns

In accordance with previous studies, Pin-tailed sandgrouse selected locations away from roads and dirt roads, due to their high sensitivity to human disturbances (Benítez-López, 2014; Benítez-López et al., 2017; Casas et al., 2016), and also possibly because of a higher predation risk near linear infrastructures (Benítez-López et al., 2015; Bischof et al., 2019). This behavior seemed to be weaker in the Short-cereal period, when human activity is likely lower and their gregarious behavior might reduce their perceived predation risks (Borbón et al., 1999; Martín et al., 2010b), and strengthen during the breeding period, when they are in pairs and need undisturbed and safe places for nesting (Mougeot et al., 2014). We also found that Pin-tailed sandgrouse generally avoided steep terrain and irrigated crops, confirming previous evidence on this behavior (Benítez-López et al., 2017; Martín et al., 2010a). They switched from avoiding olive groves during Short and Tall-cereal periods (Benítez-López et al., 2017) to selecting them and almond crops in the Stubble period (see also Tarjuelo et al., 2020a). Indeed, positive selection towards almond and olive crops was the only cause of the 13% increase in selected habitat during the Stubble period. Selection of tree land-uses during this period are likely related to the preference of shady habitats while resting under midday high summer temperatures (Herranz and Suarez, 1999), suggesting that the bottleneck on suitable habitat for feeding and breeding is likely latent during the Stubble period.

Role of fallow management for habitat selection

Despite studies proving the importance of managing vegetation structure for steppe bird conservation are increasing (Hawkes et al., 2021; Robleño et al., 2017; Sanz - Pérez et al., 2019), our results show that sandgrouse habitat selection was only slightly higher for TFM over CFM during the Short-cereal period. Pin-tailed sandgrouse has very narrow requirements, preferring fields with highly sparse vegetation (Benítez-López et al., 2017; Robleño et al., 2017). Although CFM is intensive and might end up in fields too cleared from vegetation for most steppe birds, this vegetation structure might not greatly differ from the one of TFM in the study area, where management is applied to obtain very open vegetation for Pin-tailed sandgrouse. Extensive management in TFM occurs at the beginning of the Tall-cereal period, likely minimizing the differences between CFM and TFM at that moment. Finally, the drastic habitat reduction during the Tall-cereal period limits the sandgrouse habitat choices exclusively to TFM and CFM (together with natural vegetation), thus both categories likely have an enhanced ecological value during this period. Besides, it is remarkable the higher effect size of slope and distance to roads than that of the management variables TFM and CFM for explaining bird habitat selection. This pattern reinforces the extreme importance of promoting fallows in flat and undisturbed locations.

Movement behavior of Pin-tailed sandgrouse

Pin-tailed sandgrouse responded to a decrease in suitable habitats during the Tall-cereal period by increasing their travelled distances. 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 dynamic cereal steppes (Tarjuelo et al., 2020a), indicating its value as an effective adaptative strategy to exploit resources in fragmented landscapes (Fahrig, 2007). Seasonal lack of habitats during the bottleneck, however, did not alter flying time, or, alternatively, hourly positions might not confer enough resolution to capture the flying behavior for this species. Field change rate did not increase during the Tall-cereal period, but a decreased trend can be noticed throughout the study period. The Stubble period is the core breeding season for sandgrouse, so they are likely driven by finding the optimal balance between resource acquisition and field-fidelity during nesting (Hinsley, 2000).

Conclusions and conservation implications

A key insight of our study is the critical role played by fallows and natural vegetation across the year but specially during the confirmed habitat bottleneck, acting as refuges for steppe bird species during the start of the breeding season. Conservation efforts should therefore prioritize the preservation and increase of fallows with suitable characteristics for steppe bird species, which is especially important given the alarming decline of fallows and steppe bird populations (see Tarjuelo et al., 2020b; Traba and Morales, 2019). Despite Pin-tailed sandgrouse habitat selection in our study was not stronger towards TFM than CFM, this does not invalidate TFM as a conservation measure. For instance, TFM increases the overall fallow surface and forbids agricultural management during the breeding season likely increasing reproductive success (see also Benítez-López et al., 2017). Moreover, a higher TFM surface increased the abundance of this and other species over other conservation measures and CFM in the study area (Sanz-Pérez et al., 2021). Our findings also highlight the importance of arranging fallows in optimal spatial locations (i.e., flat, undisturbed by humans, far from irrigation; see also Giralt et al., 2021) for conservation success, especially for highly sensitive species such as the Pin-tailed sandgrouse. This is noteworthy given the upcoming increase of disturbances by wind and solar photovoltaic energy projects, planned to occur in highly valuable pseudo-steppes of Spain (Serrano et al., 2020).

Seasonal resource fluctuations have proved to affect survival (Janke et al., 2015; Schlaich et al., 2016) and have carry-over effects (Swift et al., 2020). Our results revealed higher displacements during the bottleneck in suitable habitat. Further research on the physiologic and demographic consequences of altered movement patterns during the bottleneck is crucial to discover long-term bottleneck effects on the populations of Pin-tailed sandgrouse and other steppe bird species. Ensuring habitat and fitness stability in seasonal landscapes is key to preserve steppe bird populations and should therefore become a priority in conservation planning.

Author's contributions: GB, FM, DG, FS-P, RT, and AS-P conceived and designed the study. RT and AS-P implemented the analysis with the contribution of MP. AS-P led the writing of the manuscript. CS, MP, FS-P, DG, GB, FM, performed fieldwork, with the help of AS-P and RT. All the authors contributed to subsequent drafts and gave final approval for publication. FS-P, DG and GB coordinated fieldwork and GB secured funding.

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APPENDIX

Appendix A: Pin-tailed sandgrouse data

We used data on 12 Pin-tailed sandgrouse individuals which resulted in a total of 20,212 locations. We used the full set of GPS locations to perform the movement analysis on the percentage of flying locations per period (main text), and excluded flying locations (n = 737) for the rest of analyses. We also excluded locations that fell in land uses not analysed in our study (n = 510), such as locations within gravel roads or unproductive land uses.

Table A1. List of Pin-tailed sandgrouse GPS data collected during 2017-2019 in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain) to study habitat selection and movement patterns. Start and End denote the start and end date for 0which GPS locations were available. The number of locations is given for each of the three study periods. The sex of the studied individuals (F – Female; M – Male) is also provided

Logger ID	Sex	Start	End	Locations		
				Short	Tall	Stubble
PIC17	M	1/12/2018	31/1/2019	1132	1259	814
PIC15	M	17/4/2018	4/8/2018	0	1198	855
PIC02	M	1/12/2018	16/8/2019	493	1245	846
GUE05	F	8/3/2019	4/8/2019	0	633	1090
GUE04	M	8/3/2019	31/5/2019	0	1255	0
GUE03	M	8/3/2019	25/8/2019	0	618	769
GUE02	M	8/3/2019	21/4/2019	0	1258	0
GUE01	M	8/3/2019	25/8/2019	0	983	1529
CIP05	F	1/12/2016	18/1/2017	630	0	0
CIP04	M	8/3/2017	10/8/2017	0	675	756
CIP03	M	8/3/2017	10/8/2017	0	660	1125
CIP02	M	1/12/2016	14/2/2017	389	0	0
	Total N° locations			2644	9784	7784

Table A2. Home range sizes in ha calculated from MCP 99% for each individual Pin-tailed sandgrouse studied during 2017-2019 in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain). Individual and average home range sizes with associated Standard Deviations (SD) are provided for the Short-cereal, Tall-cereal, and Stubble periods.

Logger ID	Short-cereal period	Tall-cereal period	Stubble period	Mean (SD) per individual
CIP02	614.2	-	-	614.20
CIP03	-	1481.13	1178.43	1329.78 (214.04)
CIP04	-	894.08	840.83	867.46 (37.65)
CIP05	958.66	-	-	958.66
GUE01	-	1482.46	918.28	1200.37(398.94)
GUE02	-	295.62	-	295.62
GUE03	-	2579.31	1714.21	2146.76 (611.72)
GUE04	-	2281.26	-	2281.26
GUE05	-	1897.89	276.67	1087.28 (1146.38)
PIC02	1040.87	1800.51	1969.91	1603.76 (494.78)
PIC15	-	496.76	457.53	477.15 (27.74)
PIC17	489.5	413.58	403.77	435.62(46.92)
Mean (SD) per period	775.81 (265.7)	1362.26 (805.49)	969.95 (618.8)	

Appendix B: Normalized Difference Vegetation Index (NDVI)

NDVI calculation

We used NDVI data obtained from the 15th of February to the 30th of April during 2017-2019 to set up the threshold between the Pre-Bottleneck and Bottleneck periods (i.e., by identifying the period when cereal vegetation growth occurred). If available weekly or fortnightly 20 meter resolution NDVI was calculated on the cloud using the Surface Reflectance product from Sentinel 2 repository (European Space Agency, 2015; European Union, 2015), available on the Google Earth Engine Data Catalog (Gorelick et al., 2017). All data with a cloud coverage affecting up to 20% of the scene was excluded in order not to incur in bias of index values.

NDVI results

Information on the daily and weekly NDVI images revealed that the transition period for vegetation growth occurred at the interface between the end of February and beginning of March (Fig. B1). Therefore, we chose the 1st of March as a threshold and excluded all GPS locations during 5 days before and after this date to ensure that the vegetation structure was homogeneous within each period (i.e., low and cleared cereal vegetation during the Short-cereal period, high and dense cereal vegetation during the Tall-cereal period).

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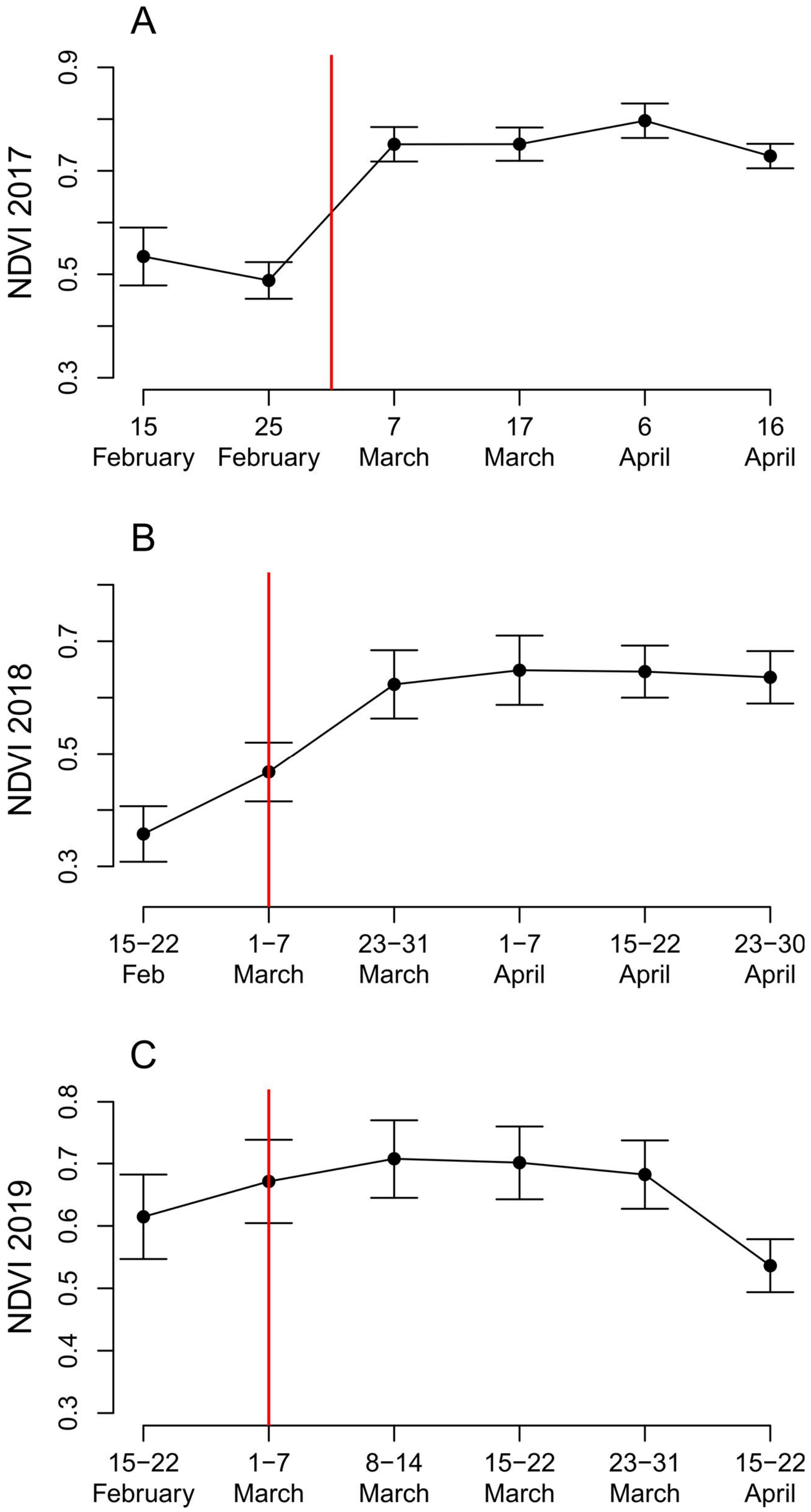

Figure B1. Evolution of NDVI values for the years 2017 (a), 2018 (b), and 2019 (c) extracted from the cereal fields within the total MCP of 12 Pin-tailed sandgrouse individuals during 2017-2019 in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain). The date that supported the decision on the division between the Short and Tall-cereal period (1st March) is shown in red

Appendix C: Habitat selection analyses

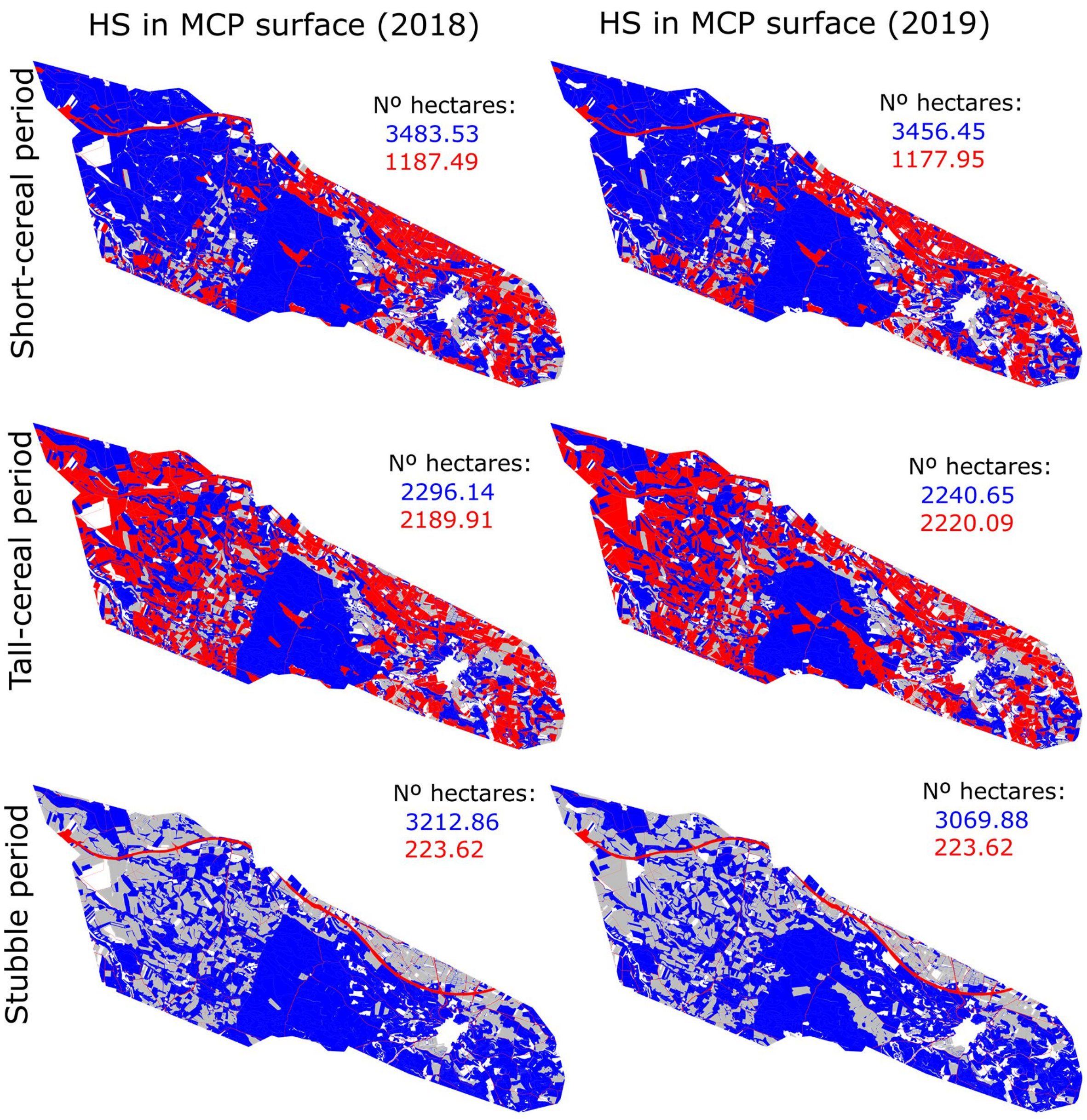

Figure C1. Land-use maps covered by habitat selected (blue), avoided (red), or used proportionate to their availability (grey) by Pin-tailed sandgrouse during each study period of 2018 and 2019 in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain). The map covers the MCP 99% built from bird locations during 2017-2019. The surface in hectares covered by each type of land use (selected or avoided) is shown on top of the maps. Please refer to main text for Habitat Selection beta coefficients and map of 2017.

Table C1. RSPF habitat selection results of Pin-tailed sandgrouse during the Short-cereal period, Tall-cereal period and Stubble period used to identify and quantify a habitat bottleneck on suitable habitat for Pin-tailed sandgrouse during 2017-2019 in the the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain). Averaged beta coefficients (β coef), Standard Errors (SE) and p-values are provided for the three study periods. Significant p-values are indicated with an asterisk.

	Short-cereal period			**Tall-cereal period**			**Stubble**		
	β coef.	**SE**	**p-value**	**β coef.**	**SE**	**p-value**	**β coef.**	**SE**	**p-value**
Intercept	-4.65	0.39	< 0.01*	-4.68	3.35	0.16	-2.38	0.23	< 0.01*
DistRoad	-0.34	0.03	< 0.01*	0.38	0.01	< 0.01*	0.76	0.05	< 0.01*
Slope	-2.04	0.13	< 0.01*	-1.00	0.03	< 0.01*	-1.12	0.06	< 0.01*
DistDirt	0.12	0.03	< 0.01*	0.46	0.02	< 0.01*	0.38	0.02	< 0.01*
NatVeg	2.41	0.34	< 0.01*	0.67	0.27	< 0.05*	0.38	0.17	< 0.05*
Forest	-12.01	5.49	< 0.05*	-12.88	25.61	0.58	-1.40	0.72	0.06
IrriHerb	-12.68	5.97	< 0.05*	-10.25	32.05	0.73	-2.51	1.78	0.15
IrriTree	-14.01	5.93	< 0.05*	-2.16	0.59	< 0.05*	-2.96	1.42	0.06
Almond	-2.25	2.71	0.39	0.13	0.27	0.64	0.40	0.18	< 0.05*
Olive	-12.24	6.11	< 0.05*	-0.80	0.31	< 0.05*	0.84	0.18	< 0.01*
Cereal	1.82	0.33	< 0.01*	-1.55	0.27	< 0.01*	-0.24	0.17	0.17
Fallow	3.24	0.36	< 0.01*	1.68	0.27	< 0.01*	0.99	0.17	< 0.01*

Appendix D: Movement patterns analyses

Table D1. Pairwise differences among study periods for movement patterns of Pin-tailed sandgrouse during 2017 – 2019 sandgrouse in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain). The difference among means of each study period and its associated Standard Errors and p-values are presented only for significant variables according to ANOVA tests and linear mixed models.

	Log Euclidean distance (m)			**Field change rate (%)**		
	Estimate	SE	p-value	Estimate	SE	p-value
Short - Tall	-0.19	0.06	> 0.05*	0.08	0.03	0.12
Tall - Stubble	-0.02	0.03	0.6	0.07	0.03	0.07
Stubble - Short	-0.22	0.06	> 0.01*	0.15	0.04	> 0.01*

Table C2. Relative importance (% of average Pin-tailed sandgrouse home range area) of each land use under selection (blue) and avoidance (red) along the Short-cereal period, Tall-cereal period and Stubble period in the 'Secans de Mas de Melons-Alfés' SPA (Lleida, Spain). Percentages were calculated within individuals MCP. The total percentage of selected and avoided habitat (obtained by summing percentages of land uses), as well as the mean and Standard Deviation (SD) for all individuals are provided➡.

		Almond	Fallow	Cereal	IrriTree	IrriHerb	Olive	OtherHerb	Forest	NatVeg	Selected	Avoided
Short-cereal period	PIC17	0.05	0.3	0.16	0.02	0.01	0.06	-	0	0.39	0.85	0.07
	PIC15	-	-	-	-	-	-	-	-	-	-	-
	PIC02	0.02	0.17	0.46	-	0	0	0.03	0.01	0.23	0.86	0.02
	GUE05	-	-	-	-	-	-	-	-	-	-	-
	GUE04	-	-	-	-	-	-	-	-	-	-	-
	GUE03	-	-	-	-	-	-	-	-	-	-	-
	GUE02	-	-	-	-	-	-	-	-	-	-	-
	GUE01	-	-	-	-	-	-	-	-	-	-	-
	CIP05	0.05	0.17	0.43	-	0	0.01	0.02	0.01	0.25	0.85	0.03
	CIP04	-	-	-	-	-	-	-	-	-	-	-
	CIP03	-	-	-	-	-	-	-	-	-	-	-
	CIP02	0.01	0.13	0.47	0	0	0	0.02	0.01	0.28	0.88	0.01
	Mean(SD)	**0.03 (0.02)**	**0.19 (0.06)**	**0.38 (0.13)**	**0.01 (0.01)**	**0 (0)**	**0.02 (0.02)**	**0.02 (0)**	**0.01 (0)**	**0.29 (0.06)**	**0.86 (0.01)**	**0.03 (0.02)**
Tall-cereal period	PIC17	0.1	0.36	0	-	0.01	0.07	-	0	0.4	0.76	0.07
	PIC15	0	0.5	-	-	0.01	0.04	-	0	0.43	0.93	0.04
	PIC02	0.06	0.22	0.26	0	0.01	0.05	0.02	0.02	0.28	0.5	0.32
	GUE05	0.06	0.22	0.32	0	0	0.03	0.01	0.02	0.27	0.49	0.35
	GUE04	0.06	0.23	0.28	0.04	0	0.03	0	0.01	0.28	0.5	0.36
	GUE03	0.06	0.18	0.24	0.01	0.01	0.07	0.02	0.02	0.28	0.46	0.32
	GUE02	-	0.41	0.07	-	0.01	0.05	-	0	0.45	0.86	0.12
	GUE01	0.06	0.24	0.27	0.01	0.01	0.04	0	0.03	0.29	0.53	0.32
	CIP05	-	-	-	-	-	-	-	-	-	-	-
	CIP04	0.06	0.25	0.23	-	0	0.03	-	0.03	0.36	0.6	0.26
	CIP03	0.07	0.13	0.47	0	-	0.02	0.01	0.02	0.23	0.36	0.49
	CIP02	-	-	-	-	-	-	-	-	-	-	-
	Mean(SD)	**0.06 (0.02)**	**0.27 (0.11)**	**0.24 (0.13)**	**0.01 (0.01)**	**0.01 (0)**	**0.04 (0.02)**	**0.01 (0.01)**	**0.01 (0.01)**	**0.33 (0.07)**	**0.6 (0.18)**	**0.26 (0.14)**
Stubble period	PIC17	0.11	0.34	0	-	0.01	0.05	-	0	0.42	0.92	0
	PIC15	0.01	0.52	-	-	0.01	0.05	-	0	0.39	0.97	0
	PIC02	0.05	0.24	0.31	0.02	0	0.02	0.01	0.02	0.27	0.58	0
	GUE05	0	0.32	0.15	-	0.01	0.05	-	0	0.45	0.82	0
	GUE04	-	-	-	-	-	-	-	-	-	-	-
	GUE03	0.09	0.1	0.08	0.05	0.01	0.17	0	0.03	0.29	0.65	0
	GUE02	-	-	-	-	-	-	-	-	-	-	-
	GUE01	0.08	0.25	0.24	0.01	0.01	0.04	0	0.02	0.3	0.68	0
	CIP05	-	-	-	-	-	-	-	-	-	-	-
	CIP04	0.01	0.26	0.2	0.01	0.01	0.05	-	0.02	0.38	0.71	0
	CIP03	0.09	0.14	0.41	0	0	0.03	0	0.02	0.24	0.5	0
	Mean(SD)	**0.06 (0.04)**	**0.27 (0.12)**	**0.2 (0.13)**	**0.02 (0.02)**	**0.01 (0)**	**0.06 (0.04)**	**0 (0)**	**0.01 (0.01)**	**0.34 (0.07)**	**0.73 (0.15)**	**0 (0)**

General

DISCUSSION

GENERAL DISCUSSION

The fate of farmland bird communities is closely tied to farming practices and agricultural policies, and the future of farmland bird populations depends on our ability to promptly detect – and understand the processes driving – changes in abundance and population trends. This thesis used a multi-scale approach to show the importance of methodological and statistical considerations when evaluating population trends (*Objective 3*) and to propose solutions to reverse the declining trends of the endangered steppe bird guild in a cereal pseudo-steppe of north-eastern Spain. I studied agricultural management of fallow fields as a conservation measure for steppe birds assuming that if agricultural practices have reduced their populations, then alternative agricultural practices can restore them (*Objective 1*) (Ormerod and Watkinson, 2000). I identified applied pathways to benefit steppe bird populations, and that can also be integrated into the legal framework of the Common Agricultural Policy. This thesis is timely, as it provides input into policy at the verge of the CAP-post 2020 reform (*Objective 2*) (e.g., Tarjuelo et al., 2020b). It is also of broad relevance, as it does not only focus on the steppe bird specialist guild, but also includes the larger farmland bird community and steppe bird species that have historically received little scientific attention (Morales and Traba, 2016).

1. Insights into bird monitoring in agriculture ecosystems

Designing monitoring programs well-suited to the characteristics of farmland ecosystems and their rich biodiversity is essential to properly track their conservation status. Farmlands experience large fluctuations in vegetation structure (Cardador et al., 2014; Catry et al., 2012) caused by varying weather conditions, land uses, and agricultural practices. Such fluctuations can lead to heterogeneous conditions in visibility when performing bird surveys. I found that fluctuations in detectability across years (Chapter I) led to higher uncertainty in trend estimates as compared to TRIM models, which do not account for imperfect or varying detection. Vegetation height is an important ecological driver for bird species in agro-systems but also prone to affect detectability (Henderson et al., 2000), so differences in crops, agricultural practices, or conservation measures that shape the vegetation structure are also likely to cause heterogeneous detection among sampling locations. If not accounted for within data analysis, vegetation effects on detectability can be confounded with population abundance or trends, potentially leading to incorrect ecological inference.

I considered imperfect detection when evaluating population trends, abundance, and conservation measures in Chapter I and II through distance sampling. However, data collection in Chapter III, that was based on a single survey and without records of detection distances, did not allow me to explicitly account for imperfect detection. Sampling for Chapter III was specifically designed to evaluate the effects of Targeted Fallow Management (TFM) by maximizing detection of target steppe bird species potentially hidden in dense vegetation (i.e., combination of point counts and zigzag sweep transects performed by fully trained observers), which minimized imperfect detectability. Specific designs are not always feasible from a technical or economic perspective and assessment of conservation measures often relies on data collected within large-scale monitoring programs, designed for surveying the entire bird community (e.g., Chapter I, II). The trade-off between accounting for the characteristics of specific species, while adequately covering a large number of species, highlights the importance of generic but also thoughtful study designs.

Moreover, monitoring programs often rely upon citizen science (Bart, 2005; Voříšek et al., 2010), which can introduce further heterogeneity in the detection process through varying observer skills (Vallecillo et al., 2020). Chapter I revealed different degrees of observer variability among species, for instance, among large-flagship (e.g., Stone curlew) and small-common species (e.g., Eurasian skylark). Such differences are expected when monitoring broad communities, as it was the case in Chapter I and II, and in most bird monitoring programs.

Monitoring programs are the foundation for estimating population trends, assigning species conservation status (e.g., IUCN categories), and evaluating the effectiveness of conservation measures to reverse those trends. Farmland bird population trends and their conservation status are decreasing at alarming rates, and there is a growing need for more systematic data collection (Maes et al., 2015) that allows modelling the detection process (Kéry and Schmid, 2004). Distance sampling is a cost-effective approach widely used in bird research (e.g., Newson et al., 2008; Rosenstock et al., 2002) – as it only involves recording distance from the observer – and also proved useful in this thesis to evaluate population trends (Chapter I), and the effectiveness of conservation measures (Chapter II). Hierarchical Distance Sampling (HDS) models implemented in a Bayesian framework are becoming common (e.g., Kéry and Royle, 2016), due to their flexibility for building complex models. With Bayesian HDS models, such as the ones used here for population trends (Chapter I) and for testing conservation measure effects (Chapter II), we also have the ability to obtain posterior distributions of variables of interest. Quantifying uncertainty is key in decision-making, and posterior probabilities are very useful in that regard, as they represent a continuous measure of the importance of environmental variables (or of whether a population is increasing or decreasing) rather than significance thresholds associated with frequentist methods (Wade, 2000).

Hierarchical models that account for imperfect detection are becoming increasingly popular among ecologists thanks to recent software developments (e.g., unmarked R package, Fiske and Chandler, 2011; JAGS, Plummer, 2003) and an increase in literature explaining its application (Kéry and Royle, 2016). However, statistical and coding knowledge are required to apply these models – often computationally intensive – and interpret their output appropriately. Together with inappropriate sampling designs, those are often the main reasons explaining why their application is not ubiquitous. Promoting collaborations between organizations in charge and statisticians/quantitative ecologists from an early stage of the monitoring program could help overcoming these limitations. Also, allocating funds to developing algorithms and approaches that minimize computing time, or investing in more user-friendly interfaces, would help to slowly transition to models accounting for imperfect detection. Species-specific research, such as the comparison between HDS and TRIM models performed in Chapter II, can help identifying species or situations where detectability is constant and accounting for imperfect detection is not required to obtain unbiased population trend estimates.

2. The conservation value of fallow land and its management.

Many farmland bird species persist despite the steady habitat loss caused by agriculture intensification, but extinction debt (i.e., species or populations expected to eventually become extinct after habitat change; Kuussaari et al., 2009) will increase if habitat is not recovered (Kleijn et al., 2011). The decrease in fallow land area is a large-scale indicator of agriculture intensification (Peco et al., 2009), and is also linked with the decline of steppe bird populations in the Iberian Peninsula (Traba and Morales, 2019). I found lower occurrence of Calandra lark and Little bustard in TFM fallow fields surrounded by high fallow surfaces (Chapter III). This suggests a dilution effect supported by the ideal-free distribution hypothesis (scattering of individuals when availability of suitable habitat is higher; Fretwell and Lucas, 1969; McMahon et al., 2010), that was reinforced by the positive correlation between the abundance of Little bustard and TFM fallow surface in Chapter II.

The bird breeding season in pseudo-steppes is characterized by the development of tall and dense vegetation, which makes cereal crops – prevalent in pseudo-steppes – unsuitable for most steppe bird species and potentially causes a habitat bottleneck (Tarjuelo et al., 2020a). I identified and quantified this habitat bottleneck for the highly specialist Pin-tailed sandgrouse in Chapter IV, where Pin-tailed sandgrouse was found to only select fallow land and natural vegetation during the period characterized by tall cereal vegetation. Using GPS tracking data allowed us to transition from a static to a dynamic habitat selection approach for the first time for this species (Martin et al., 2009), which is crucial given the high spatio-temporal variation in resource availability in cereal steppes (Catry et al., 2012).

The strong selection of fallows corroborates their essential role for Pin-tailed sandgrouse (e.g., Tarjuelo et al., 2020a) and other bird and insect species (Toivonen et al., 2015; e.g., Van Buskirk and Willi, 2004), providing essential ecosystem services (Kuussaari et al., 2011). This thesis supports their use as a conservation tool within the future CAP post-2020 (Chapter II), and also goes one step further by exploring specific management actions that can improve their conservation value for the steppe bird guild.

Promoting fallows is not enough: fallow management is key for steppe bird conservation.

Steppe birds prefer fallows due to their optimal vegetation structures and resource availability, as compared to other land uses (e.g., cereal fields during bottleneck periods; Chapter IV). However, not all fallows are equally attractive, as they often present different vegetation structures that are not always suitable for steppe birds (Moreira, 1999; Traba et al., 2015). Through the pseudo-experiment evaluated in Chapter III, I found that different agricultural practices promoted the occurrence of different steppe bird species by creating a more suitable vegetation structure than that of unmanaged fallow fields. Chapter III confirmed the conclusions of Robleño et. al (2017) on the potential of agricultural practices to meet different steppe bird species requirements. It also highlights the ecological mechanisms behind the importance of TFM as a conservation measure. The efficiency of TFM to increase occurrence of two steppe bird species (Chapter III) was corroborated by the positive effect of the surface of TFM on the abundance of the steppe bird community as demonstrated in Chapter II.

In Chapter II, I evaluated the current CAP conservation measures in the study area that attempt to promote suitable fallows for biodiversity. I found that, in contrast to TFM, fallow fields under Greening and Agri-Environmental Schemes (AES) had either no or negative effects on the abundance of steppe and farmland birds (see also Kleijn and Sutherland, 2003; Pe'er et al., 2020). AES and Greening fallows are likely unsuitable because they do not limit the number of management interventions, and farmers likely perform excessive management as they fear that harmful weeds would reduce future productivity. Excessive management can be as detrimental as lack of management, because the absence of fallow vegetation reduces food resources (Giralt et al., 2018), and exposes birds to predators (Ponce et al., 2018). Moreover, TFM likely succeeded as a conservation measure because of the combination of suitable management prescriptions

(Chapter III), and the optimal location of fallow fields (e.g., flat terrain, far from irrigation; Mañosa et al., 2021). I found a strong avoidance of steep terrain and linear human infrastructures by Pin-tailed sandgrouse in Chapter IV, confirming the importance of optimal fallow location for conservation success.

The response to the TFM conservation measure differed in the case of Pin-tailed sandgrouse. While I found a positive effect of TFM surface on the species' abundance in spring (Chapter II), individuals selected TFM and fields under AES, Greening or conventional management equally during this period (although they did show a stronger selection towards TFM in winter; Chapter IV). Three non-mutually exclusive explanations might explain this pattern. First, Pin-tailed sandgrouse has a highly restricted niche as compared to other species, preferring fields with a high proportion of bare ground (Figure 1, Introduction Chapter; Benítez-López et al., 2017). Thus, the cleared fallow vegetation structure provided by AES and Greening might not be much different from that provided by TFM in the area studied in Chapter IV (i.e., where management is targeted toward this species). However, similar vegetation structure might not translate into similar habitat quality. Greening prescriptions allow agricultural management during the breeding season, which could reduce fitness (i.e., turning them into an ecological trap; Benítez-López et al., 2017; Lopez-Antia et al., 2018) and thus does not benefit abundance at a larger scale (Chapter II). Second, the study area slightly differed between Chapter II and Chapter IV. Chapter IV is exclusively situated in the core of the Pin-tailed sandgrouse population in Catalonia ("Secans de Mas de Melons – Alfés" SPA), known to have high-quality habitat for this species due to the combination of high TFM surface and low human disturbances. However, the study area in Chapter II expands to the wider distribution range of Pin-tailed sandgrouse in the Lleida plain, including the "Secans del Segrià – Utxesa" SPA and generally, less suitable habitat. The different gradients in habitat suitability between study areas might have led – or at least contributed – to the different results. Third, the different studies took place at different spatial and temporal scales. GPS data (Chapter IV) allowed us to gain access to continuous and fine scale locations of individuals, while observation data (Chapter II) only gave us a static and snapshot representation of where individuals were located.

3. Promoting a suitable landscape mosaic for bird communities in cereal steppes

The effectiveness of conservation measures is moderated by the landscape context (Concepción et al., 2008; Kleijn et al., 2011). Iberian cereal steppes, such as the study area of this thesis, are key landscapes to host vulnerable steppe bird species that prefer open, homogeneous and structurally simple habitats (Chapter II; Pickett and Siriwardena, 2011). Thus, steppe birds would benefit from a landscape mosaic with enhanced crop structural diversity such as the one promoted by TFM (involving crop management to obtain suitable and diverse vegetation structures, Chapter III; see also Josefsson et al., 2017), rather than general crop diversity, which involves an increased amount of tree orchards and irrigated crops that are generally detrimental for these species (Giralt et al., 2021). Moreover, fallow diversity at the landscape scale guarantees a minimum amount of habitat for steppe birds in the breeding season (Giralt et al., 2018), because predicting the timing and frequency of agricultural practices to obtain suitable vegetation in fallows can be complex and jeopardized by unpredictable weather conditions.

Fallow arrangement in the landscape – in relation to other surrounding crops and landscape features – is important to ensure diversity of food resources (Benton et al., 2003), or provide some farmland bird species with habitat complementarity (e.g., Morales et al., 2008). Some evidence for this were : 1) the strong landscape effects on the occurrence of Calandra lark (Chapter III); 2) the importance of landscape composition (crop diversity) and configuration (small field sizes) to increase the abundance of both sexes of Little bustard; and 3) the increase in abundance of common species with increased landscape configurational heterogeneity (Chapter II). Spatio-temporal variation in farmland landscape features triggers behavioural changes in some species (Johst et al., 2001), as shown by a shift from avoidance to selection of extensive almond and olive groves in summer by Pin-tailed sandgrouse (i.e., likely benefitting from their shade; Chapter IV). Thus, embedding a mosaic of different fallow types in a low-complexity cereal-steppe matrix (e.g., interspersed with natural vegetation and low occurrence of extensive tree crops) can benefit the whole bird community, while maintaining a suitable landscape for steppe bird species.

4. Human dimension, conservation implications and future perspectives

Land sparing in some farmland ecosystems with high population density – such as the study area of this thesis (Cantero-Martínez and Moncunill, 2012) – is challenging, and probably not the best option for steppe bird conservation. Thus, a way forward is finding efficient pathways to integrate agriculture and conservation (land sharing). Farmers in pseudo-steppe landscapes need to cope with low productivity systems, and promoting fallow management through subsidies as I proposed in Chapter II and III would align with their interests of maintaining their fields in a productive and “tidy” state (Hauck et al., 2016), while enhancing steppe bird habitat quality. The evidence on TFM success presented in Chapter III is a solid basis for advocating policy changes and has already provided the groundwork for the forum paper of Tarjuelo et al. (2020b), that illustrates the win-win strategy that fallow management constitutes. A first and essential step is to ensure the existence and uptake by farmers of conservation schemes that promote fallow land and its management (e.g., AES, TFM). Further, advising farmers about the benefits of extensive fallow management (agricultural practices 1-2 times per year before the breeding season) is essential to foment a stronger ownership of the conservation measure, their self-perception as conservationists (see also Pe’er et al., 2017), and ultimately promote compliance of conservation measures such as TFM.

The results of this thesis are timely as their publication coincides with the transition towards the CAP post-2020. Thus, the evaluation of conservation measures from the last CAP period (Chapter II), together with the current success of the TFM conservation measure (Chapter II, III), provide useful guidelines for consideration within the next CAP reform (included in Chapter II). Indeed, the results of Chapter III have already contributed to the preliminary design of the grassland management eco-scheme in the National Strategic Plan of Spain (Ministerio de Agricultura Pesca y Alimentación, 2021). The benefits of these guidelines likely go beyond the steppe bird guild, as TFM also proved positive for the rest of the community (Chapter II).

Another feature highlighted in this thesis is the role of evaluating the effects of conservation measures in parallel with their design, as occurs in TFM (i.e., adaptive management). Allocating funds on robust monitoring programs with standardized study designs that allow accounting for imperfect detection (Chapter I) would provide a solid basis for periodic evaluations. These could further improve cost-efficiency of conservation measures in the future by making payments conditional on achieving biodiversity outcomes (i.e., switching from management-based to result-based schemes; Herzon et al., 2018), which would in turn engage farmers with policy and conservation.

With this thesis, I provide insights into the applied ecology, management and conservation of steppe bird species in the Iberian Peninsula. Yet several questions remain unsolved. For instance, food availability measures based on plant indices were neither linked to agricultural practices nor bird occurrence in Chapter III, thus, further research based on direct food availability measurements (e.g., seed biomass) would provide useful insights on the role of these variables. The TFM measure constituting the core of this thesis was a success likely because of the combination of management (Chapter III) and optimal location of fallow fields, but research on the weight of their respective contribution could provide insights for future conservation planning. Likewise, studies on the effect of fallow distribution on predation rates would be beneficial, as predation is an important source of mortality for ground-nesting species (Benítez-López et al., 2015), and clustered fallows with suitable conditions could attract predators (see Ponce et al., 2018). I focused on occurrence, abundance, and habitat selection, but further research on the demographic effects of habitat bottlenecks and agricultural practices are necessary to understand the mechanisms behind population trends. Moreover, research on the spatial distribution of the overwintering populations of these species, and the conditions therein, could help focusing on conservation needs. Finally, I especially focused on pseudo-steppe habitats of southern Europe, but bird species from other European regions that also use steppe-like habitats can benefit from robust monitoring and the conservation measures proposed here. Thus, efforts to extrapolate and validate these findings in other regions could be highly useful for conservation, which is essential in the face of the dramatic decline of farmland bird populations.

CONCLUSIONS

CONCLUSIONS

1. Applying different agricultural practices in fallow fields once or twice per year before the breeding season in optimal locations (Targeted Fallow Management conservation measure in our study area) generates suitable vegetation structures for steppe birds with different niche requirements.
2. Targeted Fallow Management (TFM) increases the occurrence of steppe bird species at the field scale (Little bustard, Stone curlew), and its abundance at the landscape scale (Pin-tailed sandgrouse, Little bustard, European roller, Stone curlew), and benefits other species of the farmland bird community (e.g., Lesser short-toed lark), showing great potential to be included into the new eco-schemes of the upcoming CAP post-2020.
3. Conservation measures are more efficient when they are targeted: Agri-Environmental Schemes and Greening applied in fallows are more generic than TFM and showed neutral or even negative effects on the bird community; they could be further improved by incorporating some features of the successful TFM conservation measure.
4. Increasing the surface of fallow land in cereal steppes is crucial for the conservation of steppe bird populations as illustrated for the Pin-tailed sandgrouse: Fallow land, together with natural vegetation, constitutes the main habitat for most steppe birds during the spring habitat bottleneck caused by cereal growth.
5. The occurrence and abundance of farmland bird species are mediated by both field-scale and the landscape processes, so taking into account the landscape context is important when designing conservation measures in fallow fields.
6. Considering imperfect detection when modelling population trends within bird monitoring programs in open farmland landscapes is important, because fluctuations in detectability across years and observers can lead to higher uncertainty in population trend estimates, as compared to models that neglect detectability.

General
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GENERAL BIBLIOGRAPHY

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APPENDIX

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ORIGINAL PAPER

The role of detectability on bird population trend estimates in an open farmland landscape

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Abstract

Monitoring programs are key to determine bird population trends and to assess environmental policies, and therefore are central to conservation biology. The European approach commonly used to estimate bird population trends (TRends and Indices for Monitoring data, hereafter TRIM) has proved useful to fulfil this task, yet it fails to account for imperfect detection and assumes constant detectability across years. We tested the role of detectability for population trend estimation in an open Mediterranean farmland context, which is a dynamic landscape likely to undergo yearly changes in detectability, by using data of 30 bird species over a nine-year study period. We evaluated species-specific population trends under the TRIM approach and hierarchical distance sampling models (hereafter HDS) that estimate true abundance by accounting for imperfect detection. When comparing both methods, 13 species presented differences in population trend estimates between TRIM and HDS models. Moreover, detectability was not constant across the bird community: observer and year affected detection, and these effects varied among species. Our study highlights the importance of accounting for imperfect detection in bird monitoring programs to ensure reliable trend estimates, providing a first insight for an open farmland bird community. Aside from trend estimates, our HDS model may prove useful as a tool to obtain site-specific abundance estimates (for intance, within Special Protection Areas) and trend probabilities of bird populations.

Keywords Detectability · Population trend · Farmland birds · Hierarchical distance sampling · TRIM · Abundance

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Introduction

Wildlife populations are in decline globally and a proper understanding of population dynamics may be decisive for the ongoing battle against biodiversity loss (Pimm et al. 2014). Among others, farmland bird species have been severely affected by global change, with agricultural intensification being the major cause of their declines worldwide, and especially throughout Europe (Donald et al. 2001; Voříšek et al. 2010), where most of the exploitable surface is dominated by agriculture (Ormerod and Watkinson 2000). Conservation measures such as agri-environmental schemes (AES; Kleijn and Sutherland 2003) aim at buffering the negative impact of agriculture intensification on bird populations. Population monitoring is essential to detect population changes, evaluate the effectiveness of such measures and inform future conservation action (Donald et al. 2007).

Bird monitoring programs are numerous across Europe (Voříšek et al. 2010) and elsewhere (Bart 2005). Obtaining results on population trends at the continental scale is challenging because of variation in field methods among monitoring programs, which are usually organized at the national level. Despite the challenge posed by integrating this information, much progress has been made in the last two decades (e.g., for the U.S. and Canada: Bart 2005; for Europe: Voříšek et al. 2010). The Pan-European Common Bird Monitoring Scheme (PECBMS) was created as an initiative to pool population trend information from national bird breeding surveys across Europe and has provided robust evidence of farmland bird population declines (Voříšek et al. 2010).

PECBMS produces national and supranational indexes, as well as multi-species indicators (Klvaňová and Voříšek 2007), by using the TRIM software (TRends and Indices for Monitoring data; Pannekoek et al. 2005). TRIM provides a user-friendly interface (i.e., the TRIM program and the recently developed ‘rtrim’ package; Bogaart et al. 2018) and uses Generalized Estimating Equations (GEE) to fit log-linear models to bird count data, while dealing with overdispersion and serial correlation (Pannekoek et al. 2005). TRIM has proved useful for estimating species-specific population trends (e.g., Gómez-Catasús et al. 2018), linking population trends with their drivers (e.g., to quantify the effect of land abandonment on bird population declines; Herrando et al. 2014), and assesing conservation status for IUCN Red List assessments (Criterion A; Maes et al. 2015).

Although TRIM has been very useful for analysing time-series data of bird surveys, its population trend estimates are based on raw bird counts. Yet, birds cannot be counted with certainty because detection is always imperfect to some extent (Kéry 2008), and therefore accounting for probability of detection lower than 1 is necessary to ensure unbiased estimates of population size. Counts may provide reliable information about population trends if detection probability remains constant over time (Thompson 2002; Kéry and Schmid 2004). In spite of the broad consensus that the assumption of perfect or constant detectability is often violated in bird (and other wildlife) surveys (e.g., Diefenbach et al. 2003; Kéry et al. 2009), this assumption is rarely checked, and the effects of its violation are rarely evaluated (but see Camp et al. 2016).

Indeed, heterogeneity in detection over time may have a variety of sources, such as weather conditions (Bas et al. 2008), year-specific changes in bird behaviour (Newson et al. 2013), fluctuations in population sizes (Kéry and Schmid 2004) or differing observer skills (e.g., in monitoring programs that rely on volunteers; Diefenbach et al. 2003; Johnston et al. 2018). Likewise, spatial heterogeneity in detection may occur when surveys are placed in different habitat types (e.g., Kéry et al. 2009) or are subject to different treatments (Archaux et al. 2012). Detectability is also species-specific (Si et al. 2018), as it varies with factors such as body size (Anderson et al. 2015) or singing behaviour (Alldredge et al. 2007). Hence, homogeneous detectability of one species cannot always be extrapolated to the entire community.

Whereas techniques that fail to take detectability into account remain popular among bird studies and monitoring programs (Rosenstock et al. 2002; Klvaňová and Voříšek 2007), there are several modelling approaches that, when combined with appropriate survey designs, allow for estimation of population parameters taking into account imperfect detection. One of these approaches is distance sampling, which is a widely used technique to estimate abundance of wild animal populations (Buckland et al. 2004; see Rosenstock et al. 2002 for application in bird surveys). Distance sampling deals with the observation component of ecological field data (i.e., imperfect detection) by estimating the probability of detection (p) of an object as a function of its distance from the observer (i.e., the detection function; Buckland et al. 2001, 2004). Hierarchical Distance Sampling (hereafter HDS; Royle et al. 2004) consists of the analysis of distance sampling data across multiple survey sites. HDS explicitly conditions the observation process on the underlying ecological process and further allows for modelling spatial variation in the detection function and abundance as a function of site-specific covariates.

Accounting for imperfect detection has proved important to obtain unbiased estimates of population trends in bird species (see Bart 2005 for marsh birds; Camp et al. 2016 for forest birds). However, few studies have tested the role of detectability for common birds (but see Newson et al. 2013), and to our knowledge none have focussed on the role of detectability on population trends of birds inhabiting open farmland landscapes, or specifically tested the effect of temporal variability in detection. While farmlands are open environments, which likely have a higher detectability than more closed habitat types (e.g., woodlands), these landscapes are dynamic and likely to undergo yearly changes (e.g., due to changes in crop types; Merriam 1988) that could cause variable detectability across years.

Here, we compare estimates of bird population trends in a farmland landscape from a TRIM and a HDS model, in order to test the effect of time-varying and imperfect detectability on trend estimates. Specifically, we studied the population trends of 30 bird species from 2010 to 2018 in an open farmland landscape of north-eastern Spain, where the coexistence of species of conservation interest has led to the designation of Special Protection Areas (SPA), and the application of generic (i.e., Agri-Environment Schemes, AES) and specific (e.g., Sanz-Pérez et al. 2019) conservation measures. Aside from the local monitoring program of our study (FarmDINDIS), that produces its own dataset, in this area there is a national (SACRE 2018) and a regional (ICO 2018) bird monitoring program that estimate population trends using TRIM. Our HDS model, which estimates true abundance and its changes across space and time, builds on the Binomial N-mixture model of Royle (2004) and the open-population HDS model of Sollmann et al. (2015), while also including the serial correlation structure from Johnson and Hoeting (2003) and an overdispersion parameter.

We predict that even in an open farmland landscape, bird detectability may vary among observers, weather conditions, and years, and that as a consequence, estimates of population trends will differ between TRIM and HDS models. Because of their different ecology and life-history traits that can influence detection, we expect different responses among species. In addition, we demonstrate how the actual abundance estimates from the HDS model can be used to assess population status of species of conservation concern within SPA. Evaluating the reliability of trend estimates from standard European bird monitoring programs is particularly important in agricultural landscapes, as farmland bird population trends are known to be bound to agricultural change (Gates and Donald 2000) and farmland is the dominant land surface in most European countries (e.g., 65% in Denmark; Ormerod and Watkinson 2000). Reliable trend estimates and true abundance information within SPA is timely now that the upcoming Common Agricultural Policy (CAP) reform (2021–2028) will bring new management regimes and conservation action.

Material and methods

Study area and design

This study was conducted in the Lleida steppe plains (~ 3580 km^2, NE Spain; Fig. S1, SI 1). The area is an open and flat agricultural landscape with semiarid Mediterranean climate and low annual rainfall (between 300 and 450 mm; Calvet et al. 2004), located 200–400 meters (m) above the sea level. Traditional agriculture practices in this area consist of extensive cultivation of winter cereal crops, annual fallow fields, and woody crops (olive and almond), interspersed with small patches of sparse natural shrub land.

From 2010 to 2018, a total of 191 line transects (Table S1; Fig. S1, SI 1) were sampled annually in May. Due to logistic limitations, only 57% of the transects was surveyed every year (transects were surveyed on average: Mean ± SD = 7.12 ± 2.95 years). Transects were 500 m long and were randomly placed throughout the whole study area, located on non-asphalted tracks to avoid trespassing on private farmland, and with a minimum separation of 1000 m to ensure independence of the data (Buckland et al. 2001). Eighty percent of the transects were located within Special Protection Areas (SPA) devoted to bird conservation (i,e., characterized by extensive agriculture; Fig. S1, SI 1; Brotons et al. 2004).

Bird surveys

Bird surveys were performed for the FarmDINDIS bird monitoring program, which aims at collecting information about local farmland bird populations and habitat characteristics in the study area. Bird surveys were conducted by 13 different professional observers (4 different observers on average per year; Table S1, SI 1) with experience in the identification of bird species in farmland landscapes. Observers conducted the surveys in the morning from 6 to 10 a.m. Surveys were not performed under the rain, when wind speed was above 20 km/h, or temperature was above 30 ºC. Each survey was conducted by a single observer who walked at a slow pace (~ 1.5 km h^{-1} with occasional pauses) along the line transect, and collected data of all bird species detected following a distance sampling protocol (Buckland et al. 2001). Birds were recorded on both sides of the transect when first observed, and the perpendicular distance from the transect line to a bird was visually estimated. Because distance sampling assumes independence of individual observations, but several of our study species often occur in groups, we considered groups of birds as the unit of observation, and recorded group size along with distance to the centre of the group. Observers recorded individuals detected visually or aurally, reported the mode of detection and marked the detection location on a map of the transect surroundings. Distance sampling assumes that distances are measured without error, which is unrealistic in a field setting. Grouping observations into distance bins can overcome distance estimation error; thus we assigned observations into five distance classes (0–25 m; 25–50 m; 50–100 m; 100–200 m; 200–500 m) with the guidance of a field map containing information on the borders of fields and type of crops surrounding the transect. The maximum truncation distance at which observations where recorded (i.e., the strip width) was 500 m. Aside from bird data, observers collected weather information at each transect that could affect the detection process, such as temperature, wind speed, clouds cover, and time of the day.

Trend assessment

We studied population trends of 30 bird species from 2010 to 2018 (Fig. 1). These species had different characteristics, ranging from small passerines (e.g., Great tit *Parus major*) to large non-passerines (e.g. Stone curlew *Burhinus oedicnemus*). We included in the analysis all species potentially breeding or foraging in the study area, with a minimum of 100 observations distributed across years. We evaluated population trends by using two different statistical approaches: a TRIM model, based on yearly population indexes derived from bird counts, and a HDS model based on abundance estimates corrected for imperfect and varying detection. For each species, we compared the population trend estimates provided by both models by assessing the direction of the trend coefficients (see below) and its significance. We considered trends significant when 95% Confidence Intervals (CI; TRIM) or 95% Bayesian Credible Intervals (BCI; HDS) did not contain zero. While we acknowledge that frequentist confidence intervals and Bayesian credible intervals do not have the exact same interpretation, we found this to be the most consistent way to assess statistical significance across the two approaches. To exploit the attributes of Bayesian trend estimation we also calculated the posterior probability of a negative trend for HDS results (Wade 2000). All analyses were performed in R version 3.5.1 (R Core Team 2018).

TRIM model

We fitted the log-linear time effects model (TRIM Model 3; Pannekoek et al. 2005), which estimates separate parameters (α, β) for each site j and year t and can be written as:

$$\ln\left(\mu_{jt}\right) = \alpha_j + \beta d_t + \gamma_t \tag{1}$$

where μ is the expected count (not corrected for detectability) at site j at time t, α is a fixed site (transect) effect, and d_t represents the centred year of study. In this version of the model, the temporal trend is decomposed into a linear trend parameter (β), that we used as an estimate of average population change, and a fixed effect (γ) that describes the deviations from the linear trend for each year. The parameter γ was set to zero in year 1 to make the model identifiable. This model investigates both whether the overall linear trend is significant and for which time-points significant deviations from the linear trend occur.

The estimation approach used by this TRIM model is generalized estimating equations (GEE) (Pannekoek et al. 2005). This method accounts for drawbacks typically found in trend analyses of counts such as overdispersion and serial correlation (Pannekoek et al. 2005).

We assessed the significance of the population trend for a given species by determining whether the 95% Confidence Interval (CI) associated with the overall trend parameter β overlapped zero (for comparison purposes with HDS). We extracted the total yearly expected counts and imputed counts (which equal the observed counts for surveyed site-year combinations and the expected count for un-surveyed site-year combinations, i.e.,

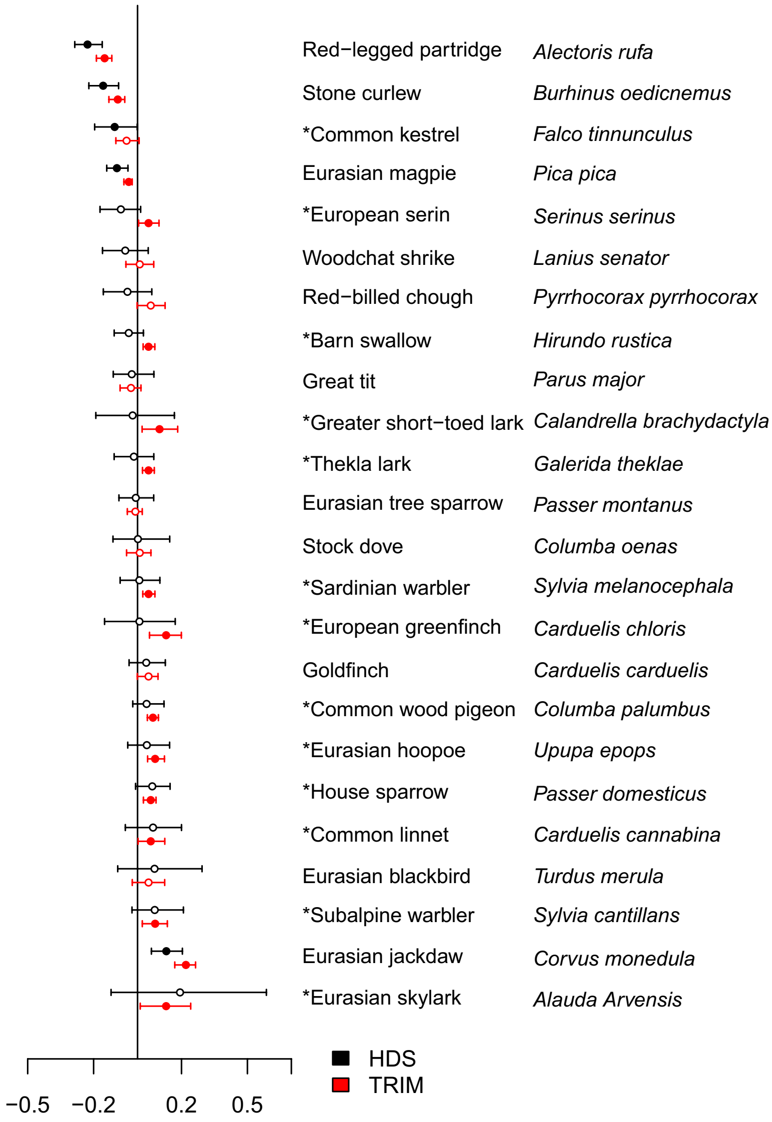


Fig. 1 Trend coefficient obtained by using HDS models (black) and TRIM models (red) on data of 24 bird species collected from 2010–2018 in Lleida (Spain). The trend coefficient of 6 species were discarded due to lack of model fit (Methods section). Filled circles show significant trends (95% Bayesian Credible Interval (HDS) or Confidence Interval (TRIM) not overlapping zero). Species for whom there are differences in the significance results obtained with both methods are indicated by an asterisk "*"

missing counts; Pannekoek et al. 2005) to plot expected and realized population trends (Fig. 2; Fig S3, SI 1). All TRIM analyses were performed with the 'rtrim' R package version 2.0.6 (Bogaart et al. 2018).

HDS model

We fitted a HDS model (Fig. S2, SI 1; Hobbs and Hooten 2015), where the process component describes local abundance N at a given transect j and year t as a random variable following a Poisson distribution:

$$N_{jt} \sim Poisson\left(\lambda_{jt}\right) \tag{2}$$

Here, λ_{jt} is the expected abundance of birds/bird groups and can be modelled as a function of an intercept and site-specific covariates. In order to obtain estimates of population change that were comparable with estimates from the TRIM approach, we built the following abundance model:

$$\log\left(\lambda_{jt}\right) = \alpha.site_j + \beta.year \times Year_t + \gamma.lam.year_t + w_{jt}\ \alpha.site_j \sim Normal(\mu_{site}, \sigma_{site})\ \gamma.lam.year_t \sim Normal(0, \sigma_{lam.year}) \tag{3}$$

$$w_{j,1} = \varepsilon_{j,1} / \sqrt{1-\rho^2} \text{ for t=1, and } w_{jt} = \rho * w_{j,t-1} + \varepsilon_{jt} \text{ for t>=2}$$

$$\epsilon_{jt} \sim Normal(0, \sigma_{\epsilon})$$

where $\alpha.site_j$ is a random site (transect) intercept, with hyperparameters μ_{site} and σ_{site}. Time is decomposed into a linear trend parameter ($\beta.year$), and a random year effect ($\gamma.lam.year_t$) that describes yearly deviations from the linear trend (i.e., by following a zero-mean normal distribution with variance $\sigma_{lam.year}$). The $Year_t$ covariate ranged from 0–8 (from the first to the 9th year of study). As for the TRIM model (see above), the parameter $\gamma.lam.year$ is set to zero for year 1 ($Year_1 = 0$) to make the model identifiable. We accounted for serial correlation by using an autoregressive model of order 1 [AR(1) following Johnson and Hoeting (2003)]. This temporal structure was included in the parameter w, which accounts for both overdispersion and serial autocorrelation by partitioning the extra-residual variance into a serial correlation $\left(\rho * w_{j,t-1}\right)$ and overdispersion (ε_{jt}) component. We estimated yearly expected and realized abundances (Fig. 2; Fig S3, SI 1) as derived parameters by summing λ or N, respectively, over all sites for a given year, and we estimated abundances within transects in SPA by summing λ over the sites belonging to each of the SPA for a given year (Table S5). Because our unit of observation was bird groups, we converted estimates of group abundance to actual abundance by multiplying λ_{jt} with average group size.

The observation model links the process (biological) model for N_{jt} (2,3) to the field data by introducing an observation error induced by imperfect detection. Specifically, the number of individuals (or groups) of a given species observed at transect j and year t, Y_{jt}, is described as a Binomial random variable:

$$Y_{jt} \sim Binomial(N_{jt}, p_{jt}) \tag{4}$$

where p is the probability of detection, which is estimated using the distance sampling framework. In distance sampling, p is assumed to be 1 at the transect line, and decreases from the observer as a function of distance x following a detection function (Buckland et al. 2001). We chose a half normal detection function as observation model:

$$g(x, \sigma) = exp\left(\frac{-x^2}{2\sigma^2}\right)$$

where σ is the scale detection parameter and can be modelled on the log scale as a function of an intercept and site-specific covariates. For some species, the half-normal detection function provided poor model fit and in these cases we used a hazard rate detection function instead:

$$g(\mathrm{x}, \sigma) = 1 - \exp\left(-\left(\frac{\mathrm{x}}{\sigma}\right)^{-\mathrm{b}}\right)$$

where b is the shape parameter. Preliminary analyses revealed that the most relevant detection covariates were observer identity and temperature (°C). Therefore, we fit the following model for σ:

Fig. 2 Population trend of the species that showed different significant results for the trend coefficient ▶ when using HDS models (black) and TRIM models (red), based on data from 2010–2018 in Lleida, Spain. The population trend of each species is represented by a continuous line. The trend coefficients (on the log scale) are showed in the legend; asterisks beside the coefficients mark significant trends (i.e, 95% BCI (HDS) or CI (TRIM) not overlapping zero). The yearly abundance estimates from the HDS model are given by black dots, and the yearly expected counts from the TRIM model are given by red dots. Years from both models that present significant deviations from the linear trend are indicated by an asterisk

$$\begin{aligned}\log\sigma_{jt} = \alpha.obs + \beta.temp \times Temp_{jt} + \gamma.sig.year_t \ \alpha.obs \\ \sim Normal\left(\mu_{obs}, \sigma_{obs}\right) \gamma.sig.year_t \sim Normal(0, \sigma_{sig.year})\end{aligned} \tag{5}$$

We included observer as a random intercept ($\alpha.obs$) with hyperparameters μ_{obs} and σ_{obs}. $\beta.temp$ is the coefficient for the temperature variable (*Temp*). In order to detect differences in detection probability among years (e.g., due to fluctuations in weather conditions or bird behaviour), we included the random effect $\gamma.sig.year_t$, with zero-mean and variance $\sigma_{sig.year}$.

Under the half-normal detection function and with binned distance observations, detection probability for each distance bin k can be calculated as the integral of *g(x)* over the break points of k:

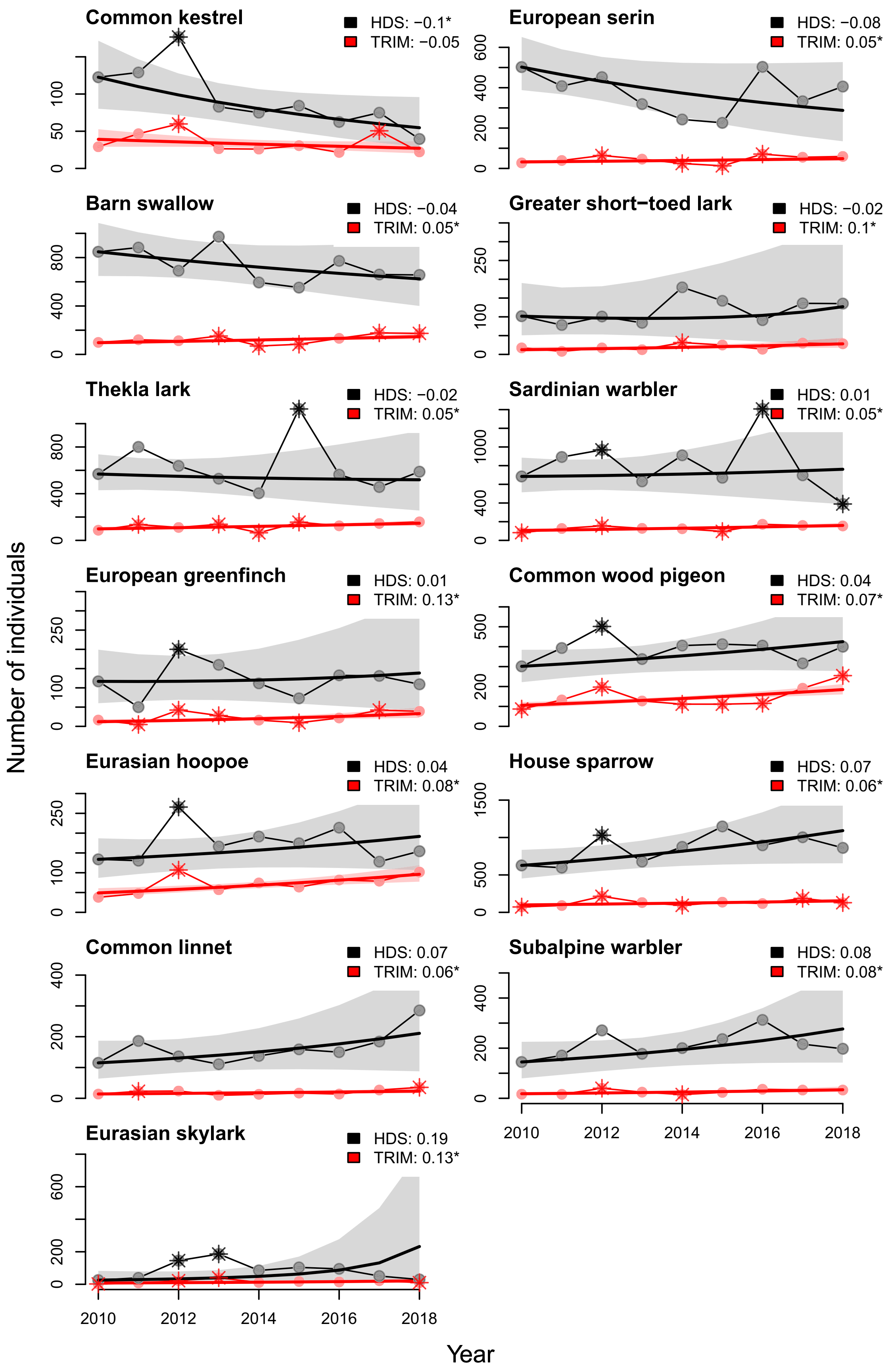
$$p_k = \frac{\int_{b_k}^{b_{k+1}} g(x)dx}{v_k}$$

where $\boldsymbol{b}$ are the $K+1$ breakpoints of the K distance categories and v_k is the width of the k-th distance category (see also Sollmann et al. 2016). Under the hazard rate detection function, detection probability p for each distance bin k was approximated as p at the mid-point distance of the bin. In our study, v_k was 25, 25, 50, 100, and 300 m from the first to the fifth distance category, respectively. Because individuals are assumed to be uniformly distributed around the transects, the individual probability of occurrence in a distance bin Ψ_k is

$$\Psi_k = \frac{v_k}{strip\,width}$$

where the strip width is 500 m. Therefore, the cell probability of detection π_k is $p_k \times \Psi_k$, and the overall probability of detection (p_{jt} from the Binomial distribution, Eq. 4) is the sum over all π_k (see also Sollmann et al. 2015; Kéry and Royle 2016).

We conducted parameter estimation using a Bayesian MCMC approach in JAGS version 4.3.0 (Plummer 2003), accessed through the 'jagsUI' R package version 1.5.0 (Kellner 2018). JAGS model codes are available in SI 2 and SI 4. We used non-informative or weakly informative priors on all parameters. For the random effects, we chose uniform (− 10, 10) for μ_{site} and μ_{obs}, and uniform (0, 10) for $\sigma_{site}, \sigma_{obs}, \sigma_{lam.year}$ and $\sigma_{sig.year}$. We chose normal (0, 0.001) for $\beta.year$ and $\beta.temp$, where 0.001 is the precision, τ. Finally, we chose uniform (0, 3) and uniform (− 1, 1) for the overdispersion σ_ϵ and serial correlation ρ parameters, respectively. We ran three parallel Markov chains with a number of iterations ranging from 170,000 to 2,000,000, burn-in ranging from 5000 to 300,000, and thinning chains from 5 to 50 depending on the species (see SI 3 for further details on model convergence). With this, we ensured convergence of structural parameters of all the single-species models according to the Gelman-Rubin statistic (i.e., values < 1.1; Gelman et al. 2013).


Common kestrel
HDS: −0.1*
TRIM: −0.05
European serin
HDS: −0.08
TRIM: 0.05*
Barn swallow
HDS: −0.04
TRIM: 0.05*
Greater short−toed lark
HDS: −0.02
TRIM: 0.1*
Thekla lark
HDS: −0.02
TRIM: 0.05*
Sardinian warbler
HDS: 0.01
TRIM: 0.05*
European greenfinch
HDS: 0.01
TRIM: 0.13*
Common wood pigeon
HDS: 0.04
TRIM: 0.07*
Eurasian hoopoe
HDS: 0.04
TRIM: 0.08*
House sparrow
HDS: 0.07
TRIM: 0.06*
Common linnet
HDS: 0.07
TRIM: 0.06*
Subalpine warbler
HDS: 0.08
TRIM: 0.08*
Eurasian skylark
HDS: 0.19
TRIM: 0.13*
Number of individuals
Year
2010
2012
2014
2016
2018

We tested whether the abundance and detection components of the model fitted the data by using Bayesian *P*-values (Gelman et al. 1996) based on Freeman–Tukey residuals, and determined model lack of fit when Bayesian *P*-values were <0.1 or >0.9 (SI 3; see also Sollmann et al. 2016). The observation component with a half-normal detection function only fit the data for 7 species (Table S6, SI. 3). For 17 species, we improved model fit by using a hazard rate detection function for modelling detection (Table S6, SI 3; JAGS model code in SI 4). Changing the detection function did not result in a better fit for 6 species (Table S6, SI 3), which were therefore excluded from the analysis.

We reported parameter estimates as the posterior means and associated standard deviations. We also reported the 95% Bayesian Credible Interval (BCI), and considered parameters as significant when the 95% BCI did not overlap zero. Finally, for the trend parameter beta, we calculated the posterior probability of a negative population trend as the proportion of all posterior samples with values below zero (Fig. 5). Because posterior distributions for the standard deviation from the observer and year random effects (σ_{obs}, $\sigma_{sig.year}$) (uniform(0,10)), were skewed (Figs. 3, 4), we also reported the posterior mode (Figs. 3, 4) and used both (the mode and the mean) to draw conclusions about these variables. We considered that a given species had a higher variability among observers and/or years (i.e., as compared with the rest of the studied species), when both the SD estimates of the posterior mean and mode were above the 3rd quantile of the estimates distribution across all species (Table S3, SI 1).

Results

We evaluated the trends of 30 farmland bird species over 10 years, using data from a total of 1360 line transect surveys (Table S1, SI 1). Species occurrence on transects was variable, with Corn bunting *Emberiza calandra* and Crested lark *Galerida cristata* detected in the highest proportion of transects (mean of the proportions of transects where they were present per year = 82% and 79%, respectively; Table S2, SI 1), and Greater short-toed lark *Calandrella brachydactyla* and Eurasian skylark *Alauda Arvensis* the lowest (5% and 6%, respectively; Table S2).

Forty-three percent of all the analysed species (Common kestel *Falco tinnunculus*, European serin *Serinus serinus*, Barn swallow *Hirundo rustica*, Greater short-toed lark *Calandrella brachydactyla*, Thekla lark *Galerida theklae*, Sardinian warbler *Sylvia melanocephala*, European greenfinch *Carduelis chloris*, Common wood pigeon *Columba palumbus*, Eurasian hoopoe *Upupa epops*, House sparrow *Passer domesticus*, Common linnet *Carduelis cannabina*, Subalpine warbler *Sylvia cantillans* and Eurasian skylark *Alauda Arvensis*) showed different trend results when using TRIM and HDS models (Figs. 1, 2). In the case of Common kestrel, the HDS model returned significant negative trend estimates while the CI from the TRIM model overlapped zero, while the remaining 12 species presented the opposite pattern (the TRIM model returned significant trend estimates and the BCI from the HDS model overlapped zero; Figs. 1, 2). Three species showed a significant negative trend that was consistent across both approaches, one species showed a significant positive trend, and seven species showed non-significant trends (Fig. 1). Trend coefficients had the same signs across approaches for all species except European serin, Barn swallow, Greater short-toed lark, and Thekla lark (Figs. 1, 2), for which the trend was significantly positive when using TRIM, and marginally negative (i.e., with BCI overlapping zero) when using HDS. For the Woodchat

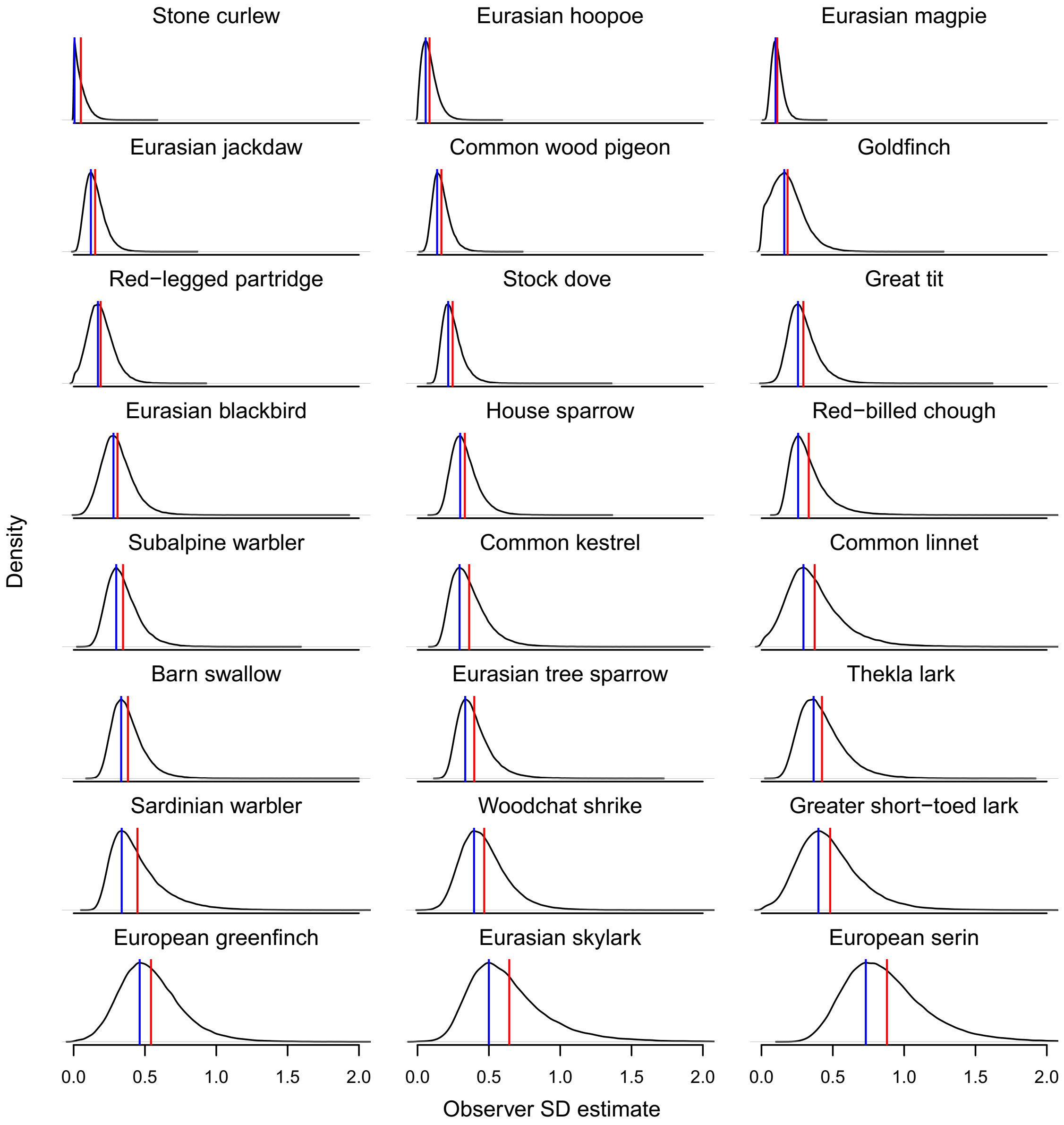


Fig. 3 Posterior distribution for the Standard Deviation (SD) of the observer random effects (σ_{obs}) from a Hierarchical Distance Sampling model fit to bird observation data from Lleida, Spain. The mean and mode of the SD estimate are indicated in red and blue, respectively. Species-specific plots are ordered according to increasing values of the mean observer SD estimate

shrike *Lanius senator* and the Red-billed chough *Pyrrhocorax pyrrhocorax*, the trend coefficients had different signs with no significant estimates with neither TRIM or HDS. The TRIM model resulted in a higher number of significant annual deviations from the linear trend than the HDS model (Fig. 2).

Temperature did not affect the detection process of any of the studied species, and was therefore discarded from the observation model when it impaired convergence (Table S4, SI 1). The species that presented highest variability in detection among observers, based on estimates of the standard deviation of the observer random effect, were European serin, Eurasian skylark, European greenfinch, Greater short-toed lark, Woodchat shrike, Thekla lark and Sardinian warbler (Fig. 3). Likewise, the species that presented highest variability in detection across years were Eurasian skylark, Sardinian

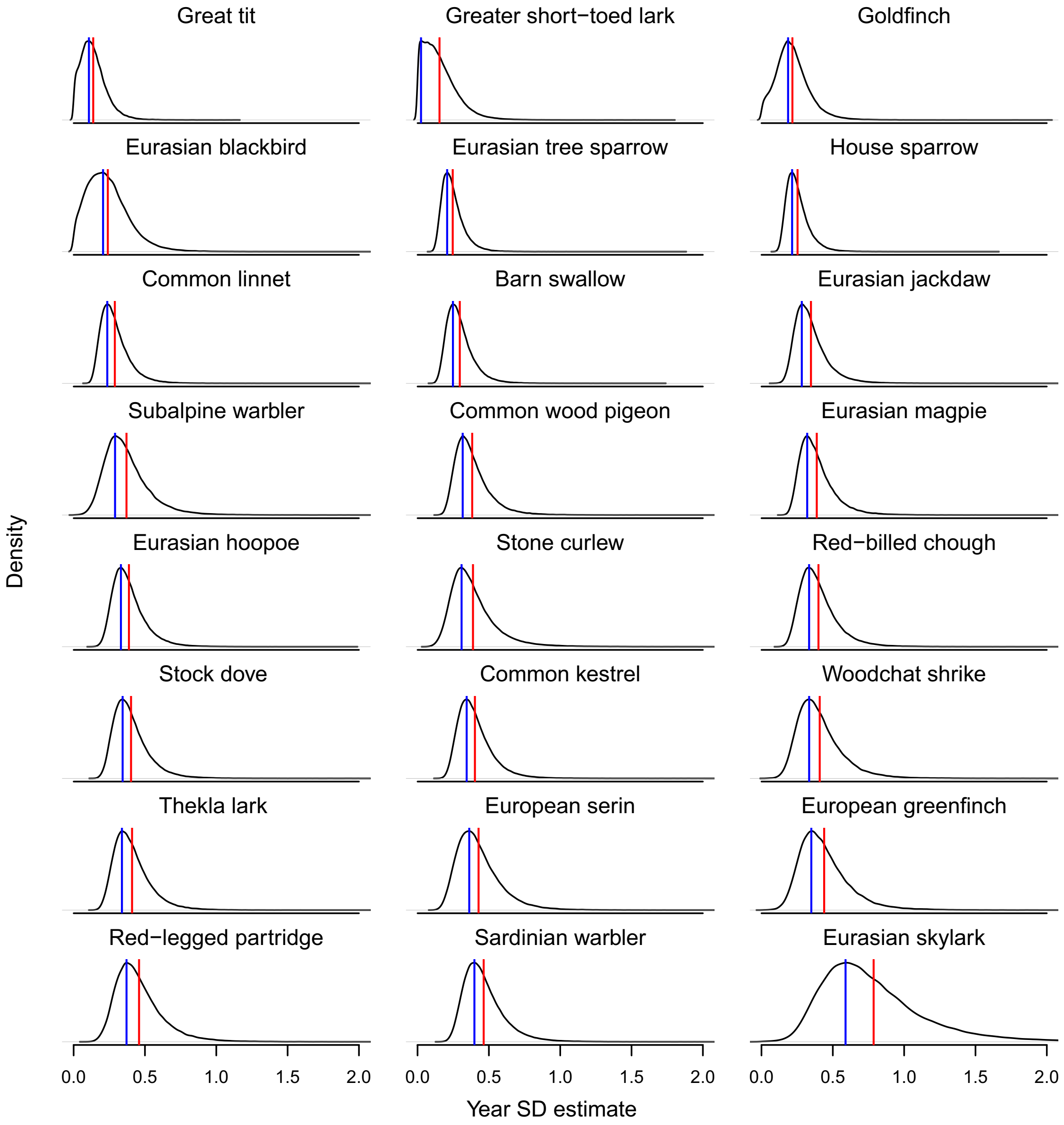


Fig. 4 Posterior distribution for the Standard Deviation (SD) of the year random effects ($\sigma_{sig.year}$) from a Hierarchical Distance Sampling model fit to bird observation data from Lleida, Spain. The mean and mode of the SD estimate are indicated in red and blue, respectively. Species-specific plots are ordered according to increasing values of the mean year SD estimate

warbler, Red-legged partridge *Alectoris rufa*, European greenfinch, European serin and Thekla lark (Fig. 4).

Discussion

Accounting for imperfect detection in monitoring programs has proved important to make inference about population trends of several taxa, including mammals (e.g., Moore and Barlow 2011), reptiles (e.g., Kéry et al. 2009) and birds (e.g., Bart 2005 for marsh birds; Berthiaume et al. 2009 for raptor birds; Camp et al. 2016 for forest birds). Our study occurred in a dynamic farmland landscape, where changes are common in terms of both human-related factors, such as crop rotations (Mas and Verdú 2003), and abiotic factors such as precipitation and temperature (Lobell and Field 2007). These changes have the potential to generate different spatial patterns in the vegetation structure on a yearly basis, which could influence the detection process on a specific transect (e.g., for ground-nesting species such as the Stone curlew, whose detection probability may depend on vegetation height; de Juana 2005). Our results showed that even in an open farmland landscape, where detectability could be expected to be high and relatively constant, detection varied considerably across species, and was affected by observer and year of study. Moreover, almost half of the studied species showed different population trend estimates when using HDS (i.e., accounting for imperfect detection) and TRIM models. Five of the species showing different population trend estimates (Eurasian skylark, Sardinian warbler, European greenfinch, European serin, and Thekla lark) were the ones presenting higher among-year variability in detection, meaning that temporal heterogeneity in detection could have biased some of the population trend estimates in our system. Yearly fluctuations in detection could be, for instance, associated with the singing behaviour of these and other species, which in turn may be influenced by factors such as weather conditions (Crick and Sparks 1999) or population size or density (Laiolo and Tella 2008), therefore adding extra variation to the detection process.

Another potential source of heterogeneity in detection commonly recognized in bird surveys is the variation in the skill level of observers (Ralph and Scott 1981; Diefenbach et al. 2003; Johnston et al. 2018). Observer effects are likely stronger in large-scale monitoring programs based on citizen science (Bart 2005; Voříšek et al. 2010) and relying on multiple volunteer observers with variable backgrounds. Our study was performed by hired professional observers, yet we found different degrees of observer variability among species. Moreover, our results point towards species mostly detected aurally (e.g., the Eurasian skylark, European greenfinch and Greater short-toed lark) showing higher detection variance among observers. Identifying bird species by their singing behaviour is more challenging than visually, so for most species differences in observer experience may be more pronounced. In contrast, temperature did not affect the detection process. Our field protocol avoided conducting census at very high temperatures, so temperatures where probably not extreme enough to affect bird activity in our study context. Care should be taken to extrapolate this conclusion to other areas or future years, as high temperatures have proved to affect bird singing and displaying activity (e.g., Gudka et al. 2019), and extreme temperatures due to climate change will affect the farmland dynamics (e.g., the yield of annual crops; Wheeler et al. 2000) and birds' ecology (Crick and Sparks 1999; e.g., Gudka et al. 2019 for displaying time).

In general, the TRIM model estimated more significant trends and more significant annual deviations from the trend than the HDS model. This can be explained by the different levels of uncertainty associated with trend estimates from the two approaches, with uncertainty from the HDS model being higher for all the studied species. These results are in accordance with other studies evaluating the effect of detectability on animal population trends such as the one of Camp et al. (2016) and Kéry et al. (2009); they are also expected, as incorporating a detection component into the model increases model complexity (i.e., the number of parameters), which translates to increased parameter uncertainty. Indeed, a higher uncertainty in HDS models seems to explain the different trend estimates between TRIM and HDS for 12 of the studied species. While these higher levels of uncertainty may seem undesirable from a management perspective, they likely provide a more honest representation of our state of knowledge of the studied species. Properly accounting for uncertainty when estimating trends is important for conservation, since underestimating uncertainty could lead to suboptimal decisions in a decision-making framework (for example, by assigning an erroneous IUCN category to a species; Connors et al. 2014; Maes et al. 2015). Indeed, incorrectly classifying a population as decreasing will divert conservation funds from populations with higher extinction risk, while considering a population as stable when is declining could lead to the eventual loss of such population because remedial action is not taken (D'Eon-Eggertson et al. 2015).

The Bayesian HDS models also provided posterior probabilities for negative population trends (Fig. 5), which represent a continuous measure of the importance of the trend (i.e., rather than significance thresholds associated with frequentist methods; Wade 2000). For instance, the Woodchat shrike and the Great tit had non-significant trends with either HDS or TRIM models (Fig. 1), but showed a probability of decline of 86% and 73% respectively (Fig. 5), which may prove useful to inform management decisions.

For 11 species, accounting for imperfect detection did not change trend estimates. Yearly fluctuations in detection may not be pronounced enough to be reflected on these population trends within the time frame of our study. Alternatively, the high visibility provided by open farmlands may have led to near-perfect detection of these species, thus making accounting for missed individuals less influential. Indeed, a preliminary analysis showed that a high truncation distance was required for the detection curve of some species to decrease, suggesting they remain highly visible even at several hundred meters' distance, so we recommend setting wide transect strips (e.g., up to 500 m, like in our study) for distance sampling study designs in open farmlands.

In addition to evaluating the effect of ignoring imperfect detection when estimating trends, the HDS approach presented here provides a tool to estimate and monitor true abundance (i.e., black dots in Fig. 2, S3; SI 1). The framework has been used to estimate abundance for a multitude of taxa (e.g., Moore and Barlow 2011 for Fin whales *Balaenoptera physalus*; Sollmann et al. 2015 for Scrub jays *Aphelocoma insularis*), and could be useful to address ecological questions regarding bird ecology in farmland landscapes. In our system, obtaining site-specific estimates of abundance could help evaluating the effectiveness of ongoing conservation actions (such as agri-environmental schemes; Cantero-Martínez and Moncunill 2012; Sanz-Pérez et al. 2019), and inform on how these management actions are contributing to increase the habitat suitability and the carrying capacity of Special Protection Areas (SPA). In fact, providing population abundance estimates in each SPA is one of the requirements of the Standard Data Forms (SDFs) for the European Commission (European Community Bird Directive 79/409/ECC and 147/2009/ECC; European Comission 2000). SDFs provide the list of all bird species relevant for a site to be officially designated as SPA. Having an updated SDF of the target species is essential to design site-specific conservation actions, as well as verifying the relevance of the target population in a wider context (Battisti and Fanelli 2015). We have provided an example of the potential of our HDS model in this sense by providing the site-specific abundance estimates within transects related to SPA areas in our study zone (Table S5, SI 1) for four of the studied species.

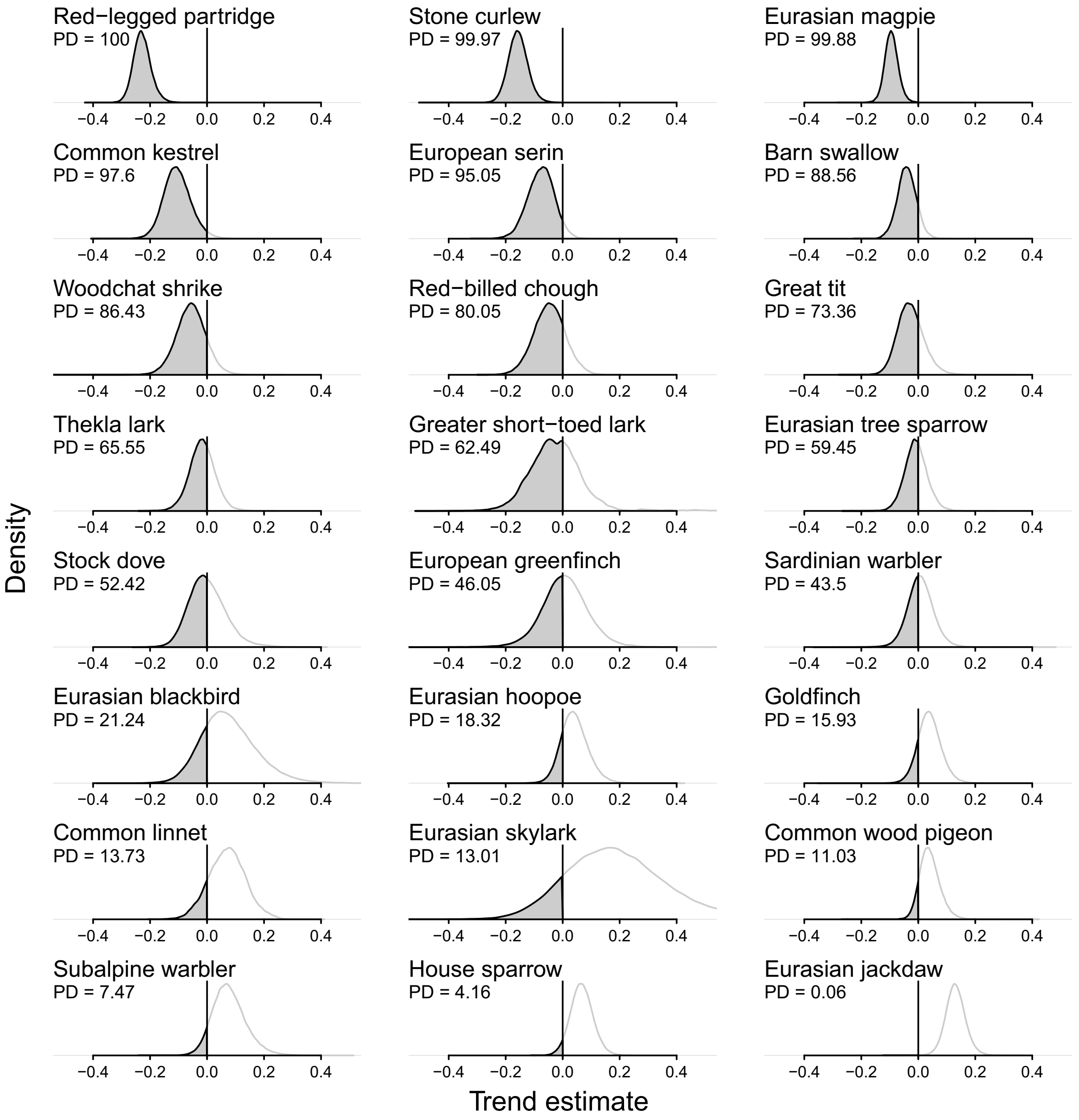


Fig. 5 Posterior distribution for the beta coefficient of the trend estimate from a Hierarchical Distance Sampling model fit to bird observation data from Lleida, Spain. The area under the curve of the posteriors below zero (i.e., probability of negative trend) is shaded in grey. The Probability of Decline (PD) is presented for each species. Species-specific plots are ordered according to increasing values of the trend estimate

Conclusion

There is a global consensus that scientists play a key role not only in developing new methodologies, but also in questioning and evaluating current ones (Johnson 2008). Learning more about the detection process will garner insight in the role of detectability for abundance and trend estimation in different contexts, and advance towards the improvement of monitoring programs, which are a cornerstone of conservation biology. To our knowledge, this is the first study to test the role of imperfect and variable detection probability in population trend estimation in an open farmland bird community, and to evaluate the reliability of TRIM, the principal European approach for estimating bird population trends. For most of the studied species TRIM appears to be valid to determine trend direction and magnitude. However, if traditional significance levels are used to determine whether a population is in risk, TRIM may produce overly confident results because it ignores the added uncertainty due to imperfect detection, which is the case for 43% of our studied species. Therefore, we recommend that, even in open landscapes where visibility is high, monitoring programs should adjust their sampling designs to include detectability in their analysis.

Using methods that take imperfect detection into account in bird monitoring programs would ensure reliable trend estimates, which would pay off its more complex implementation in citizen-based surveys. In bird monitoring programs there is always a trade-off between making the surveys feasible and appealing to volunteers and using methodologies that provide accurate estimates. Collecting data that allows accounting for imperfect detection as well as its analysis is not always straightforward, and coordinators of monitoring programs are sometimes sceptical about accounting for detectability because they consider it irrelevant or find the analyses too complex. TRIM has an easy application, yet this is conditional on detectability being constant across years. Therefore, collecting data in a way that allows accounting for imperfect and variable detection (e.g., through distance sampling, which does not require temporal replicates; Buckland et al. 2001) and using methods that integrate detectability, is highly recommended.

Accounting for imperfect detection may be of even greater importance in habitats in which detection is lower, such as forests and shrublands, which also encompass big part of European monitoring efforts for common bird species (Klvaňová and Voříšek 2007), or mountain areas, which are important for regional monitoring programs (ICO 2018).

Ensuring unbiased population trends estimates is especially important for threatened species. Given the increase in agriculture intensification during the last decades, the farmland bird community is suffering from an abrupt decline (BirdLife International 2018). Thus, a proper assessment of their population trends and true abundance will be essential to correctly assign farmland bird species into IUCN categories and to design species-specific conservation actions.

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Author's contributions R.S, D.G., F.S-P, and A.S-P conceived and designed the study, with G. B's suggestions. A.S-P and R.S implemented the analysis. A.S-P wrote the manuscript with the help of R.S, D.G., F.S-P and G.B. All authors contributed to subsequent drafts and gave final approval for publication. D.G coordinated fieldwork and G.B secured funding.

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Compliance with ethical standards

Conflict of interest The authors have no conflict of interest to declare.

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RESEARCH ARTICLE

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Fallow management increases habitat suitability for endangered steppe bird species through changes in vegetation structure

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Abstract

1. In the face of the dramatic worldwide decline of farmland bird populations, the preservation of fallow fields is a conservation measure encouraged through subsidies (e.g. agri-environmental schemes, AES). Beyond the general benefits of increasing fallow availability for endangered steppe bird populations, there is a lack of knowledge on how fallow management can contribute to meeting species-specific habitat requirements.
2. We used occurrence data from three steppe bird species protected at the EU level (Stone Curlew *Burhinus oedicnemus*, Little Bustard *Tetrax tetrax* and Calandra Lark *Melanocorypha calandra*), framed in a quasi-experimental approach covering an unprecedented spatio-temporal scale that included 612 fallow fields over a 3-year study period in an agricultural Mediterranean landscape (Spain). We used path analysis to explore the mechanisms by which common agricultural practices affected species-specific occurrence. We examined partial effects of agricultural practices on vegetation structure and food availability, and the partial effect of these variables on bird occurrence compared to control fields (no agricultural practices applied).
3. Agricultural practices had a significant effect on the presence of the three studied species. Through changes in the vegetation structure, Shredding + Herbicide and Tillage increased the occurrence of the Stone Curlew and Shredding increased the occurrence of the Little Bustard. The occurrence of Calandra Lark was mostly affected by landscape variables.
4. *Synthesis and applications*. Our study highlights that, in addition to the acknowledged positive role of fallow availability, applying a limited number of specific agricultural practices before the breeding season can further increase bird occurrence by changing the vegetation structure. Using path analysis, we explored the mechanisms driving the occurrence of three steppe bird species under different agricultural practices. Such information is key to providing specific recommendations for future conservation management of endangered species within agri-environmental schemes.

KEYWORDS
agricultural practices, agri-environmental schemes, bird occurrence, conservation, fallow management, path analysis, steppe birds, vegetation structure

1 | INTRODUCTION

Agricultural lands have become a major conservation focus due to the large proportion of global biodiversity which rely on them for persistence (Flynn et al., 2008). The severe decline in biodiversity and farmland bird populations across Europe (Donald, Sanderson, Burfield, & van Bommel, 2006) and the Iberian Peninsula (Santos & Suárez,) has been attributed to the intensification of agriculture since the 1970s, which has compromised the quality of habitats, food supplies, and nesting sites (Wretenberg, Pärt, & Berg, 2010).

In agricultural landscapes, the presence of key features such as cereal, ploughed fields or non-cropped lands (i.e. fallow fields, hereafter FFs) plays an important role in the persistence of farmland bird populations (Henderson, Cooper, Fuller, & Vickery, 2000). FFs are particularly important, since they enhance feeding opportunities by supporting a greater abundance of invertebrates (Moreby & Aebischer, 1992) and weeds and seeds (Henderson et al., 2000), optimize foraging efficiency, and reduce the predation risk by reducing vegetation cover and height (Whittingham, Devereux, Evans, & Bradbury, 2006).

Fallow fields are essential for steppe birds (McMahon, Giralt, Raurell, Brotons, & Bota, 2010; Morales, Traba, Carriles, Delgado, & de la Morena, 2008; Moreira, 1999), which reinforces their conservation value (i.e. given unfavourable conservation status of steppe birds at the European level; Burfield, 2005). Steppe birds' strong dependence on FF stems from their narrow niche requirements (Robleño, Bota, Giralt, & Recasens, 2017; Traba, Morales, Carmona, & Delgado, 2015), which are exclusively met within these landscapes as they resemble the original steppes in which these species evolved (Santos & Suárez, 2005). This explains the increasing impact of global change and agricultural intensification on steppe bird populations, since these processes act as ecological filters against specialist species (Gámez-Virués et al., 2015).

Habitat selection in farmland bird species, which is driven by the minimization of predation risk and the maximization of foraging efficiency and reproductive success (Green, Tyler, & Bowden, 2000; Traba et al., 2015), has been shown to be influenced by fallow vegetation structure (Whittingham et al., 2006). FFs are usually managed seasonally by farmers for agronomic purposes (i.e. to control weeds and prepare the soil for subsequent crops), which results in vegetation structures that may not always meet the narrow habitat requirements of steppe birds during the breeding season. Consequently, using agricultural practices a limited number of times before the breeding season can manage the vegetation structure of FF (Fried, Kazakou, & Gaba, 2012) and benefit farmland bird conservation. Although extensive information on species-specific requirements is available (Morales & Traba, 2016), comprehensive evaluations on the effect of agricultural practices on the habitat requirements of farmland and specifically steppe-land bird species are rare (but see Barré, Le Viol, Julliard, & Kerbiriou, 2018).

Such knowledge is crucial to promote FF management and improve conservation action effectiveness (e.g. within agri-environmental schemes (AES), where farmers are subsidized to promote FF; Kleijn & Sutherland, 2003). For example, the cost-efficiency of AES has been questioned (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011; Kleijn & Sutherland, 2003), partly because benefits of FF strongly depend on the vegetation structure (Henderson et al., 2000).

Within a quasi-experimental context, we evaluated the effect of different agricultural practices (commonly used by farmers in our study area and Spain; ESYRCE, 2017) applied to FF compared to control FF (no agricultural practices), on the occurrence of three steppe bird species having different niche requirements in northeastern Spain. Using path analysis, we built a causal network to disentangle the indirect effects (i.e. through vegetation structure and food availability) of agricultural practices on the presence of Stone Curlew *Burhinus oedicnemus* (SC), male Little Bustard *Tetrax tetrax* (LB) and Calandra Lark *Melanocorypha calandra* (CL) (see Supporting Information S1 for details).

2 | MATERIALS AND METHODS

2.1 | Study area

The study area was an agricultural mosaic landscape in the Lleida steppe plains (Catalonia, NE Spain; Supporting Information S2: Figure S5), covering approximately 3,580 km^2 of semi-arid habitat. This area was dominated by extensive cultivation of winter cereal crops interspersed with woody crops, small patches of sparse shrub land and annual FFs. The latter are mainly promoted (for among others, steppe-land bird conservation purposes) by regional AES (Cantero-Martínez & Moncunill, 2012) and a local conservation measure occurring in Special Protection Areas (SPA), which purpose is to compensate the construction of the irrigation project Segarra-Garrigues.

We conducted our research in 612 FFs (average size ± *SD* = 3.11 ± 2.87 ha) from 2015 to 2017, covering 1,925.74 ha (Supporting Information S2: Tables S4 and S5). All FFs were funded through the local compensatory conservation measure and were located within six SPA (Supporting Information S2: Figure S5).

2.2 | Agricultural practices

Fallow fields were managed in a quasi-experimental manner by applying one agricultural practice (Cantero-Martínez & Moncunill, 2012; Supporting Information S2: Table S4) from February to early April (before breeding season). These were: chisel ploughing to a minimum tillage of 10 cm (hereafter Tillage), cutting the vegetation at 5–10 cm height (hereafter Shredding), Shredding with subsequent application of a glyphosate herbicide spray at a rate of 2–4 L/ha, depending on vegetation density (hereafter Shredding + Herbicide), or sowing alfalfa (*Victoria R1* variety) at 20 kg/ha dose (hereafter Alfalfa).

Apart from this experiment, farmers in our study area regularly implement these practices in FF one to three times per year (Cantero-Martínez & Moncunill, 2012) to control for weeds on future and surrounding crops. Alfalfa is also a common crop on irrigated land, but in this study, it was never harvested as it had conservation purposes (e.g. Bretagnolle et al., 2011). FFs with no agricultural practices from February to early April were considered as control fields (hereafter Control). Agricultural practices were assigned randomly to the FFs, with a certain dependence on each farmer's context (e.g. capability in terms of machinery; Supporting Information S2: Figures S6–S8).

We sought a similar vegetation structure in all FFs (i.e. a yearly reset of the system) by applying a shredding treatment in September-November in FF with >50% cover and >30 cm height, before the application of the agricultural treatments described above. This preparatory resetting protocol was applied based on previous knowledge of the response of vegetation to the different agricultural practices.

2.3 | Bird occurrence

We chose three steppe bird species protected at the EU level (Stone Curlew (SC), Little Bustard (LB) and Calandra Lark (CL); Annex I of the EU Birds Directive: Directive 2009/147/EC 2009), with different intrinsic characteristics and habitat requirements (Supporting Information S3). Bird censuses were performed by trained observers during May, the peak of the target species' breeding season. Censuses took place from after dawn until 10:00 a.m. in good weather conditions. We used two sampling methods for each field (Bibby, Burguess, Hill, & Mustoe, 2000), namely: (a) A point count sampling, where visual and auditory observations of all detected target species were recorded during 10 min. (b) A variation of the line transect method (Bibby et al., 2000), which consisted of walking in a zigzag pattern through the FF to detect elusive species (e.g. SC and LB). The presence/absence of individuals of each species in either of the two methods was used as species occurrence per FF. Due to the low detectability of LB females (Morales, Traba, Delgado, & Morena, 2013), we only analysed male presence.

2.4 | Environmental variables

We used three groups of variables, namely: vegetation structure, food availability and landscape, to explain bird occurrence (Supporting Information S2: Table S6). We also included the size of the FF (m^2) as a covariate when modelling species occurrence (McMahon et al., 2010).

2.4.1 | Vegetation structure

We measured vegetation structure using 3–6 (i.e. proportional to the field size) 2 × 2 m plots in each FF. In each plot, one measure of vegetation height (cm) and the proportion of dead and live vegetation cover were visually estimated by approximating the measure to the nearest 5 cm and 5% value, respectively. Each variable was averaged among plots to obtain a unique field measure (Supporting Information S2: Table S6). We also calculated a Simpson Diversity Index derived from the cover of each dominant plant species (i.e. >20% cover within the plot). We considered this value as a pseudo plant diversity index (only dominant species were used for the index) for each FF.

We characterized within-field heterogeneity in the FF by visually estimating the proportion of the FF area covered by 10 different categories of vegetation structure (i.e. vegetation cover and height combinations) (Supporting Information S2: Table S6). This proportion was approximated to the nearest 5% value. We estimated field heterogeneity in each FF with the Levin's index of niche breath, by substituting species with FF ID and dietary items with vegetation structure categories.

2.4.2 | Food availability

We estimated orthopteran biomass using the regression equations derived by Hódar (1996), from orthopteran counts performed in two transects of 20 m long × 2 m wide per FF.

We calculated leaf and seed availability indexes by combining information about functional traits and the cover of dominant plant species identified in the plots (see Robleño et al., 2017; Supporting Information S2: Table S6). The Leaf Availability Index was estimated as [vegetation cover × height × Specific Leaf Area (SLA, mm^2/mg)], and Seed Availability Index was estimated as [vegetation cover × height × seed mass (the average individual weight of 1,000 seeds)], weighted by flowering period (Robleño et al., 2017).

2.4.3 | Landscape variables

To control for landscape heterogeneity (i.e. configuration and composition), we extracted landscape characteristics within an average circular home range size of each target species (i.e. buffer of 500 m-radius for LB and SC and 200 m-radius for CL; Caccamo, Pollonara, Emilio Baldaccini, & Giunchi, 2011; Ponjoan, Bota, & Mañosa, 2012; Suárez-Seoane et al., 2002).

Configuration

Using the regional Geographic Information System of Farming Land (SIGPAC; Supporting Information S2: Table S6), we calculated Total Border Length (TBL) as the sum of the field perimeters. We also calculated the Mean Perimeter-Area Ratio (MPAR) as indicator of field regularity (Supporting Information S2: Table S6), by calculating the Perimeter-Area Ratio of each field as the ratio of the field perimeter to the perimeter of a circular field of the same area (Donald, Evans, Buckingham, Muirhead, & Wilson, 2001), and then averaging the field values within each buffer.

Composition

Using a crop-land use map annually updated by the regional government (Unique Agrarian Statement/DUN; Supporting Information S2: Table S6), we calculated the proportion of fallow land and crop diversity using the Shannon Diversity index on relevant cover categories for the target species (see Supporting Information S2: Table S6 for a description of the land cover categories).

2.5 | Statistical analyses

We performed a confirmatory-exploratory path analysis (Supporting Information S1; Grace, 2006) using piecewise Structural Equation Modelling (SEM) to investigate how the effect of different agricultural practices on bird occurrence was mediated by the changes in vegetation structure and/or food availability. Piecewise SEM links information of multiple component models for different response variables and allows rigorous estimation of indirect effects in a single causal network (Shipley, 2009). We constructed this network based on previous knowledge of the system for each target species and agricultural practice, that represented our partial hypotheses (Supporting Information S1; Grace et al., 2012). We only included variables with a Pearson correlation coefficient <0.5. We then used Shipley's (2009) directional separation approach (D-sep), which consists of the following two main steps.

The first step consisted of constructing the path model as a set of hierarchical linear mixed models. Regressions related to the first part of the path (i.e. linking agricultural practice with vegetation and food variables; Supporting Information S1) were modelled with an identity link function using the 'lme' function (nlme R package; Pinheiro, Bates, DebRoy, & Sarkar, 2018), and regressions related to the second part (i.e. linking all explanatory variables with bird presence/absence; Supporting Information S1) were fitted with a logit link function using the 'glmmPQL' function (MASS R package; Venables & Ripley, 2002). We included year as random intercept and a Gaussian correlation structure (corGaus(form = ~Lon_x + Lat_y)) in all models to account for the spatial clustering of the fields (Lefcheck, 2016; Supporting Information S2: Figures S6–S8). We created a path model for each of the agricultural practices and used Control as a reference by including the agricultural practice as dummy variable (1—Agricultural practice; 0—Control). All variables were standardized (mean ± *SD* = 0 ± 1) in order to compare their effect size.

The second step consisted of fitting the overall path model using the R package *piecewiseSEM* (Lefcheck, 2016). This approach applies the D-sep test to estimate the overall goodness-of-fit by combining the significance of missing paths and correlated errors into a single chi-squared distributed Fisher's *C*-statistic (Shipley, 2009).

Once the best path model validated, we estimated the standardized model parameters of causal effects. Parameter estimates are given in the link function scale and expressed as mean ± *SE*. All analyses were conducted using R v. 3.3.3 (R Core Team, 2017).

3 | RESULTS

The proportion of species presence per agricultural practice was highest in Alfalfa fields for LB (31.25%, Supporting Information S2: Table S8), and in Shredding + Herbicide fields for CL (65%, Supporting Information S2: Table S8) and SC (40%, Supporting Information S2: Table S8). The lowest proportion of species presence was found in Alfalfa fields for SC (7.5%), in Control fields for CL (25.64%), and in Shredding + Herbicide fields for LB (10%).

3.1 | Stone Curlew

The presence of SC was affected by the vegetation variables in all paths, but was not affected by the food variables (Supporting Information S1: Table S2). Across all agricultural practices, SC benefited from a decrease in cover and height (Figure 1a; Table 1). It was the only species positively affected by plant diversity (Supporting Information S1: Table S2). Shredding + Herbicide had the strongest positive effect on the presence of SC compared to Control (OE_{SH} = 2.22, Table 1). This positive effect occurred because of the decrease in cover and height (Supporting Information S1: Figure S3, Table S2). Tillage was the second-best agricultural practice for SC (OE_T = 0.63, Table 1), due to its negative effect on cover and height (Figure 1a; Supporting Information S1: Table S2). Shredding and Alfalfa had a lower positive effect (Table 1) on SC presence. SC presence was not affected by any of the landscape variables (Table 2).

3.2 | Little bustard males

Little bustard occurrence was not affected by food variables, but did increase with lower vegetation heights in half of the agricultural treatments (Supporting Information S1: Table S2; Figure 1b). Shredding resulted in the highest LB occurrence, due to the reduction in vegetation height (OE_S = 0.21, Table 1; Figure 1b). Shredding + Herbicide had no overall effect on LB occurrence as compared to Control (Table 1). Tillage had a negative effect on LB occurrence (OE_T = −0.05, Table 1), because the benefit of decreased vegetation height was countered by the decrease in vegetation cover (Table 1; Supporting Information S1: Table S2). Alfalfa had a direct negative effect on LB presence that was not explained by any of the included variables. From the landscape variables, the presence of LB was hindered by the compositional variables (i.e. fallow land proportion and crop diversity) and field regularity (MPAR) (Table 2).

3.3 | Calandra lark

Calandra lark (CL) was generally not affected by any of the vegetation or food variables (Table 1). Shredding + Herbicide and Shredding had a direct positive effect, and Alfalfa had a direct negative effect in CL presence that was not mediated by any of the included variables (Table 1). CL was the species most affected by the landscape variables. Its presence was positively affected by TBL and negatively

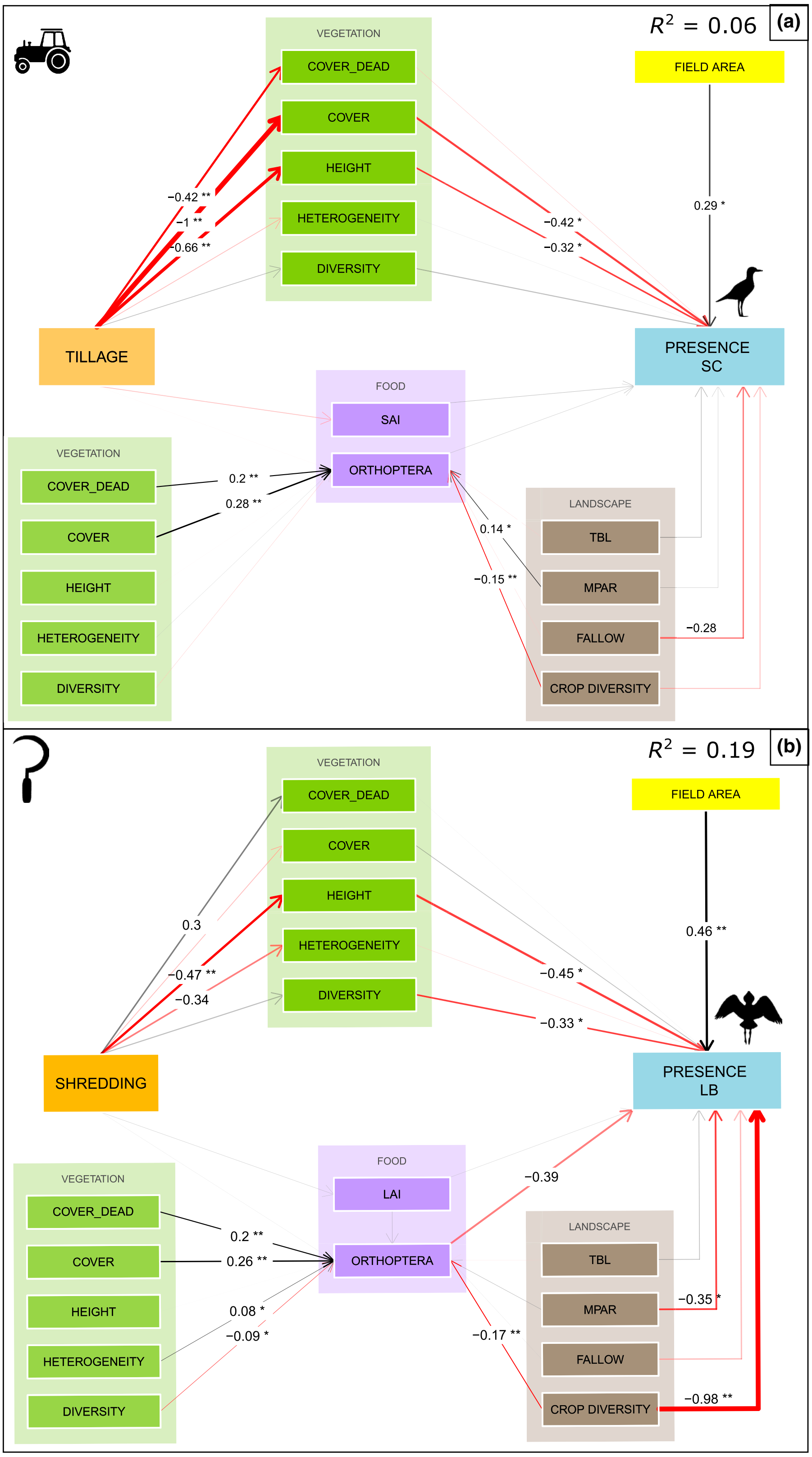

FIGURE 1 Results of path analyses for agricultural practices highlighted as relevant for conservation implications on the studied species (see discussion section), exploring (a) the effect of Tillage on the Stone Curlew (SC) presence and (b) the effect of Shredding on the Little Bustard (LB) presence. Conditional R^2 is shown in the top-right corner of each path. Thickness of black (positive) and red (negative) paths is proportional to standardized path coefficients. Path transparency is proportional to the *p*-value significance level. Standardized path coefficients with $p < 0.10$ are shown according to the criteria: $p < 0.01$**;$0.01 < p < 0.05$*;$0.05 < p < 0.10$

TABLE 1 Standardized effects of the significant paths between the agricultural practices Shredding + Herbicide, Shredding, Tillage and Alfalfa, predicted for the Stone Curlew (SC), Little Bustard (LB) and Calandra Lark (CL)

Species	Agricultural practice	Path (agricultural practice → (Variable) → Species)	Indirect effect	Overall effect
 SC	Shredding + Herbicide (S + H)	S + H → Cover → SC	1.27	**2.22**
		S + H → Height → SC	0.95	
	Shredding (S)	S → Height → SC	0.22	0.22
	Tillage (T)	T → Cover → SC	0.42	0.63
		T → Height → SC	0.21	
	Alfalfa (A)	A → Diversity → SC	−0.29	0.28
LB 	Shredding (S)	S → Height → LB	0.21	**0.21**
	Tillage (T)	T → Cover → LB	−0.39	−0.05
		T → Height → LB	0.34	
	Alfalfa (A)	A → LB	−0.83	−0.83
CL 	Shredding + Herbicide (S + H)	S + H → CL	1.5	**1.5**
	Shredding (S)	S → Height → CL	0.08	1.08
		S → CL	1	
	Alfalfa (A)	A → CL	−0.93	−0.93

The indirect effects are the coefficients of the significant agricultural practices on each species mediated by the vegetation/food variables, obtained by multiplying the partial standardized path coefficients. The overall effects are the total effect of the agricultural practices on each species, obtained by summing all indirect effects. The strongest positive effects are shown in bold

affected by field regularity (MPAR), fallow land proportion and crop diversity (Table 2).

4 | DISCUSSION

Despite the number of studies showing positive effects of fallow availability on steppe and farmland birds (e.g. Henderson et al., 2000; Van Buskirk & Willi, 2004), managing field vegetation structure is considered as key to improving habitat quality and halting, or even reversing, the farmland bird populations decline (McMahon et al., 2010; Morales et al., 2008; Wilson, Whittingham, & Bradbury, 2005). We used a unique quasi-experimental setup, covering an unprecedented spatio-temporal scale, to evaluate how the use of common agricultural practices applied in FFs can increase the occurrence of three steppe bird species with different ecological requirements (Supporting Information S3). Our study does not only emphasize the role of vegetation structure for steppe birds within FFs (e.g. Moreira, 1999), but also highlights the benefits of applying common agricultural practices at a specific timing (i.e. before the breeding season) and frequency (two times per year), to meet the habitat requirements of different bird species. Specifically, our comprehensive analysis highlights that the use of Shredding + Herbicide and Shredding increased the occurrence of the three studied species, in two of them (i.e. SC and LB males) through a change in the vegetation structure, and in the case of CL for causes unexplained by either of the included variables. The use of Tillage also increased SC through a change in the vegetation structure rather than a change in food availability.

Our study shows species-specific responses to different vegetation structure. Vegetation structure may either protect or expose an individual to predators (Whittingham et al., 2006), extreme weather conditions (Walsberg, 1985) or influence its feeding behaviour (Wilson et al., 2005). Therefore, these specific responses are likely caused by different evolutionary strategies developed by species to deal with environmental pressures (Wilson et al., 2005). Unmanaged FFs usually develop important vegetation growth (Supporting Information S2: Table S7), which does not meet the habitat requirements of steppe birds (Whittingham et al., 2006). The production of excess vegetation in Control (unmanaged) FFs is likely due to the long-term over-fertilization and lack of livestock which characterize these farmlands.

We did not detect any effect of plant-food variables on species occurrence, possibly because leaf and seed availability was not limiting, and/or because it was not the main driver of microhabitat selection for the studied species. Indeed, Traba et al. (2015) found that these species tend to minimize predation risks by selecting a particular vegetation structure, even when this choice limits their access to food. We did not have access to direct measures of food availability, and had to rely on indexes that may have only partially captured plant-food availability within each FF. We did not find an effect of orthopteran biomass in the studied species' occurrence, although orthopterans represent a part of the diet of the SC (Amat, 1986; Green et al.., 2000) and the LB (Jiguet, 2002; but see Bretagnolle et al., 2011). However, it is possible that our measure did not capture the whole effect of invertebrate availability, as bird's diet can also include other taxa such as coleopterans.

TABLE 2 Standardized path coefficients and 95% confidence intervals shown for the 12 path analyses for each species (from left to right: Stone Curlew, Little Bustard and Calandra Lark) and each agricultural practice (from top to bottom Shredding + Herbicide, Shredding, Tillage, Alfalfa)

							
		β	95% CI	*β*	95% CI	*β*	95% CI
	TBL	−0.03	−0.47 to 0.41	0.23	−0.74 to 1.2	0.31	−0.13 to 0.75
	MPAR	0.20	−0.29 to 0.70	−0.02	−1.37 to 1.32	**−0.67***	−1.08 to −0.08
	Fallow	−0.35	−0.91 to 0.21	−0.49	−1.93 to 0.96	−0.08	−0.77 to 0.61
	Crop diversity	−0.50	−1.11 to 0.11	0.41	−2.40 to 1.59	**−0.90****	−1.53 to −0.26
	Field area	**0.84****	0.33–1.34	−0.34	−1.78 to 1.10	**1.03****	0.44–1.61
	TBL	−0.05	−0.43 to 0.32	0.14	−0.20 to 0.49	**0.3**	−0.02 to 0.61
	MPAR	0.32	−0.08 to 0.73	**−0.35***	−0.70 to 0.009	**−0.76****	−1.14 to −0.38
	Fallow	−0.13	−0.54 to 0.28	−0.27	−0.63 to 0.08	**−0.48****	−0.84 to −0.11
	Crop diversity	−0.21	−0.62 to 0.21	**−0.98****	−1.39 to −0.57	**−0.46****	−0.79 to −0.12
	Field area	**0.35***	0.06–0.63	**0.46****	0.16–0.76	**0.73****	0.46–0.99
	TBL	0.15	−0.16 to 0.42	**0.32***	0.01– 0.62	0.21	−0.06 to 0.48
	MPAR	0.06	−0.26 to 0.37	**−0.50****	−0.82 to −0.17	**−0.82****	−1.16 to −0.47
	Fallow	**−0.28**	−0.61 to 0.06	**−0.39****	−0.70 to −0.09	**−0.29***	−0.58 to −0.01
	Crop diversity	−0.17	−0.48 to 0.14	**−0.84****	−1.17 to 0.52	**−0.40****	−0.67 to −0.14
	Field area	**0.29****	0.05–0.54	**0.41****	0.14–0.68	**0.58****	0.34–0.83
	TBL	0.06	−0.37 to 0.49	0.28	−0.07 to 0.61	**0.62****	0.22–1.02
	MPAR	0.33	−0.16 to 0.81	**−0.61****	−1 to −0.21	**−0.55***	−1.01 to −0.07
	Fallow	−0.24	−0.70 to 0.23	**−0.35**	−0.72 to 0.01	**−0.57***	−1.04 to −0.11
	Crop diversity	−0.18	−0.68 to 0.30	**−0.68****	−1.04 to −0.31	−0.16	−0.53 to 0.20
	Field area	0.04	−0.32 to 0.39	**0.65****	0.29–1	**0.43****	0.13–0.73

Path coefficients are presented for partial paths between the landscape variables total border length (TBL), Mean of the Perimeter-Area Ratio (MPAR), Fallow, Crop diversity and Field area, and the presence of target species. Standardized path coefficients with $p < 0.10$ are shown according to the criteria: $p < 0.01$**; $0.01 < p < 0.05$*; $0.05 < p < 0.10$.

Our study design was partially conditioned by each farmer's limitations to apply certain agricultural practices (Supporting Information S2: Figures S6–S8). We attempted to overcome this limitation by including a spatial correlation structure in all path models. Likewise, we dealt with the potential bias produced by the different management histories of FF by establishing a vegetation resetting protocol (see Section 22). Despite using a combination of point count sampling and zigzag line transects to ensure detection of birds possibly hidden in the vegetation, our data collected using a single survey method did not allow us to explicitly account for imperfect detection, which is another possible source of bias of our study. We encourage further research on this topic to improve upon these shortcomings.

Stone Curlew was the species with the strongest requirements in terms of vegetation structure (low vegetation cover and height). This preference has been previously documented (Green et al., 2000), and attributed to an anti-predator behaviour linked to its lack of vision above eye level (Martin & Katzir, 1994). Its downward visual orientation optimizes foraging (Aebischer, Green, & Evans, 2000), but requires a wide visual field at ground level to detect predators and prey. Our results indicate that Shredding + Herbicide creates optimal habitats for SC presence due to the sparse and heterogeneous vegetation structure produced by the combination of both practices. However, given the detrimental impact of herbicides on biodiversity and the environment (Boatman et al., 2004), we do not recommend the use of herbicide-related practices. Based on our results, Tillage may be the best alternative because it also promotes sparse vegetation (Wilson et al., 2005), facilitates camouflage by exposing the substrate colour (Green et al., 2000), and increases food accessibility by unearthing invertebrates (Ponce, Bravo, & Alonso, 2014).

Little Bustard males benefited from the restrictions in vegetation height but not in vegetation cover provided by Shredding, probably due to their conflicting needs of visibility for displaying and courtship, and significant cover of short green plants for feeding (Morales et al., 2008). Agricultural practices did not affect LB male occurrence through food availability despite its known preferences for food-rich territories to afford the costs of mating activities (Faria, Rabaça, & Morales, 2012; Traba, Morales, García dela Morena, Delgado, & Krištín, 2008). This finding may be reasonable for this species, because unploughed FFs and moderate management (e.g. moderate grazing; Faria et al., 2012) have been shown to provide an equitable balance between food and conspicuousness for LB

(Morales et al., 2008). Alfalfa had a negative effect on LB, despite this species being generally benefited by legume fields (Bretagnolle et al., 2011; Ponce et al., 2014). Drought conditions after the sowing date in some years of the study period may have undermined the competitive capacity of alfalfa, leading other weeds to dominate and produce a similar structure to control fields (see also Robleño et al., 2017). We therefore encourage the use of a drought-adapted alfalfa ecotype, or other leguminous species, in future studies testing leguminous crops as a fallow management treatment. While fallows are important nesting and foraging areas (Morales et al., 2013; Tarjuelo et al., 2013), cereal stubbles are also a key foraging habitat for LB females and their chicks (Tarjuelo et al., 2013). Therefore, the positive response of LB males to Shredding may not necessarily lead to increased breeding success, and different vegetation structures might be needed to meet the requirements of each sex (Morales et al., 2008).

Calandra Lark occurrence was not affected by the vegetation structure (see also CL abundance response; Supporting Information S1.2). This could be related to its generalist behaviour at the microhabitat scale (McMahon et al., 2010; Morgado et al., 2010), which allows CL to breed within different types of vegetation structure (Delgado & Moreira, 2002). The direct effects from Shredding and Shredding + Herbicide that were not mediated by the vegetation and food variables encourages further research on the effect of agricultural practices on this species (but see Supporting Information S1.2 for CL abundance response).

The occurrence of CL and LB tended to decrease when fallow land availability surrounding the FF was higher. This could be caused by the scattering of individuals when the availability of suitable habitat is higher (i.e. dilution effect; see also McMahon et al., 2010). Moreover, the negative effect of crop diversity could be expected for grassland specialists favoured by homogeneous landscapes (Moreira et al., 2012; Morgado et al., 2010). The presence of CL was mainly driven by the landscape context, which further reinforces the importance of considering landscape effects in field-scale analyses (Kleijn et al., 2011).

4.1 | Conservation implications

Our study provides an evaluation of the effectiveness of common agricultural practices for the conservation of three steppe bird species. Although the importance of FFs is recognized, to our knowledge, this is the first study showing how different agricultural practices applied on FFs, when targeted towards specific-species requirements, could increase steppe bird occurrence. Indeed, the best management solution for these species points to a mosaic of fallows managed by Tillage or Shredding with a limited number of applications (one or two times per year), before the breeding season. This might be a good incentive to involve farmers in steppe bird conservation, because they usually prefer to avoid the excess of weeds and support agricultural management.

Moreover, our results suggest that increasing the availability of FFs as promoted by generic AES, might not be sufficient to protect the entire steppe-land bird community. A substantial amount of money is allocated to steppe bird conservation in AES (e.g. 3,526,147 € in Catalonia from 2010 to 2016; Gencat, 2018), and therefore improving cost-efficiency of AES by applying species-specific management measures should be prioritized (Kleijn & Sutherland, 2003).

This study not only reinforces the idea that agricultural practices can be used as a conservation tool for farmland birds (Barré et al., 2018) and biodiversity (Conover, Dinsmore, & Burger, 2014), but also highlights the important aspects of endangered steppe bird species ecology that can be directly applied to improve conservation actions in farmland areas. Understanding the mechanisms (e.g. shelter, visibility, food availability) by which agricultural practices determine species occurrence may prove useful when inferring conclusions about other systems, where these and other agricultural practices (e.g. livestock grazing) may be needed to meet the species requirements. Our methodological approach may prove useful for future research which evaluates how agricultural practices affect steppe bird species, and also in terms of demographic parameters such as reproduction and survival.

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AUTHORS' CONTRIBUTIONS

D.G., F.S.-P., G.B., I.R. and A.S.-P. conceived and designed the study with C.M. and S.M.'s suggestions. A.S.-P. and C.M. implemented the analysis. A.S.-P. wrote the manuscript with the help of D.G. and F.S.-P. All the authors contributed to subsequent drafts and gave final approval for publication. F.S.-P., D.G. and G.B. coordinated fieldwork and secured funding.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository, https://doi.org/10.5061/dryad.85b47d1 (Sanz-Pérez et al., 2019).

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SUPPORTING INFORMATION

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