



# Modelling the effectivity of a land sparing strategy to preserve an endangered steppe-land bird population in cereal farmland: Scopes and limits

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## ARTICLE INFO

### Keywords:

Fallow  
Demographic modelling  
Adaptive management  
Farmland conservation  
Land-sharing  
Land-sparing  
Little bustard (*Tetrax tetrax*)

## ABSTRACT

Agricultural intensification and the disappearance of fallow land have been identified as a major driver of biodiversity loss in European farmland. In particular, the dramatic population decline of the little bustard (*Tetrax tetrax*), a flagship bird species in western European cereal farmland, has been largely attributed to the loss of this crucial habitat. Demographic modelling showed that low breeding success and reduced female survival were co-responsible for the little bustard population decline in a NE Iberian cereal pseudo-steppe. An equilibrium finite rate of change can be achieved by raising either female adult survival or fecundity. In both cases, the required increases fall within a biological meaningful range, but a combination of both would be more feasible in practice. Setting farmland aside as managed fallow can boost fecundity to the required equilibrium value, but the potential of this management action is seriously reduced as mortality increases. Socio-economically acceptable amounts of spared-land can only be achieved if actions to reduce mortality are undertaken in combination with providing fallow land. Actions to reduce both natural and anthropogenic mortality have so far been neglected by little bustard conservation programs. Both are needed if we seek to guarantee the long-term viability of the species and an acceptable share of conservation effort from stakeholders. Our results show that the holistic adaptive management approach adopted here can be used to evaluate the effectiveness and limitations of conservation decisions and to provide insights for conservation projects.

## 1. Introduction

Agricultural intensification is one of the main drivers leading to the loss of biodiversity in the world (Emmerson et al., 2016; Raven and Wagner, 2021). The demise of bird populations in farmland has been particularly well-documented and studied (Donald et al., 2006; Henderson et al., 2020; Jeliaskov et al., 2016). The process involves the simplification of the landscape matrix and the increased use of inputs on farmland, which results in the loss of food and shelter for birds, as well as increased sources of anthropogenic mortality. From a biodiversity point of view, the traditional practice of fallow in Mediterranean farmland (Suárez et al., 1997), although primarily addressed to maintain soil fertility, was a sort of land sparing strategy that resulted in highly

heterogeneous and biodiversity-rich agricultural landscapes. The disappearance of this traditional practice with the arrival of chemical fertilizers has been claimed to be one the main causes of farmland bird population decline (Traba and Morales, 2019). Therefore, setting aside farmland as fallow land can be a good way to halt this process, particularly when other Agri-environmental Schemes (AES) based on land-sharing approaches have not succeeded (Kleijn and Sutherland, 2003; Tarjuelo et al., 2021).

The little bustard (*Tetrax tetrax*, T. Foster 1817, Aves, Otidae) is a ground-nesting bird inhabiting natural steppes, pastures, cereal steppes or other herbaceous crops from western Europe to western China (Morales and Bretagnolle, 2022). It exhibits an exploded lek breeding system in which no permanent pair bonds are established (Bretagnolle et al.,

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<https://doi.org/10.1016/j.biocon.2023.110386>

Received 22 March 2023; Received in revised form 15 November 2023; Accepted 19 November 2023

Available online 28 November 2023

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2022b). Females are solely responsible for laying, incubating and caring for the precocial chicks (Bretagnolle et al., 2022a). These feed exclusively on arthropods (Jiguet, 2002) and progressively shift to the preponderantly herbivorous adult diet (Bravo et al., 2017; Cabodevilla et al., 2021). A recent review of its population status and trends around the world found alarming patterns in most cases, particularly in Western Europe (Morales and Bretagnolle, 2021, 2022). In Iberia, the stronghold of the European population, the decrease of little bustard populations has been quantified at c.50 % of breeding males in only 10 years (García de la Morena et al., 2018; Silva et al., 2018). The species is listed as Vulnerable in Europe and Near Threatened on a global scale (BirdLife International, 2018). It is included in Appendices I and II of the Convention on Migratory Species and Wildlife (CMS, 2020) and has recently been officially upgraded from Vulnerable to Endangered in Spain, as proposed by López-Jiménez et al. (2021). Agricultural changes, in conjunction with mortality factors, are ultimately responsible for this decline (Iñigo and Barov, 2010; BirdLife International, 2018; Mañosa and Morales, 2021; López-Jiménez et al., 2021). Reduction of fallow availability associated with agricultural intensification (Traba and Morales, 2019) and increased urban and industrial development (Arroyo et al., 2022) result in partial or complete habitat loss and a reduction of the habitat carrying capacity, leading to sharp decrease in reproductive success (Lapiedra et al., 2011; Cuscó et al., 2021b). Predators, poaching or power line collisions are the main factors of mortality (Marcelino et al., 2018) and seem to affect females more than males, as suggested by the male skewed sex ratios observed in many Western European populations (Serrano-Davies et al., 2022).

Previous knowledge on the reproductive biology and population dynamics of the species (Bretagnolle and Inchausti, 2005; Inchausti and Bretagnolle, 2005; Morales et al., 2005; Lapiedra et al., 2011; Cuscó et al., 2021b) pointed to nest losses and low chick-survival as one of the main causes underlying the decline of the species in farmland habitats. Accordingly, several conservation initiatives have been implemented to improve breeding success. A land-sharing approach, based on the implementation of an agri-environment scheme (AES) promoting the voluntary adoption of friendly agricultural practices in alfalfa crops, was adopted in Western-Central France, to try to make farming compatible with little bustard populations. These practices included 1) converting annual crops into grassland and fodder crops, 2) preventing mowing of alfalfa and set-aside fields, and 3) prohibiting the use of insecticides and herbicides in grassland (Bretagnolle et al., 2011; Berthet et al., 2012). Although effective, this approach was found to have some limitations, due to biological and socio-economic reasons (Berthet et al., 2017; Bretagnolle et al., 2018), and a land-sparing approach has already been proposed as a more suitable alternative (Berthet et al., 2012; Bretagnolle et al., 2018). A land-sparing approach was also adopted (Mañosa et al., 2021) in Catalonia (NE Iberia), where the species experienced a dramatic decline in recent decades (Cuscó et al., 2021a). A specific conservation program was initiated in 2014 focusing on increasing the availability of fallows (both with native spontaneous vegetation or with sowed alfalfa) across the strongholds of the species's breeding range, by renting, setting aside and managing farm plots within Special Protection Areas (SPA) in the Lleida Plain. The management of these leased fallows that is required in order to meet the specified conservation objectives (Robleño et al., 2017; Sanz-Pérez et al., 2019) was provided by the competent conservation authority in a controlled and planned way. Fallow land availability was presumed to increase fecundity, as it might provide suitable green cover for displaying males (Giralt et al., 2018; Sanz-Pérez et al., 2019), shelter for nests, as well protection and food, mainly orthopterans (Estrada et al., 2017) for the chicks. The program achieved its planned target of c.3400 set-aside hectares in 2019, with an estimated annual cost of c. €385–415/ha (including land leasing, fallow management and administrative and coordination costs). At local level, the presence of these managed fallows significantly increased the abundance of little bustard males and other steppe bird species (Sanz-Pérez et al., 2021). Here, we use a demographic modelling approach to

evaluate the potential impact of this measure at the population level, as compared to other potential conservation actions. The integration of population monitoring and modelling in an adaptive management framework (Keith et al., 2011) allowed us to forecast the results of competing conservation strategies, in order to validate or reformulate the current practice (Morris and Doak, 2002; Williams et al., 2002; Dolman et al., 2015; Sergio et al., 2020). This approach is particularly suitable for the little bustard, a species for which obtaining field data is especially difficult. We specifically aimed 1) to investigate whether increasing fecundity alone had the potential to achieve the expected conservation results; 2) to explore the potential of fallow management to achieve the required increase in fecundity; 3) to explore the demographic results of reducing different sources of mortality and 4) to identify the optimal strategy to set the population to demographic equilibrium.

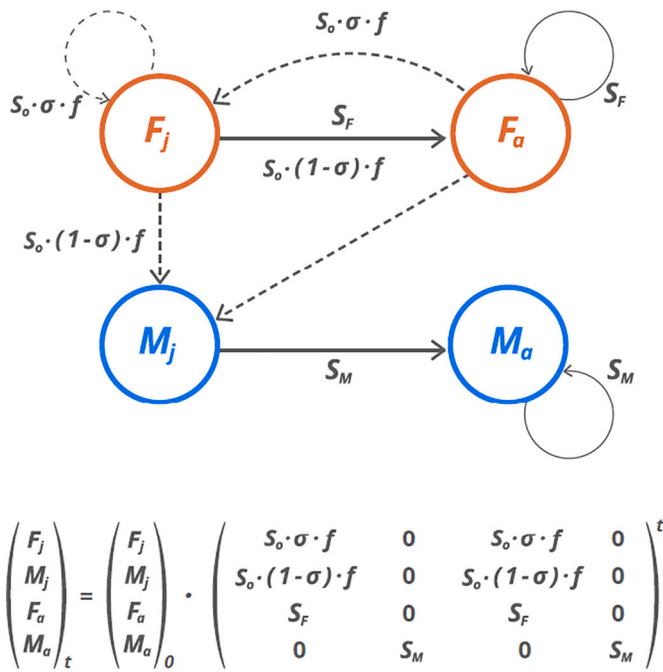
## 2. Material and methods

### 2.1. Study area

The study was conducted in the Lleida Plain, in Catalonia, NE Spain (Mañosa et al., 2021), which is representative of a standard Iberian cereal pseudo-steppe. The Lleida Plain is a flat c.4000 km<sup>2</sup> area situated on the edge of the Ebro basin, at 164–489 m a.s.l. Climate is semiarid Mediterranean, with an average annual rainfall of 300–400 mm and an average temperature of 7–8 °C in winter and 24–25 °C in summer. The central part of the area (c. 2500 km<sup>2</sup>) is devoted to irrigated farmland, including fruit tree orchards, alfalfa and maize fields, while the periphery (c. 1500 km<sup>2</sup>) consists mainly of a mosaic of rain-fed crops, including c. 800 km<sup>2</sup> of cereal pseudo-steppes, 474 km<sup>2</sup> of which are included in 8 Special Protection Areas (SPA). Agricultural practices on rain-fed crops have intensified and increasing proportions of the landscape are shifting from rain-fed to irrigated crops. However, the area holds the last breeding population of little bustard in Catalonia (Cuscó et al., 2021a), which was estimated at 1500 males in 2002 (García de la Morena et al., 2006) but was reduced to only 650 males in 2016 (García de la Morena et al., 2018).

### 2.2. The demographic model

We built a pre-reproductive pulse, age-structured matrix demographic model which assumed that individuals were counted each year just before nesting (15th April, for convention) (Fig. 1). The model included four age and sex compartments: young females ( $F_j$ ), young males ( $M_j$ ), adult females ( $F_a$ ) and adult males ( $M_a$ ). Young were all birds in their second calendar year, while adults were on their third calendar year or more. Females were assumed to breed on the second calendar year (young and adult females breed) and males not before their third calendar year (only adult males breed) (Cramp and Simmons, 1980; Mañosa et al., 2022). Males and females survive from one year to the next with  $S_M$  and  $S_F$  probabilities. The model considered that both young and adult females reproduced with identical fecundity  $f$  (numbers of chicks >30 days old per female). The proportion of females at hatching,  $\sigma$ , was assumed to be 0.5 (Inchausti and Bretagnolle, 2005). We further assumed that fledged chicks survived to next spring with probability  $S_0$ . We incorporated this parameter into the model as  $S_0 = S_e \cdot [(S_M + S_F) / 2]^{8/12}$ , where  $S_e$  is the survival from fledging (30 days) to independence (assumed to take place on 15th August). Although we did not have a previous reference value for  $S_e$ , nor a specific estimate for it, we set 0.8 as a default value, consistent with the proportion of chicks surviving between 30 and >45 days old reported by Bretagnolle et al. (2018). In the current conditions, changes in the choice of this parameter do not have much effect on the viability of the population (Fig. 3f).



**Fig. 1.** Diagram showing the relationship between the age and sex groups considered in the demographic model and its formal matrix expression (see text for details).  $F_j$ : Number of juvenile females;  $F_a$ : Number of adult females;  $M_j$ : Number of juvenile males;  $M_a$ : Number of adult males;  $S_o$ : first winter survival;  $\sigma$ : sex ratio at hatching;  $S_M$ : annual male survival;  $S_F$ : annual female survival;  $f$ : fecundity.

### 2.3. Estimation of the demographic parameters

Breeding and survival parameters from the Lleida Plain little bustard population were obtained based on data compiled from two tagging programs, one based on tagging 20 males (2002–2005) and 23 females (2004–2006) with VHS transmitters (Ponjoan et al., 2012; Lapiedra et al., 2011) and another one based on tagging 18 females with GPS-GSM transmitters from 2009 to 2013 (Cuscó et al., 2021b). In all cases, capture and tagging was done under permission of the competent authority of the Generalitat de Catalunya. The following parameters were estimated:

- Fecundity ( $f$ ). The average number of chicks >30 days old produced by every female alive at the start of the nesting season. This was estimated as the product of four sequential and independently estimated parameters: Laying rate (LR): the proportion of females initiating laying in relation to the total number of females alive at the beginning of the breeding season; Hatching rate (HR): the probability that a female that has laid at least one clutch manages to hatch a brood; Fledging rate (FR): the probability that a female with a brood manages to fledge at least one young >30 days old; Number of chicks at fledging (FS): the average number of chicks per successful brood. We only included data of those females tracked between 2003 and 2013, before the set-aside conservation program was launched in 2014, and considering only those breeding attempts for which we had full information on their outcome. The interannual variance of fecundity was estimated following the method of White as explained in Morris and Doak (2002).
- Male ( $S_M$ ) and female ( $S_F$ ) adult annual survival rate. We used a mortality table approach implemented in SPSS version 25.0 (IBM Corp, 2017) to calculate, for every 365 days interval, the number of birds at risk at the start of the interval and the number of dead birds during that specific interval. When the exact fate of a bird during a

given year interval was not known, or when the transmitter failed, data were censored to the right from the date of the last reliable information received for this bird. We used the above-mentioned values to compute the average annual survival and the corresponding interannual variability using the Kendall method (Morris and Doak, 2002) using R (R Development Core Team, 2019). Only data from birds older than one year were used, and dead birds or those likely to be dead as a consequence of capture myopathy (Ponjoan et al., 2008) were excluded from the analysis.

### 2.4. Modelling the population trajectories, stochastic growth rates and the sensitivity analysis

We used the Unified Life Models (ULM) software (Legendre and Clobert, 1995) for the construction and analysis of the described matrix model. We incorporated environmental stochasticity into the model by considering that survival rates ( $S_F$ ,  $S_M$ ,  $S_o$ ) and fecundity ( $f$ ) showed some random interannual variability. For survival rates, this variability was described and incorporated into the model using a beta1f distribution, with an average equal to the actual values of  $S_F$ ,  $S_M$ ,  $S_o$  and an interannual coefficient of variation corresponding to the maximum interannual CV obtained for adult survival rates. We considered that  $f$  followed a Gaussian distribution with mean  $f$  and a coefficient of variation corresponding to the interannual CV of fecundity. The stochastic finite growth rate ( $\lambda_s$ ) was calculated by projecting 1000 Monte Carlo trajectories 50 years ahead. The population trajectories (2002–2052) were plotted separately for males and females, considering the 2002 initial population estimates for the study area. The initial number of adult males was around 1500 individuals (García de la Morena et al., 2006). The initial number of females was estimated based on the number of males and assuming a ratio of 0.357 females/total number of birds in the population (Serrano-Davies et al., 2022), resulting in 835 females. We used a graphical approach to evaluate the effect of a given change in a population parameter or management action on the finite rate of population growth, by using the landscape tool in ULM, which allowed us to draw isoline maps of the finite growth rate  $\lambda$  in relation to selected pairs of parameters.

### 2.5. Modelling the effect of semi-permanent herbaceous vegetation on fecundity

Semi-permanent herbaceous fields like fallows or pastures are critical habitat for steppe birds' reproduction since these are positively selected habitats for nesting and chick rearing (Traba et al., 2022b). From 2012 to 2019, we conducted brood counts on 7 farmland areas, totalling 6363 ha using the methodology described in Tarjuelo et al. (2013), to obtain an indirect measurement of the annual breeding success. These areas were the same across the years and, assuming that the number of females was not increasing (which is a conservative assumption), the variation in the number of broods and number of chicks was an indicator of population's fecundity. We standardized the number of chicks and broods counted each year in relation to the value of the initial year, so that we obtained a relative fecundity index ( $K$ ) for each year. Then, assuming that fecundity can raise only to an asymptote, we adjusted a logarithmic equation to the relationship between this index and the percentage of semi-permanent herbaceous vegetation each year (computed in relation to the total counted area), which changed mainly according to the land devoted to fallow. The resulting equation was then incorporated into the model, which allowed us to modify the input value of fecundity as a function of the percentage of semi-permanent herbaceous vegetation.

### 2.6. Modelling the effect of reducing illegal killing, car-crashing, overhead powerline collision or natural mortality on population viability

Marcelino et al. (2018) estimated that, in Iberia, the minimum

annual mortality rate attributable to natural factors was 8.7 %, to vehicle collisions 1 %, to illegal hunting 3 %, to collisions with power lines 3.4 %. This adds up to 16.1 % annual mortality rate, 54.1 % (i.e. 8.7/16.1) of which would be attributable to natural causes, 21.1 % to collisions with power lines, 18.6 % to illegal killing and 6.2 % to car-crashing. To estimate how a given theoretical perceptual reduction of any of these sources of mortality, derived from mitigation actions (from 0 to 100 % reduction), would reduce the total mortality rate, these values were multiplied by their above-mentioned share of mortality and subtracted from the initial mortality rate, to obtain the resulting estimated mortality rate after mitigation. This allowed us to analyse the effect of specified percentage reductions on individual mortality causes or combinations thereof on the finite rate of population growth. The latter calculations assume that all mortality causes are additive and that no compensation exists.

### 3. Results

#### 3.1. Estimated demographic parameters of the population

During the period 2005–2013, we recorded a total of 36 potential breeding opportunities from 25 different VHF and GPS tagged females, of which only 31 initiated laying, which gives an average ( $\pm$  SE) laying rate (LR) of  $0.8611 \pm 0.0576$ . Only 16 of these managed to hatch a brood, which gives an average ( $\pm$  SE) hatching rate (HR) of  $0.516 \pm 0.090$ . Only 8 of the initial broods managed to fledge at least one chick  $>30$  days old, which gives an average ( $\pm$  SE) fledging rate (FR) of  $0.500 \pm 0.129$ . The average ( $\pm$  SE) number of chicks per successful brood (FS) was  $1.500 \pm 0.177$ . The resulting average ( $\pm$  SE) fecundity value ( $f$ ) was  $0.333 \pm 0.111$ , with an interannual variance estimate of 0.0466 (CV = 64.8 %). The estimated male annual survival rate ( $\pm$  se) was  $S_M = 0.861$  (CI: 0.652–0.955;  $n = 20$ ) and the corresponding value for females was  $S_F = 0.672$  (CI: 0.478–0.821;  $n = 42$ ), with interannual variation coefficients of 4.1 % and 5.2 % respectively.

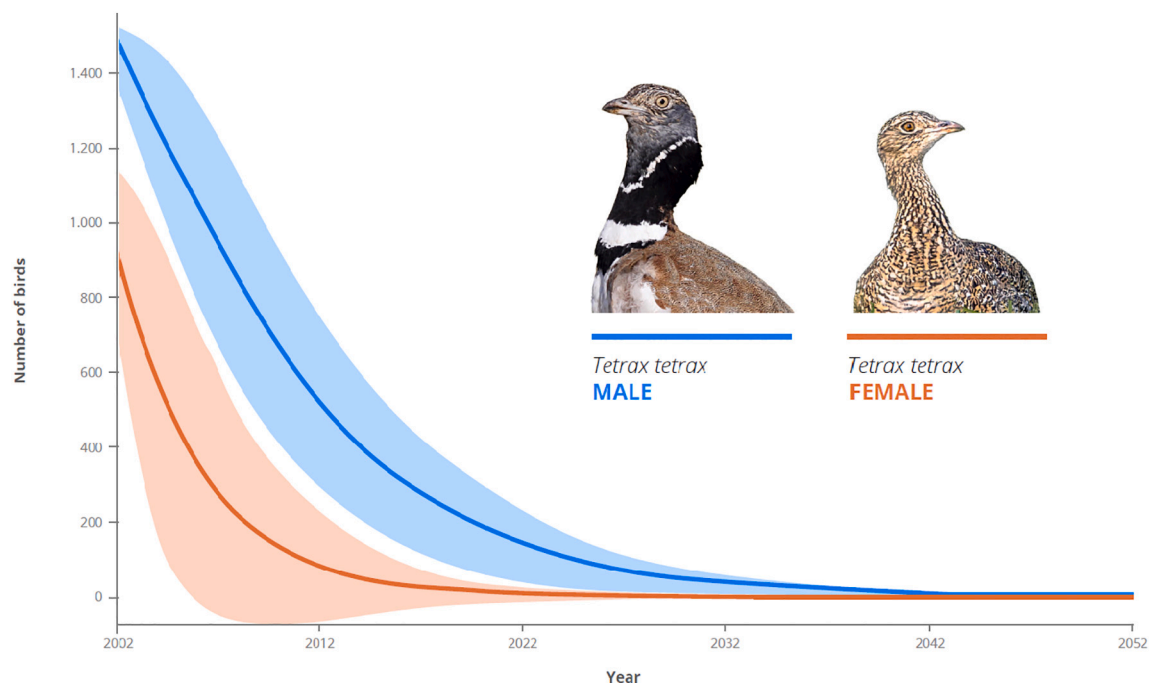
#### 3.2. Model output and sensitivity analysis

Considering the observed population parameters, the resulting stochastic growth rate of the little bustard population in the Lleida Plain was  $\lambda_s = 0.861$  (–13.8 % annual change). The simulation showed that the number of females declined sharply and became virtually zero even when relatively large numbers of males remained in the population (Fig. 2). According to the  $\lambda$ -isoline landscapes (Fig. 3), increasing male survival alone would not bring the population to stability, while increasing either female adult survival ( $S_F$ ) or fecundity ( $f$ ) alone would make it possible to balance the population. Increasing the number of chicks raised per female slightly over 1, or female survival over 0.88, would suffice. In both cases, however, these are relatively high values in comparison to the starting values (threefold increase in fecundity and 62 % reduction in mortality). A combined increase in female survival and fecundity at the same time would involve more realistic values. Increasing the number of fledglings per successful brood would not be enough to increase fecundity to the necessary level. Rather, this would require the proportion of females that produce a successful brood to be raised to  $\approx 0.65$ . Increasing the proportion of females that start laying would have negligible effect on  $\lambda$ .

#### 3.3. The effect of providing semi-permanent herbaceous vegetation or reducing mortality factors on the population balance

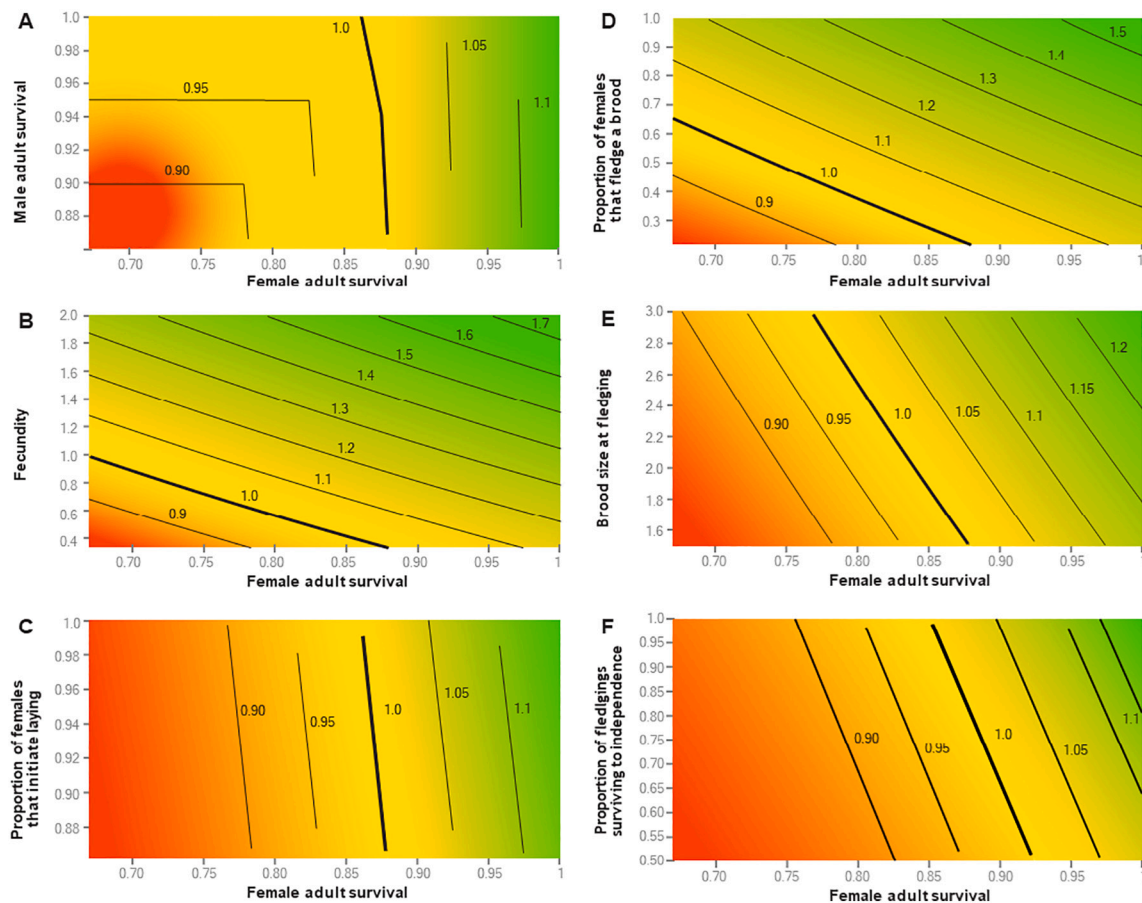
Increasing the percentage of semi-permanent herbaceous vegetation had significant effects on the number of successful broods, the mean size of those broods and the overall fecundity (Fig. 4). In the current low-female-survival scenario, a minimum of 20–22 % semi-permanent herbaceous vegetation land would be needed to stabilize the population (Fig. 5). However, this amount would be halved if female survival were raised to 0.75.

In the hypothetical absence of actions to increase breeding success, the required increase in female survival to bring the population to stability could not be achieved by acting on either natural mortality factors or anthropogenic mortality factors alone; only a combined reduction of



**Fig. 2.** Simulation of the population trajectory of the total number of mature males (blue) and mature females (orange) little bustards in the Lleida Plain. The estimates stem from the population model described in the text, starting with an initial population as estimated in the Lleida Plain in 2002 (1500 adult males and 835 mature females). Colour bands show 2-sigma intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)





**Fig. 3.** Isolines of finite rates of population increase ( $\lambda$ ) resulting from different combinations of female survival rate ( $S_F$ ) and several other demographic parameters: A) male adult survival ( $S_M$ ); B) fecundity ( $f$ ); C) the proportion of females that initiate laying (LR); D) the proportion of females that fledge a brood (LR·HR·FR); E) brood size at fledging (FS); and F) the proportion of fledglings surviving to independence ( $S_e$ ). In panels A–E the origin of coordinates is centred on the actual estimated parameter values. In panel F, the Y-axis is expanded below the current value.

both could lead to the necessary drop in the mortality rate (Fig. 6, top panel). When the combined action between specific mortality factors is analysed in more detail (Fig. 6, middle and bottom panels), we see that any conservation scenario based on mortality mitigation alone would require reducing natural mortality and, at least, either power line collisions or illegal killings, although reducing all of them at the same time seems a more efficient option (Fig. 6, top panel).

#### 4. Discussion

The aim of our research was to evaluate the efficiency of a land-sparing strategy in a cereal steppe area as a way of reverting the declining trend of a little bustard population, and to evaluate the potential effect of reducing different sorts of mortality factors. The theoretical population decline derived from our model (−13.8 % annual change), although slightly steeper, coincides with the estimated rate of decline for the species reported by the Common Bird Monitoring Program for the same area and period (−11 % annual rate between 2002 and 2021; ICO, 2022). It also coincides with the decline reported when comparing the national counts in 2002 and 2016 (García de la Morena et al., 2006, 2018). This indicates that the model can be used to make reasonable inferences about the population's dynamics and fate.

We found that increasing female survival and fecundity (mainly through improving breeding success) were, out of all the model's parameters, those that contributed most significantly to guaranteeing population stability. Not surprisingly for a polygynous bird, female survival was found to be much more important than male survival. In our case, this has important implications because female survival was

found to be much lower than that of males. Although no previous evidence for sex biased mortality in the little bustard existed (Inchausti and Bretagnolle, 2005; Marcelino et al., 2018), our results suggest that this might occur in our population, as in other western European areas where consistent male biased sex-ratios have been recently reported (Serrano-Davies et al., 2022). This results in the number of breeding females declining very quickly and becoming extinct well before males which, as a result of their relatively longer potential life span (Mañosa et al., 2019), may persist in the form of functionally extinct populations.

Previous demographic research has already stressed the high sensitivity of little bustard populations to low adult survival (Morales et al., 2005; Inchausti and Bretagnolle, 2005) and the high vulnerability of this species to human induced mortality factors (Marcelino et al., 2018; Silva et al., 2022a). However, the main conservation programs specifically addressed to preserve little bustard populations in Western France (Bretagnolle and Inchausti, 2005; Berthet et al., 2012; Berthet et al., 2017) or in the Lleida Plain in Catalonia (Mañosa et al., 2021) so far have aimed primarily to increase recruitment (by improving breeding success through habitat management or through captive breeding reinforcement), rather than adult survival (Traba et al., 2022a). This was because the values of adult survival required were considered to be unrealistically high (Inchausti and Bretagnolle, 2005; Morales et al., 2005) or because the mortality issues were more difficult to address. However, our model indicates that both breeding success and female survival are equally important to determining the fate of the populations. Ideally, both need to be improved at the same time, because working on improving only one of them would require achieving very high values of the managed parameter to obtain population

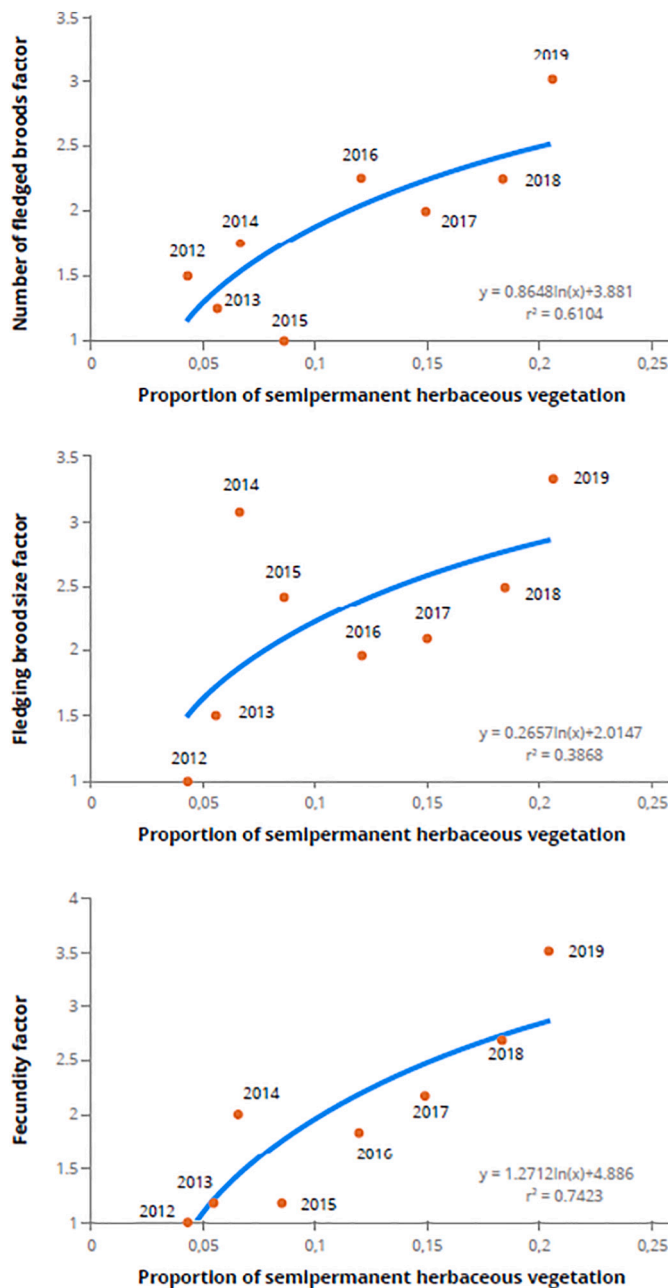


Fig. 4. Relationship between the percentage of semi-permanent herbaceous vegetation and the number of fledged broods (top panel), the mean size of the broods at fledging (middle panel) and overall fecundity (bottom panel). The Y-axis shows the relative factor increase of each parameter in relation to the lowest value, which takes the value of 1.

sustainability (female adult survival >0.88 or fecundity >1.0 chick/female). This suggests that the optimal approach would be to target female survival and fecundity at the same time, in a combined strategy where more sensible and realistic values of both parameters would suffice to obtain desired population outcomes.

The estimated value of female adult survival in our population is low yet similar to values previously reported (Inchausti and Bretagnolle, 2005; Marcelino et al., 2018). The models predict that raising female survival to values similar to those of males would suffice to balance the population. Interestingly, our analysis suggests that any strategy aiming to increase survival to this necessary level should include both the reduction of natural and anthropogenic mortality, because reducing just one of them would not suffice. Enforcing the law and increasing

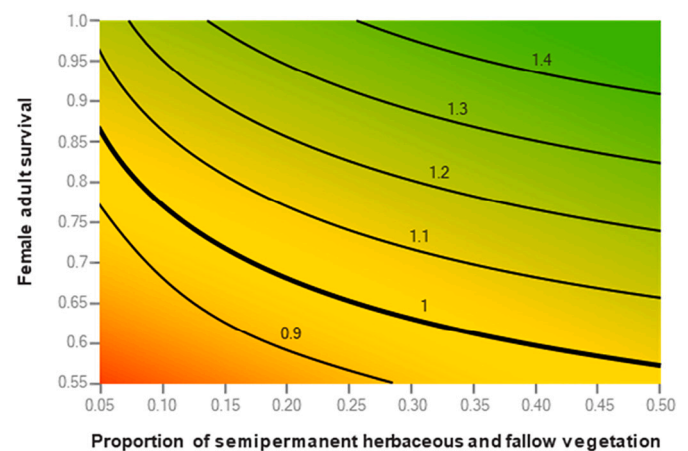
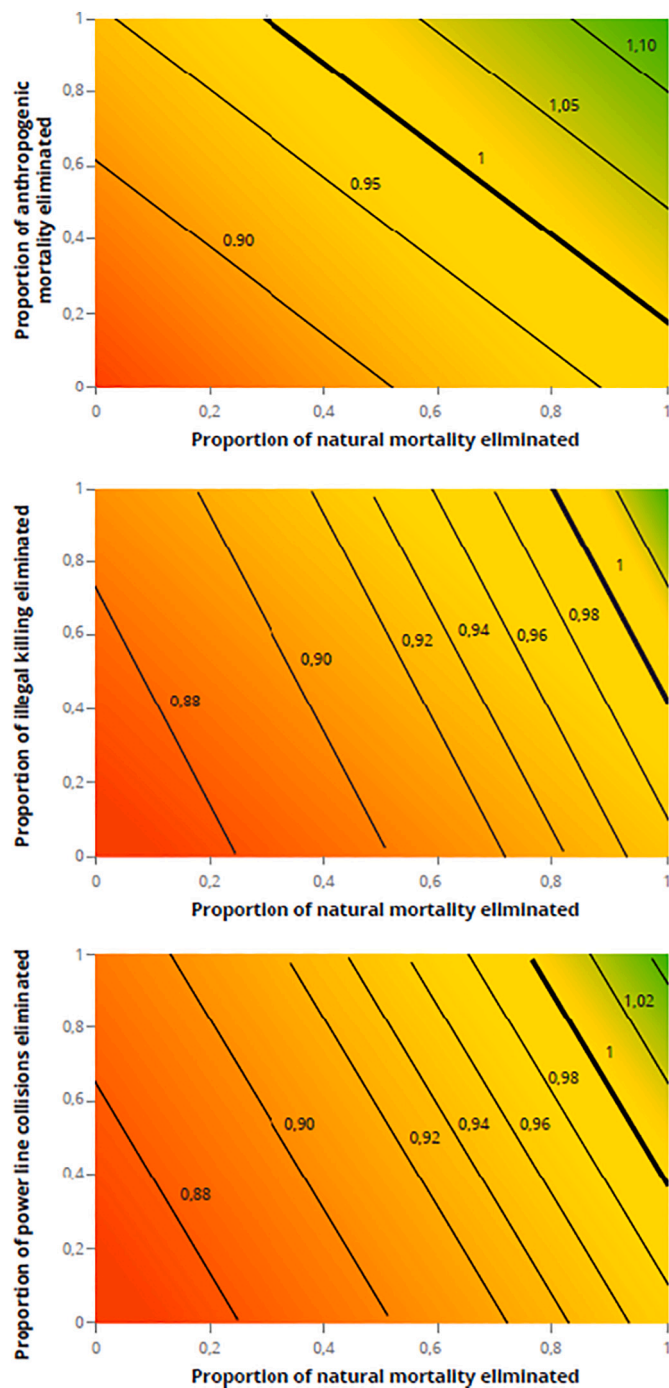


Fig. 5. Combined effect on the finite rate of population change ( $\lambda$ ) of the proportion of semi-permanent herbaceous and fallow land and adult female survival.

awareness and education among hunters would contribute to eliminating illegal killing, which occurs mainly outside the breeding season, on the summer or winter grounds, mostly outside protected areas (Traba et al., 2022a). Marking can eliminate 9–65 % of power line casualties (Barrientos et al., 2012; Marques et al., 2020), but only by grounding the dangerous lines would it be possible to eliminate this mortality factor (Silva et al., 2022b). The effect of natural mortality on the population is comparable to the effect of all the anthropogenic factors together. However, before being able to take actions to reduce it, more research is needed to understand how and when natural mortality occurs, including the relative importance of predation, climate, diseases or parasites. Measures to reduce mortality should involve not only the breeding areas, but also the non-breeding areas, where little bustards spend most of the year (Cuscó et al., 2018). These are highly productive yet very humanized areas, devoid of any protection (Traba et al., 2022a), and where little bustards are exposed to a high risk of predation, illegal killing or collision with vehicles or man-made structures. Unfortunately, it is often difficult to implement the necessary conservation measures to reduce mortality.

Based on the threshold value of 10–20 % of grassland needed to preserve grasshopper populations, Berthet et al. (2012) suggested that sparing 15 % of farmland as grassland, scattered across the landscape, would be enough to increase chick survival to preserve the little bustard population on Western France. Our modelling results, based on empirical data obtained in the Lleida Plain, supports this early suggestion, indicating that providing spared-land as managed fallow can have positive effects on the dynamics of the little bustard population, by directly affecting fecundity (probably by improving the female condition, laying frequency and relaying rates, as well as hatching success and chick survival).

We have no evidence that the fallow fields we provided acted as an ecological trap (Battin, 2004; Hale and Swearer, 2016). Such effect on farmland birds has been associated to linear habitats (Bro et al., 2004), very different to the large fallow fields in our program (Sanz-Pérez et al., 2019), usually grouped forming plots of several hectares. In our study area, female little bustards preferred fallow fields to nest (Cuscó et al., 2021b), and these fields were not moved or destroyed by farming practices. Moreover, we have no evidence that predation rates were higher in these fields. Nest predation by corvids decreases substantially when vegetation height > 30 cm (Bravo et al., 2022), which is below the average vegetation height where little bustard nest (Mañosa et al., 2021; Traba et al., 2022b). In France, such a trap effect has been reported (Bretagnolle et al., 2018), but it was associated to farming practices, not to predation. Finally, our empirical evidence indicates a positive global effect of fallow on breeding success, so any small reduction on hatching



**Fig. 6.** The effect on the finite rate of population change ( $\lambda$ ) of different combinations of reduced natural mortality and anthropogenic mortality factors. The possible paired combinations that do not bring the finite rate of increase  $>1$  are not shown.

success derived from an eventual ecological trap effect was probably cancelled by increased chick survival or landscape-scale positive effects (Hale et al., 2015). Although the current program for providing fallow fields did not take the spatial context into account, this topic is being currently addressed (Revilla-Martín et al., 2023), so that the efficiency of the measure can be improved in the future.

According to previous knowledge on the species's breeding biology (Lapiedra et al., 2011), the positive effect of fallow land availability on breeding success was an expected result. However, when working within the context of an adaptive management scenario (Walters, 1986; Keith

et al., 2011), involving policy makers, managers and researchers, we were able to monitor the results of the adopted land-sparing strategy and generate an empirical relationship between the management action and the population outcome. This resulted in a better understanding of the system and allowed us to evaluate the expected scopes and limits of the action. Moreover, an increased amount of fallow may have positive effects on other demographic parameters. In particular, fallow plots, especially if they are within SPAs and far from power lines, roads and hunting areas, may provide safe resting and feeding sites and contribute to increasing the female condition and survival, reducing predation risk and increasing young survival during the winter.

However, with a low female survival probability and relatively intensive cereal farming scenarios, a proportion of 20–22 % fallow land would be needed to obtain the necessary breeding success just to compensate for the high adult mortality reported. Although this value has already been attained under the Lleida Plain scheme (Mañosa et al., 2021), any further increase in mortality or random fluctuations in fecundity would imply significantly endangering the population. The necessary area of fallow land could probably be reduced if less intensive farming practices were adopted. Reducing the input of herbicides and fertilizers on crops, or the frequency of tillage, would help to increase food availability (weeds and arthropods) within the crop fields. The creation of conservation headlands -strips along the edges of cereal fields where herbicides, pesticides and fertilizers are only used selectively (Dicks et al., 2020)-, could be a sensible practice to achieve this objective. The restoration of field margins that have been eliminated as a result of plot concentration practices, would probably help to increase food availability within the fields (Vickery et al., 2009; Concepción et al., 2012; Fahrig et al., 2015; Alignier et al., 2019) and provide fundamental thermal microrefugia for little bustards in summer (Ramos et al., 2023). Finally, delaying harvest after the third week of June, when most first and second clutches have had the opportunity to hatch, would provide safe nesting cover from mid-April to mid-June and good brood-rearing cover from mid-May to the end of July (Cuscó et al., 2021b).

The land-sparing strategy adopted so far in the Lleida Plain seems capable of increasing fecundity to the necessary level for population stability. However, its ability to counteract any further reduction in survival is limited. First because, if survival is reduced, the proportional increase of fallow land required to maintain the population at balance is disproportionately much higher (Fig. 5). Secondly, because removing increasing amounts of land from farming would involve increasing budgets for leasing and managing, which may not be sustainable in the long term (Cardador et al., 2014). And, finally, because farmers may not accept more land being set aside, as they depend on enough land for their activity to be economically sustainable. Reducing mortality (either natural or anthropogenic) would significantly reduce the amount of fallow needed to achieve population stability and is associated budget and social costs. Therefore, the combined strategy of improving breeding success by land sparing, on one hand, and reducing mortality on the other, seems to offer several advantages when compared to strategies focusing only on one these actions. Firstly, it allows adapting to environmental or even political uncertainties that may unpredictably limit the viability of each of the individual strategies (i.e. Morales et al., 2022). Secondly, it allows for a more sensible distribution of conservation effort among stakeholders (in this case, farmers to provide fallow land to increase productivity and powerline industries to mark or bury the lines to reduce mortality). Thirdly, while setting land aside requires a recurrent annual budget, actions to reduce mortality, although initially difficult or expensive (Silva et al., 2022b), are permanent measures that does not involve this recurrent investment.

## 5. Conclusions

The adaptive management approach, involving policy makers, researchers and farmers, as well as continuous monitoring and modelling, allowed us to set up an ambitious land-sparing scheme in Catalonia



(Mañosa et al., 2021). According to information currently available, it seems to have significant potential to achieve stable finite rates of increase in a farmland little bustard population. However, in the current scenarios of low female survival and intensive cereal farming, the necessary amount of fallow land needed would be relatively high and potentially unsustainable in the long term. The necessary area of fallow land, and the associated budget, could be reduced substantially only if female survival is raised, by eliminating illegal killing, power line casualties and natural mortality. Strategies focusing on one management action alone may be subject to socio-economic and political constraints that may put the global strategy at risk. Consequently, we advocate for a polyhedral strategy, based on the implementation of a land-sparing scheme combined with land-sharing practices (preserving or restoring of natural and seminatural features within the agricultural landscape, using less intensive farming practices) and alongside the reduction of mortality factors. Anthropogenic and natural mortality have similarly significant effects on reducing female survival and both need to be tackled if little bustard populations are to be preserved for the future generations. Our results confirm that the adaptive management approach, simultaneously considering and modelling several processes involved in population decline, even with limited information, can prove very useful for evaluating the effectiveness and limitations of conservation decisions and for providing guidelines on conservation projects. This can enhance conservation practice and create realistic scenarios for success both in terms of ecological outcomes and the balanced distribution of conservation efforts among stakeholders.

### Funding information

This research was funded by the Ministry of Science and Technology (CGL2004-06147-C02-01/BOS), the Ministry of Science and Innovation (CGL2009-13029/BOS), REGSEGA, Infraestructures de la Generalitat de Catalunya, and Departament de Recerca i Universitats de la Generalitat de Catalunya (2021-SGR 00302).

### CRediT authorship contribution statement

**Santi Mañosa:** Conceptualization, Methodology, Data curation, Formal analysis, Funding acquisition, Writing – original draft, Writing – review & editing. **Gerard Bota:** Conceptualization, Methodology, Data curation, Funding acquisition, Writing – review & editing.

### Declaration of competing interest

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

### Data availability

Data will be made available on request.

### Acknowledgements

This study is based on the information obtained in the course of many research projects, in which many people has been involved either directly or indirectly. We are grateful to Anna Ponjoan, Oriol Lapiedra, Francesc Cuscó, Roger Guillem and Carlos Santiesteban, among others, for their contributions to different parts of the work, and to Antonio Hernández-Matías for help with survival estimates and R scripts. Gerald Puig edited and improved the presentation of the figures. We also thank the editor and an anonymous reviewer for their constructive comments on an early version of the manuscript, and Jackie Morrow for the final style and grammar correction. We would especially like to thank Teresa Fainé, from Infraestructures de la Generalitat de Catalunya, for her support and for believing in the need to do this work, and also Carme

Bernat, from Aigües Segarra Garrigues (ASG), for managing and making the fallow scheme a reality. We also thank the Fundació Bosch i Gimpera for taking some of the administrative tasks involved in the project.

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