



Research article

Using spatially explicit individual-based models to prioritize conservation strategies: A case study on the little bustard



Tiago Crispim-Mendes^{a,b,c,d,*}, Ana Teresa Marques^{b,c,d}, Francesco Valerio^{a,b,c},
Sérgio Godinho^a, Ricardo Pita^a, João Paulo Silva^{b,c,d,e}

^a MED – Mediterranean Institute for Agriculture, Environment, and Development, CHANGE – Global Change and Sustainability Institute, Institute for Advanced Studies and Research, Universidade de Évora, Pólo da Mitra, Ap. 94, 7006-554, Évora, Portugal

^b CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661, Vairão, Portugal

^c BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661, Vairão, Portugal

^d CIBIO – Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, 1349-017, Lisboa, Portugal

^e Estação Biológica de Mértola (EBM), Rua Baptista da Graça 1, 7750-329, Mértola, Portugal

ARTICLE INFO

Keywords:

Anthropogenic mortality

Cost-effective

Management

Movement ecology

Tetrax tetrax

ABSTRACT

Steppe birds are among the most threatened terrestrial birds worldwide, requiring urgent, well-planned, and cost-effective conservation strategies to halt population declines. The little bustard (*Tetrax tetrax*) is one of those species that has experienced sharp population declines across its western range, yet the effectiveness of different management interventions remains poorly understood. Predictive models, such as Individual-Based Models (IBM), provide powerful tools to anticipate and assess the effectiveness of conservation scenarios for endangered species, supporting evidence-based management decisions.

In this study, we developed a spatially explicit demographic IBM to evaluate conservation strategies for the little bustard in Extremadura, Spain, where the species faces a skewed sex ratio towards males, habitat degradation and high anthropogenic mortality. Our model integrates high-resolution habitat suitability data with demographic parameters to simulate individual behaviours and interactions with the environment, forecasting habitat use and population dynamics under different management strategies.

The model calibration process supported the hypothesis that nest, chick, and adult survival positively correlate with habitat suitability. Notably, our results suggest that the unbalanced sex ratio is partially driven by low female survival rates in less favourable habitats. We simulated conservation strategies focused on habitat improvement and the mitigation of anthropogenic mortality over 50 years (2022–2072). The results indicate that habitat enhancements alone are insufficient to reverse population declines without complementary efforts to reduce anthropogenic mortality. This finding emphasizes the need for an integrated, long-term conservation strategy that combines habitat management with proactive measures to mitigate human-induced mortality, ensuring the sustainable recovery of little bustard populations.

More broadly, this study highlights the value of IBMs as high-resolution, spatially explicit decision-support tools for conservation planning, offering critical insights into prioritizing and implementing cost-effective strategies.

1. Introduction

Biodiversity is currently facing substantial declines worldwide, primarily driven by both human-induced environmental changes and

climate change, which severely disrupt species distribution and abundance (Díaz et al., 2019; Lees et al., 2022). In particular, anthropogenic activities such as agriculture, urbanization, and infrastructure expansion are driving habitat loss and degradation, representing key threats to

* Corresponding author. MED – Mediterranean Institute for Agriculture, Environment, and Development & CHANGE – Global Change and Sustainability Institute, Institute for Advanced Studies and Research, Universidade de Évora, Pólo da Mitra, Ap. 94, 7006-554, Évora, Portugal.

E-mail address: tfc@uevora.pt (T. Crispim-Mendes).

<https://doi.org/10.1016/j.jenvman.2025.124790>

Received 18 November 2024; Received in revised form 1 March 2025; Accepted 1 March 2025

Available online 6 March 2025

0301-4797/© 2025 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

biodiversity (Powers and Jetz, 2019). Moreover, the increasing frequency and intensity of hazardous events, including droughts and heat waves, not only directly stress species but also degrade ecosystems, thereby further accelerating biodiversity loss and triggering climate change-induced range shifts (Synes et al., 2020; Valjarević, 2024). Consequently, effective conservation strategies are imperative for mitigating these threats and sustaining both species and ecosystems (Zurell et al., 2022). However, limited time and financial resources often constrain conservation efforts (McCarthy et al., 2012), requiring targeted, precise, and well-founded methods to maximize positive outcomes (Wintle et al., 2011). This requires identifying priority areas for conservation and accurately assessing the level of intervention needed to reverse species decline, thereby optimizing resource allocation and enhancing conservation effectiveness (Gann et al., 2019).

Identifying the most cost-effective conservation actions requires a comprehensive understanding of spatiotemporal patterns in wildlife population distribution and abundance, which is essential to better anticipate the impacts of conservation interventions (Guisan et al., 2013; Zurell et al., 2022). Although long-term field experiments are typically required to test optimal solutions, such experiments are often unfeasible for species experiencing rapid population declines that demand immediate conservation action. In this context, predictive models that leverage the existing scientific knowledge of target species provide a timely and cost-effective alternative to traditional, field-based approaches (Cook et al., 2010; Pollock et al., 2020). Predictive modelling, and particularly Individual-Based Models (IBMs), can significantly contribute at all stages of conservation planning, from problem framing and intervention design to implementation and impact evaluation (Travers et al., 2019). Such tools are essential for quickly evaluating and prioritizing alternative management strategies (DeAngelis and Diaz, 2019; Seaborn et al., 2023).

IBMs are particularly valuable tools as they can forecast population responses to different management strategies and help prioritize conservation actions (DeAngelis and Diaz, 2019; Seaborn et al., 2023). Unlike conventional approaches, these models embrace the complexity of ecological systems by integrating individual heterogeneity with environmental dynamics, thereby enabling forecasts of population responses to management scenarios with unprecedented precision (McLane et al., 2011; Railsback and Grimm, 2019). By adopting a bottom-up approach, IBMs simulate the behaviour and interactions between individuals and their environment, which drive emergent patterns and dynamics (Grimm and Railsback, 2005; Stillman et al., 2015). Despite their immense potential, the widespread adoption of IBMs in conservation is often constrained by challenges such as data scarcity, model complexity, and high computational demands, limiting their broader adoption (An et al., 2021; Gray et al., 2023). These limitations can hinder model precision, especially when comprehensive behavioural and environmental data are lacking. However, recent advances in animal tracking, remote sensing, and computational power are gradually overcoming these obstacles (Regos et al., 2022; Ustin and Middleton, 2021; Vedder et al., 2021). In parallel, the development of standardized frameworks such as the ODD protocol (Grimm et al., 2006, 2010, 2020) and specialized tools for calibrating and evaluating complex IBMs with multiple data sources (e.g. Salecker et al., 2019) have further strengthened the reliability and robustness of model outcomes. These advances have led to the progressive adoption of these models as conservation support tools, ranging from the management of endangered mega-herbivores (Boult et al., 2018) and bird species (Drenske et al., 2023; Heinrichs et al., 2018) to freshwater fish populations (Ayllón et al., 2016; Galic et al., 2023) and invasive predators (Hradsky et al., 2019).

Grassland birds are among the most endangered terrestrial vertebrates in Europe, primarily due to habitat transformations resulting from intensified agriculture and livestock practices (BirdLife International, 2022; Lees et al., 2022). In particular, the Iberian Peninsula represents a crucial stronghold for numerous grassland bird species,

many of which exhibit unfavourable conservation status (Traba and Morales, 2019). Among these species, the little bustard (*Tetrax tetrax*) stands out due to its dramatic population decline in recent decades, primarily caused by habitat loss (Morales and Bretagnolle, 2022). As a result, the species has been classified as Vulnerable at the European level (BirdLife International, 2021). Similar to other Iberian populations, the little bustard has faced a concerning decline in the Extremadura region over the last decades (García de la Morena et al., 2006, 2018). This decline is coupled with low breeding success, skewed male-biased sex ratios (Serrano-Davies et al., 2023), and elevated adult mortality rates from anthropogenic sources, including illegal hunting, roadkill, and notably power line collisions, recognised as the leading cause of "non-natural" mortality (Marcelino et al., 2018). These challenges underscore the urgency of conservation efforts to safeguard the little bustard population and its critical habitats.

Stochastic population models have previously been developed to test the viability of the French little bustard population (Inchausti and Bretagnolle, 2005; Morales et al., 2005a) and to evaluate the effects of population reinforcement (Bretagnolle and Inchausti, 2005). More recently, this modelling approach has been applied to assess the effectiveness of a land-sparing strategy in preserving the species in Catalonia, Spain (Mañosa and Bota, 2023). However, none of these models incorporate detailed individual behaviour throughout the annual cycle or account for spatially explicit and dynamic landscape features, thereby limiting their spatial context.

In this study, we aimed to develop a management support tool to identify conservation strategies to halt the decline and rehabilitate the little bustard populations within an important conservation area for the species: the region of Extremadura (SW Spain). Using an IBM, we simulated individual behaviours and their interactions with the environment to forecast habitat use and population dynamics under different management strategies, assessing their potential impacts on the population. Specifically, our key objectives were: 1) to develop and evaluate a high-resolution, spatial-explicit IBM tailored to the little bustard population of the Extremadura region; and 2) to assess the model's potential and usefulness in informing cost-effective conservation plans for the species, with a particular focus on mitigating anthropogenic mortality and enhancing habitat suitability in selected locations over a 50-year timeframe (2022–2072).

The model developed in this study represents a major advancement in conservation planning for the little bustard in Extremadura and beyond, featuring unprecedented high spatio-temporal resolution, full annual cycle coverage, and a detailed representation of individual behaviour. Moreover, it serves as a powerful tool for assessing the impact of anthropogenic threats, supporting more effective, evidence-based management strategies.

2. Methods

2.1. Study area and study species

The Extremadura region is an autonomous administrative entity with authority over biodiversity management, functioning as an integrated management unit. It is subdivided into two provinces: Badajoz in the south, and Cáceres in the north. The region is characterized by a meso-Mediterranean climate, with warm, dry summers and cold, humid winters, based on 30 years of climate data (Rivas-Martínez et al., 2002). The landscape is heterogeneous and fragmented, predominantly characterised by livestock and agricultural activities. Despite the designation of several Special Protection Areas (SPAs), the little bustard has experienced an alarming population decline over the last decades (García de la Morena et al., 2006, 2018; Traba et al., 2022). Between 2016 and 2022, the density of breeding males declined by approximately 65%, resulting in an overall decrease of about 80% compared to 2005 (Silva et al., 2024). This represents an increase in the annual decline rate of male densities from 5% between 2005 and 2016 to 11% between 2016

and 2022.

The little bustard is a medium-sized steppe bird that inhabits natural steppes as well as agricultural landscapes (Morales and Bretagnolle, 2022). In Western Europe, it primarily occupies dry farmland with varying levels of agricultural intensification, from extensive landscapes with long-term fallows and pastures to highly intensive farmland dominated by cereals and irrigated crops (Traba et al., 2022). The species exhibits polygynous behaviour, employing an “exploded-lek” mating system in which only females provide parental care (Jiguet et al., 2000). Its annual cycle comprises three distinct phenological phases – breeding, post-breeding, and winter – characterized by territorial behaviours and lek formations during the breeding phase, and gregarious behaviour during the other phases (Faria and Silva, 2010; Silva et al., 2004, 2007).

The Iberian population displays partial migration, with some individuals being strictly sedentary and others exhibiting various migratory patterns influenced by factors such as food availability and environmental conditions (Traba and Morales, 2019). Migration movements are synchronized with the species’ phenological phases, involving regular migrations with varying timing and spatial range, and a strong philopatric tendency (Alonso et al., 2019; García de la Morena et al., 2015). However, when habitat conditions change, males may slightly adjust their locations to find optimal habitats that meet their requirements (Delgado et al., 2010; Morales et al., 2005b). Male little bustards predominantly undertake migratory movements in June/July, immediately following the breeding season, during the Iberian summer, when temperatures peak and vegetation becomes particularly dry (García de la Morena et al., 2015; Silva et al., 2007). While breeding females are still solely rearing their chicks, breeding males and other non-breeding individuals begin flocking in post-breeding areas (Silva et al., 2014). Females and their chicks join these flocks once the chicks are capable of flight. In wintering quarters, flocks grow in size, accommodating migrants from different breeding populations (Silva et al., 2004).

In Western European little bustard populations, there is compelling evidence of low breeding success and a male-biased sex ratio (Serrano-Davies et al., 2023). As a lekking species with no male parental care, the number of breeding events is constrained by the number of breeding females, making population viability highly sensitive to female shortages (Jiguet et al., 2000).

2.2. Model overview

We developed an Individual-Based Modelling (IBM) framework using NetLogo 6.3.0 (Tisue and Wilensky, 2004; Wilensky, 1999) to simulate a real-world scenario for the little bustard in Extremadura. In the Supplementary Material (Appendix A), we provide a TRACE document (“TRANSPARENT and Comprehensive model Evaluation”; Augusiak et al., 2014; Grimm et al., 2014; Schmolke et al., 2010) demonstrating that our model was carefully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose. A complete, detailed model description, following the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006, 2010, 2020), is provided in Section 2 (“Model description”) of the TRACE document (Appendix A). The code for our model is accessible at: https://github.com/TCrispimMendes/IBM_Decision-Support_Tool_for_Little_Bustard_in_Extremadura.

Below, we present a brief overview of the model’s structure and processes, as recommended by Grimm et al. (2020). All simulations for calibrating, validating, and analysing the model were performed using the “nlrx” package (Salecker et al., 2019) in R (version 4.1.1, R Core Team, 2021).

We simulated various scenarios with diverse conservation management approaches, including adjusting the extent and location of intervention areas to enhance habitat suitability and incorporating varying levels of mitigation for anthropogenic mortality. To ensure model

realism, we considered patterns of phenology, age structure, socio-spatial organization, reproduction, survival, migration, and dispersal. We assessed the model performance based on its ability to replicate the species’ demographic patterns in Extremadura from 2005 to 2022 (see Sections 2.7.8, 3 and 8 in Appendix A, for detailed information).

The model incorporates different entities, including habitat cells, several entities related to little bustards, categorized as males, females, their nests, and flocks, as well as a global environment entity (“Observer” in NetLogo). Females and males are modelled separately due to their differences in behavioural traits and survival rates during the breeding phase (Jiguet and Bretagnolle, 2014; Morales et al., 2008; Serrano-Davies et al., 2023). By explicitly modelling nests and flocks, the model provides a more accurate representation of processes linked to nest failure and group dynamics during the gregarious phenological phases, respectively. The state variables characterizing these entities are detailed in Table 1.

Spatially, the model represents the Extremadura region at a

Table 1

List of entities intervening in the model, with their state variables and corresponding status or measure unit.

Entity/State Variable	Description	Variable type (possible values)
Habitat cells		
location	Cell location	Numeric (spatial coordinates)
HS	Current habitat suitability value of the cell	Numeric (decimal between 0 and 1)
occupants	Current number of occupants of the cell	Numeric (integer)
intervened	Indicates whether a habitat cell had a habitat improvement intervention	Boolean (True; False)
Male little bustards		
ID	Unique identification code	Numeric (integer)
location	Location in the local patch	Numeric (spatial coordinates)
age	Age	Numeric (weeks)
migration_pattern	Migration pattern	Categorical (See Section 3.1 in Appendix A for details)
breed_local	Breeding location	Numeric (spatial coordinates)
post-breed_local	Post-breeding location	Numeric (spatial coordinates)
wint_local	Wintering location	Numeric (spatial coordinates)
Female little bustards		
ID	Unique identification code	Numeric (integer)
location	Location in the local patch	Numeric (spatial coordinates)
age	Age	Numeric (weeks)
migration_pattern	Migration pattern	Categorical (See Section 3.1 in Appendix A for details)
breed_local	Breeding location	Numeric (spatial coordinates)
post-breed_local	Post-breeding location	Numeric (spatial coordinates)
wint_local	Wintering location	Numeric (spatial coordinates)
nest_tries	Number of nest attempts	Numeric (integer)
Nests		
female	Female’s ID	Numeric (integer)
Flocks		
size	Number of individuals within the flock	Numeric (integer)
Global environment		
date	Date in current time-step	Date (day/month/year)
phenological_phase	Current phenological phase	Categorical (“breeding”; “migration_post-breeding”; “post-breeding”; “migration_winter”; “winter”; “migration_breeding”)
nesting_prob	Current nesting probability	Numeric (decimal between 0 and 1)
migration_prob	Current migration probability	Numeric (decimal between 0 and 1)

resolution of 250×250 m, comprising 1004×1128 square cells. Temporally, the model operates on a weekly time step, simulating the little bustard's distinct phenological phases and associated behavioural traits throughout the yearly cycle. The choice of this spatio-temporal resolution is justified by the need to accurately capture the fine-scale habitat preferences and movement patterns of the little bustard, enabling the realistic depiction of habitat utilization, as well as critical life-history events such as breeding and migration dynamics. The model's time horizon is divided into two phases. The first phase, the implementation phase (01-04-2005 to 01-04-2022), spans 17 years and was dedicated to calibration, sensitivity analysis, and validation. This period was chosen as it encompasses the species' national censuses of 2005 (García de la Morena et al., 2006) and 2016 (García de la Morena et al., 2018), as well as the regional census of 2022 (SEO, in prep), ensuring sufficient data for robust model calibration and validation. The second phase, the main experiment phase (01-04-2022 to 01-04-2072), extends over 50 years and simulates population dynamics under different conservation management scenarios, using the model's 2022 population estimates as the starting point.

The key processes driving the model are linked to specific behaviours and life-history events of the species. These processes are executed according to the phenological phase of the simulation (Fig. 1), which is updated at each simulation step alongside the corresponding changes in habitat suitability values. Migration and mating probabilities are adjusted during the migration and breeding phases, and reproductive states are updated at the beginning of the breeding phase. The reproductive process consists of two main phases: nesting and hatching. During the nesting phase, breeding females construct a nest, which, if successful, leads to the hatching of chicks three weeks later. During the migration phase, which occurs between phenological phases, individuals migrate to the same location where they spent the corresponding phase in the previous year, making slight adjustments based on changes in habitat suitability and spatial distribution of other individuals. The distances between the locations during different phenological phases vary based on each individual's migration pattern, which

is defined at the beginning of the simulation and remains unchanged throughout the simulation (data derived from GPS tracking; see Table S.3.2 and Section 3.1 in Appendix A for details). Additionally, during the migration phase to the breeding grounds, individuals may disperse to a new breeding location (see Table 2 and Section 3.1 in Appendix A). Survival probabilities at each time step differ among groups of individuals or agents, including nests, chicks, adults, and breeding females (Fig. 2 and see Section 2.7.7 in Appendix A).

The model incorporates several key design concepts to ensure the necessary realism and complexity for its intended purpose. The most important concepts pertain to phenology representation, socio-spatial organization, and the relationship between key demographic parameters of individuals and habitat suitability. Regarding phenology representation, the model recreates the little bustard's annual cycle and population dynamics based on decision rules that reflect the species' complex behaviours across its phenological phases (breeding, post-breeding, and winter), including migration periods. The annual cycle is thus temporally segmented to align with the different phenological phases, each characterized by phase-specific habitat suitability. This is achieved by incorporating high-resolution suitability maps (250×250 m) for each phenological phase, derived from annual predictions generated by species distribution models (SDMs) developed by Crispim-Mendes et al. (2024). Habitat cells are characterized by a suitability value, calculated from the mean suitability of surrounding cells within a variable-sized buffer for each phase. This approach accounts for the average home range size of individuals in each phenological phase, effectively eliminating the challenge of incorporating small-scale movements, as cells act as the centroids of individual home ranges. This dynamic habitat characterization is crucial for guiding socio-spatial organization and migration movements, as well as reproduction and survival.

Regarding socio-spatial organization, the model is grounded on the "exploded-lek" mating system described for the species (Jiguet and Bretagnolle, 2014; Morales et al., 2014). During the breeding phase, the model enforces territoriality, allowing only one individual per habitat

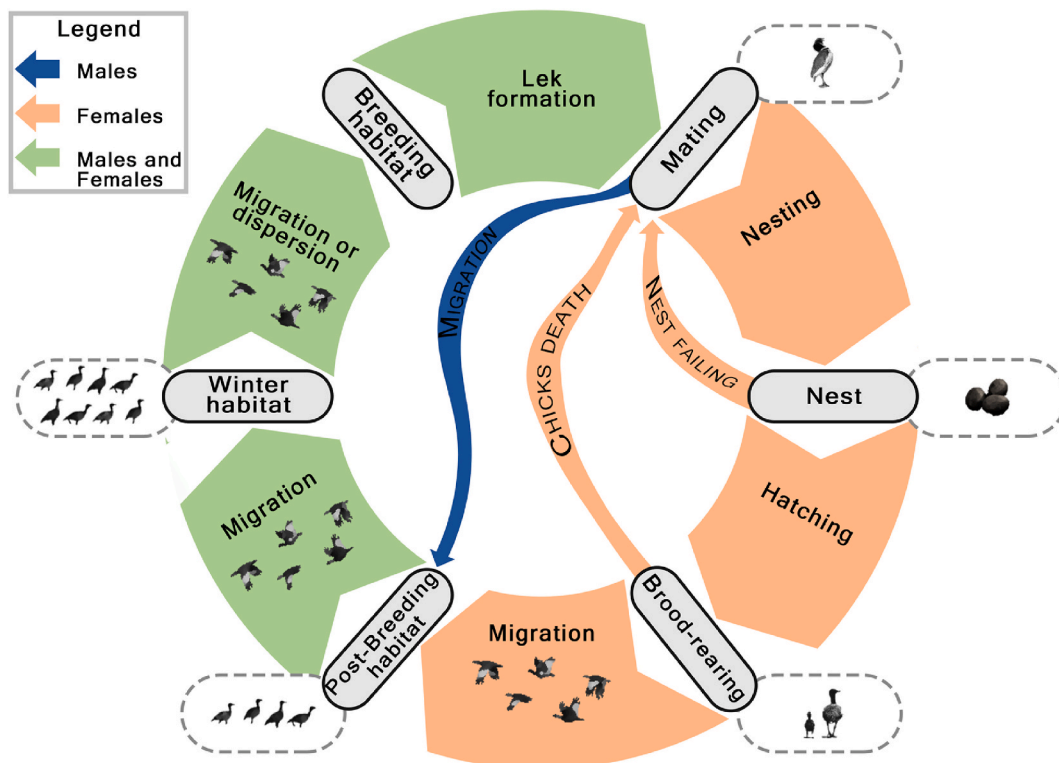


Fig. 1. Flow diagram illustrating the yearly-cycle processes incorporated in the model.

Table 2

Summary of parameter information used in the IBM, including value ranges and sources, indicating whether they were derived from the literature or calibrated. Seasonal parameters are categorized as B – Breeding; PB – Post-Breeding; W – Winter.

Parameter	Values	Source
Initialization		
Suitability maps	0–1	Crispim-Mendes et al. (2024)
Minimum suitability	B – 0.33	Calculated (see Section 3.2 in Appendix A)
threshold	PB – 0.29	
LB Densities in 2005 by suitability	W – 0.28	
LB Sex-ratio in 2005	Logarithmic regression	Calculated based on Crispim-Mendes et al. (2024); García de la Morena et al. (2006) (Section 3.3 in Appendix A)
LB Age distribution	0.716 females/male	García de la Morena et al. (2006)
	Stable age distribution	Calculated (see Section 3.4 in Appendix A)
Home range		
Home range radius	B – 745 m	Silva et al. (2024)
	PB – 1.339 m	
	W – 1.726 m	
Reproduction		
% Non-breeding females	18%	Calibrated (see Section 6 in Appendix A)
Brood-size	2.11 ± 0.85 chicks	Bretagnolle et al. (2018)
Probability of clutch replacement	1st clutch – 67%	Cuscó et al. (2021)
	2nd clutch – 57%	
Survival		
Nests' survival	Logarithmic regression	Calibrated (see Section 6 in Appendix A)
Chicks' survival	Logarithmic regression	Calibrated (see Section 6 in Appendix A)
Breeding females' survival	Logarithmic regression	Calibrated (see Section 6 in Appendix A)
Adults' survival	Logarithmic regression	Calibrated (see Section 6 in Appendix A)
Annual anthropogenic mortality	17.7 %	Silva et al. (2024)
Migration and dispersal		
Migration pattern percentages	("SD"; "MDS"; "MDSW"; "LDSA"; "LDSB"; "LDSW")	Silva et al. (2024) (see Section 3.1 in Appendix A)
Migration distances	Dependent on migration pattern and phenological phase	Silva et al. (2024) (see Section 3.1 in Appendix A)
Dispersal distances	51.67 ± 19.41 km	Silva et al. (2024)
Chicks' migration age	8 weeks	Guesstimated based on Silva et al. (2024) and Bretagnolle et al. (2022)
Flocks		
Conspecific attraction radius	PB – 1500 m	Calibrated (see Section 6 in Appendix A)
Maximum flock size	W – 2750 m	
	PB – 100	Guesstimated based on Morales et al. (2022) and Silva et al. (2024)
	W – 300	

cell (250 × 250 m). In contrast, gregarious behaviour emerges during the other phenological phases, where the species forms flocks, based on predefined flock-search radii (see Table 2 and Section 2.7.5 in Appendix A). The inclusion of different proportions of migration patterns identified in the Extremadura region (including intra-regional movements and dispersal beyond Extremadura, see Table 2 and Section 3.1 in Appendix A), along with adaptive traits related to habitat selection and response to changes in suitability (e.g. Crispim-Mendes et al., 2024), enhances the model's realism in representing spatial resource use variability throughout the annual cycle.

Habitat suitability directly impacts breeding success (in females) and individual survival, as the model assumes that higher habitat suitability positively affects nest success and survival rates. The model applies

distinct survival rates for chicks and adults, as well as for breeding females and other adults during the breeding and chick-rearing phases. These differences are supported by empirical observations of sex ratio imbalances in populations inhabiting degraded locations (Serrano-Davies et al., 2023). The relationship between agents and habitat suitability is supported by the variables included in the SDMs, which are expected to correlate with survival probability. These variables encompass topography and vegetation characteristics known to influence food availability and exposure to predation. By incorporating these ecological factors, the model enhances realism, allowing population dynamics to respond directly and emergently to habitat quality changes, whether driven by natural variability (intra- and inter-annual fluctuations) or anthropogenic impacts (habitat degradation or improvement). Together, these design principles establish a solid scientific framework for modelling the behaviour and population dynamics of little bustards in Extremadura, fully aligning with the model's conservation objectives.

2.3. Model development

2.3.1. Calibration

During model development, we calibrated parameters with limited empirical support, including the percentage of non-breeding females and the conspecific attraction radius during post-breeding and winter phases (see Table 2). Additionally, we inferred the relationship between survival at different life stages and habitat suitability using Logarithmic Regression. This required calibrating parameters A and B in the equation:

$$\text{Weekly Survival} = A + B \ln(\text{Habitat Suitability})$$

Where A represents the survival probability under optimal habitat suitability conditions (habitat suitability = 1), and B determines the slope of the curve, reflecting the strength of the correlation between survival and habitat suitability.

For the calibration process, we employed the rejection Approximate Bayesian Computation (ABC) algorithm (Beaumont et al., 2002; van der Vaart et al., 2015), which is particularly well-suited for complex models like IBMs (Beaumont, 2010). For further details, see Section 6 in Appendix A.

2.3.2. Sensitivity-analyses

We conducted a local sensitivity analysis using the Morris screening method (Morris, 1991), which applies an individually randomized one-factor-at-a-time design to estimate the impact of parameter variations on model outputs. This method was applied to assess the model's response to variations in both literature-derived (five parameters) and calibrated parameters (11 parameters). Input parameters were varied by ±10% from their default values, with 100 trajectories computed per parameter to ensure robust sensitivity estimates. Although this method does not enable a quantitative evaluation of the relative significance of inputs with respect to one another, it effectively identifies the most sensitive parameters by assessing their overall impact on model output (μ^*) and by detecting linear, additive, or nonlinear effects, as well as interactions among parameters (σ) (Campolongo et al., 2007; Morris, 1991; Thiele et al., 2014). This level of analysis provides sufficient insight to fulfil the objectives of this study. For further details, see Section 7 in Appendix A.

2.3.3. Validation

We validated the model against demographic data from the Extremadura region and other Iberian and French populations. Specifically, we compared model outputs from 100 simulation runs against male abundance estimates in the provinces of Cáceres and Badajoz, based on the 2016 national census (García de la Morena et al., 2018) and the 2022 regional census (SEO, in prep). Additionally, we validated

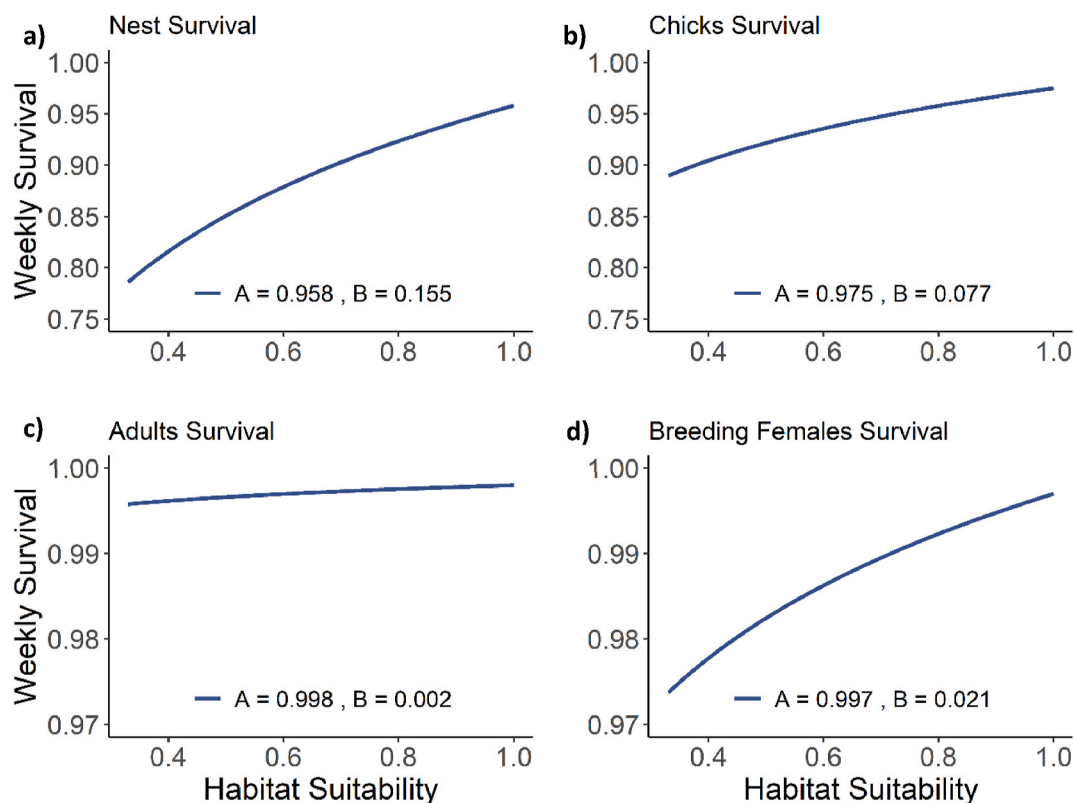


Fig. 2. Calibrated survival curves for different life stages of the little bustard as a function of habitat suitability, derived from logarithmic regression: $\text{Weekly Survival} = A + B \ln(\text{Habitat Suitability})$. The parameters A and B represent the mean values of the posterior distributions obtained through the rejection-ABC calibration process.

various reproductive, survival, and socio-spatial organization parameters. For detailed information, see Section 8 in [Appendix A](#).

2.4. Simulation experiments

For the main experiment, we used the calibrated model to run 50-year simulations (2022–2072), evaluating different management strategies to identify cost-effective conservation measures. The primary goal was to increase productivity and effective population size in Extremadura, aiming to reverse the current population decline over the medium to long term. We tested different criteria for selecting locations to implement habitat suitability improvements and explored various levels of anthropogenic mortality mitigation.

Population data was collected at years 5 and 10, and subsequently at 10-year intervals. Simulations were initialized using a database generated during the model validation process, which included the location and state variables of individuals in 2022 for each of the 100 simulation runs (2005–2022). Habitat suitability maps were calculated as the median suitability over the last 10 years (2012–2022) for each phenological phase, remaining constant throughout the simulation period.

2.4.1. Conservation interventions

To design conservation interventions, we prioritized areas with higher male breeding densities, which also coincide with greater nesting densities (Silva et al., 2024). We then evaluated several hierarchical decision rules to define conservation interventions based on habitat suitability (considering location, number, extent, and magnitude of improvement) and mitigation of anthropogenic mortality, aiming to identify the most cost-efficient management strategies. We began by defining the potential intervention locations, testing two scenarios: i) Intervening only within Special Protection Areas (SPAs); and ii) Intervening both inside and outside SPAs. Next, we examined different

proportions of male locations within these areas (0.25, 0.5, 0.75, and 1). After selecting intervention sites based on the centroid of male home ranges, we assessed different management area sizes, considering radii of 250 m, 750 m, and 1250 m (corresponding to 1, 3, and 5 habitat cells, respectively). Lastly, we tested different habitat suitability increments (0.1, 0.2, and 0.3) to simulate breeding habitat improvements.

In parallel, we evaluated the reduction of overall anthropogenic mortality using a tiered approach, where each tier represents a different annual probability of mortality due to anthropogenic causes (4 tiers in total): i) 0.06 – Current anthropogenic mortality probability (control scenario, no intervention); ii) 0.04 – Intermediate reduction (e.g., implementing power line marking); iii) 0.02 – Greater reduction (e.g., a combination of power line burial and marking); and iv) 0.00 – Complete elimination of anthropogenic mortality. The 0.06 mortality scenario serves as a baseline without mortality reduction. The 0.04 scenario represents an intervention strategy involving power line marking, while the 0.00 scenario assumes the burial or rerouting of power lines alongside stricter hunting regulations. The 0.02 scenario represents a mixed strategy, where some power lines are buried, and others are marked. We assumed that future power lines would be planned to minimize collision risks for bustards, excluding scenarios involving increased anthropogenic mortality.

We tested 288 different conservation management strategies, each replicated 10 times, resulting from the various combinations of interventions. Strategies were considered effective if they produced an annual population growth >1 .

To identify the most cost-effective strategies, we ranked them based on the ratio between the observed annual population growth rate and the intervention area used for habitat suitability enhancement. This ranking was conducted at each data collection year and for each anthropogenic mortality tier, considering only combinations that maximized habitat suitability improvement (0.3).

3. Results

3.1. Model development

3.1.1. Calibration

The calibration process enabled the establishment of a correlation between habitat suitability and individual survival at various life stages of the little bustard. Notably, during the incubation period, nest failure exhibited a strong correlation with low habitat suitability, emphasizing the critical nature of this life stage for the species. This stage, characterized by the lowest weekly survival rate under optimal habitat suitability conditions ($A = 0.958$), also revealed the strongest correlation with suitability ($B = 0.155$) (Fig. 2a). Similarly, during the chick development stage, spanning from birth to 8 weeks of age, a significant correlation was observed with habitat suitability ($B = 0.076$), alongside the second lowest weekly survival probability under optimal conditions ($A = 0.974$) (Fig. 2b).

Adult breeding females displayed a lower weekly survival probability under optimal habitat suitability conditions during the breeding phase ($A = 0.996$) when compared to non-breeding individuals and breeding females outside the breeding phase ($A = 0.998$). Additionally, the correlation with habitat suitability was substantially stronger for breeding females ($B = 0.021$) compared to other adult individuals ($B = 0.002$) (Fig. 2c and d).

Regarding the percentage of non-breeding females, the calibration process indicated a value of 18.5%, with the posterior distribution showing significant variation between 15% and 23%, suggesting a low model sensitivity to this parameter (see Table S.6.2 in Appendix A). Concerning the conspecific attraction radius during the post-breeding and winter phases, the calibration results indicated a radius of 20 patches (5 km) for the post-breeding phase and 33 patches (8.25 km) for the winter phase (see Table S6.2 in Appendix A).

3.1.2. Sensitivity analyses

The sensitivity analyses unveiled that the most crucial parameter (with high μ^* values) for the annual growth rate was the survival rate of adults under optimal habitat suitability conditions, followed by anthropogenic mortality and the survival of breeding females during the breeding season (see Figure S.7.1 in Appendix A). Additional parameters that influenced the annual growth rate included the survival rates of chicks and nests. However, these parameters were strongly influenced by the values in other parameters (high σ values). With the exception of adult survival, all remaining parameters exhibited non-monotonic effects on the growth rate, characterized by high μ^* values and low μ values.

Regarding the influence on the population sex ratio, the sensitivity analyses highlighted the importance of parameters such as adult survival, survival of breeding females during the breeding season, and anthropogenic mortality, followed by the survival rates of chicks and nests (see Figure S.7.2 in Appendix A). All of these parameters were significantly influenced by the choice of other parameter values. Finally, concerning the influence of parameters on time to extinction, adult survival and anthropogenic mortality emerged as the most important parameters (see Figure S.7.3 in Appendix A).

3.1.3. Validation

Our model successfully replicated the estimated number of males in the provinces of Cáceres and Badajoz from the 2016 and 2022 censuses, with the results slightly falling below the lower confidence interval for the number of males in Badajoz in 2016 (see Figure S.8.1 in Appendix A). Additionally, the model satisfactorily approximated the number of individuals per flock during the post-breeding and winter phases (see Figure S.8.10 in Appendix A).

The model's nest failure rate (41%; see Figure S.8.2 in Appendix A) fell within the ranges reported in other studies (Berthet et al., 2012; Bretagnolle et al., 2011; Cuscó et al., 2021; Lapedra et al., 2011), as did

the average number of juveniles per breeding female (0.76 juveniles; e.g. Bretagnolle et al., 2018; Bretagnolle and Inchausti, 2005; Cuscó et al., 2021; Tarjuelo et al., 2013). Similarly, the median chick survival (0.5; see Figure S.8.5 in Appendix A) and breeding success (0.56; see Figure S.8.6 in Appendix A) aligned with values from previous research (e.g. Bretagnolle et al., 2018; Cuscó et al., 2021; Lapedra et al., 2011). However, the model slightly overestimated the number of juveniles per female (0.65; see Figure S.8.3 in Appendix A), compared to other studies (Bretagnolle et al., 2011; Cuscó et al., 2021; Inchausti and Bretagnolle, 2005; Lapedra et al., 2011).

The model also replicated the empirical average sex ratios (median sex ratio = 0.54; see Figure S.8.7 in Appendix A) and median annual male survival rates (75%; see Figure S.8.8 in Appendix A). The male survival rate was slightly higher than the average estimated for the Extremadura region (Silva et al., 2024) but fell within the expected ranges (Inchausti and Bretagnolle, 2005; Marcelino et al., 2018). Regarding site fidelity, the model produced values consistent with those recorded in Extremadura, both at the home range (83%) and core area (46%) levels (see Figure S.8.9 in Appendix A).

3.2. Optimal management strategy

The analysis of various simulated management strategies (Table 3) revealed significant disparities in the annual growth rate (λ) over the 50-year simulation period, with most strategies failing to achieve annual population growth rates greater than 1 (Fig. 3). The results emphasize that while improving habitat suitability is essential for reversing population decline, substantial and lasting recovery can be greatly enhanced by reducing anthropogenic mortality.

This trend is particularly pronounced when interventions to improve habitat suitability are confined to SPAs. In these scenarios, only 14 out of the 36 strategies achieved growth rates greater than 1 under any mortality reduction scenario (Fig. 3). However, when no measures were taken to reduce anthropogenic mortality, only 3 strategies produced positive growth. These required intervention areas covering at least 67,645 ha (equivalent to five habitat cells surrounding the home range centroids of 50% of breeding males) and a minimum suitability increase of 0.3. Even the most comprehensive strategy, covering 101,638 ha (five habitat cells surrounding the home range centroids of 100% of breeding males) within SPAs, failed to achieve growth rates of 1 in the first decade without mitigation of anthropogenic mortality, with values below 1.02 by year 50. For growth rates greater than 1 after 10–20 years, intermediate reductions in anthropogenic mortality (mortality rates of 0.04 or 0.02), combined with broader intervention areas (at least five habitat cells around selected males) and suitability increases of 0.3, were necessary. Restricting interventions to a radius of one habitat cell, or implementing smaller suitability increases (0.1), consistently resulted in declining populations.

Expanding intervention areas beyond SPAs produced better results. In these cases, 20 out of 36 strategies achieved growth rates greater than 1 in at least one mortality reduction scenario (Fig. 3). Strategies without mortality mitigation required larger areas (at least 87,249 ha, equivalent to three habitat cells surrounding the home range centroids of 50% of breeding males) and higher suitability increases (≥ 0.2) to sustain population growth. Only scenarios with complete anthropogenic mortality mitigation achieved growth rates greater than 1 with minimal intervention (one habitat cell radius or suitability increases of 0.1).

Despite targeted efforts, 67% of the scenarios still showed declining trends (annual growth < 1) after 50 years (see Figure S.9.1 in Appendix A), particularly those with smaller intervention radii (1 or 3 habitat cells), limited suitability increases (0.1 or 0.2), and minimal or no anthropogenic mortality mitigation (mortality rates of 0.04 or 0.06). Moreover, 2% of the scenarios risk near-extinction levels (< 50 individuals) within 30 years, increasing to 26% after 40 years and 73% after 50 years, with 5% leading to effective extinction by 2073 (see Figure S.9.2 in Appendix A).

Table 3

Comparison of simulated management strategies and associated intervention metrics for habitat suitability enhancement. Metrics include the total intervention area within the study region (Total Intervened Area), the intervention area located within Special Protection Areas (Intervened Area SPAs), and the percentage of total SPA area that is intervened (% Area of SPAs). Additionally, the table presents the percentage of females whose home-range centroids fall within the intervention area in the first year of intervention (2023; % Females inside), along with the average percentage increase in habitat suitability at intervened locations where suitability increased by at least 0.3 (% HS increase).

Location	Fraction of males	Radius	Total Intervened Area (ha)	Intervened Area SPAs (ha)	% area of SPAs	% Females inside	% HS increase	
SPAs	0,25	1	3.302	3.302	1	7	56	
		3	16.484	16.484	4	18	58	
		5	40.982	40.982	11	23	61	
	0,5	1	6.219	6.219	2	13	56	
		3	28.769	28.769	7	27	59	
		5	67.645	67.645	17	31	62	
	0,75	1	8.788	8.788	2	18	57	
		3	38.452	38.452	10	32	59	
		5	86.786	86.786	22	34	63	
	1	1	11.157	11.157	3	23	57	
		3	46.750	46.750	12	34	60	
		5	101.638	101.638	26	36	64	
	All	0,25	1	9.351	3.417	1	18	58
			3	48.911	17.411	4	47	61
			5	126.740	43.882	11	57	66
0,5		1	17.778	6.314	2	34	59	
		3	87.249	29.590	8	71	62	
		5	215.813	70.292	18	81	68	
0,75		1	25.296	8.939	2	49	59	
		3	117.502	39.486	10	85	62	
		5	280.461	89.798	23	93	69	
1		1	32.121	11.246	3	62	59	
		3	143.215	47.638	12	94	63	
		5	332.013	104.589	27	100	70	

Among the strategies deemed most efficient (Fig. 4), most were still unable to recover the population to the estimated numbers from 2005, even after 50 years. This was especially evident in scenarios where habitat suitability improvements were restricted just to leks within the SPAs. The only strategy that achieved the 2005 population size involved the complete elimination of anthropogenic mortality combined with the highest level of habitat suitability improvement (0.3) across 100% of breeding male locations. However, targeting 75% of breeding male locations throughout the entire region allowed the population to approach the 2005 size within 40 years, even without mitigating anthropogenic mortality. Similarly, with interventions at 50% of breeding male locations, this goal could be reached within 50 years. If anthropogenic mortality is reduced, the 2005 population size could be achieved 10–20 years earlier, depending on the extent of mortality reduction.

4. Discussion

The IBM developed for the little bustard population in the Extremadura region has provided valuable insights into how the species' demography relates to its significant population decline, particularly highlighting the effects of a skewed sex ratio, low breeding success, and low adult survival. This modelling approach not only highlights key biological aspects requiring intervention but also optimizes management efforts. Additionally, the IBM framework facilitates the assessment of different management actions and their implementation costs through a cost-effectiveness analysis, enabling the prioritization of strategies that best align with conservation objectives.

For the little bustard in Extremadura, our findings demonstrate that the most effective management strategies (i.e. those that minimize conservation efforts while maximizing long-term species recovery) rely on coordinated actions that simultaneously enhance habitat suitability and reduce anthropogenic mortality.

4.1. IBM and population demography in Extremadura

During model development, calibration confirmed a positive correlation between habitat suitability and the survival of nests, chicks, and

adult little bustards. This aligns with previous studies showing high nest failure rates in low-suitability areas, primarily due to nest destruction, predation, and abandonment (Bravo et al., 2017; Bretagnolle et al., 2018; Cuscó et al., 2021). Low breeding productivity in these areas likely results from limited food availability, inadequate herbaceous cover, and high predation pressure (Lapedra et al., 2011; Serrano-Davies et al., 2023), which contribute to higher chick mortality and increased risks for adult females during nesting and chick-rearing phases (Cuscó et al., 2021; Serrano-Davies et al., 2023).

Our findings suggest that low female survival rates in less suitable habitats contribute to the skewed sex ratios observed in little bustard populations. This highlights the breeding phase as the most critical period in the species' annual cycle, during which habitat suitability plays a crucial role in sustaining the population stability. Enhancing habitat suitability during this phase could improve reproductive success and female survival by reducing energy expenditure and mitigating the risks associated with repeated breeding attempts (Mañosa et al., 2022). Additionally, sensitivity analyses highlighted anthropogenic mortality as a key driver influencing breeding success, sex ratio, and overall population growth.

Although this study provides a preliminary theoretical framework for evaluating conservation strategies, the results yield critical insights that can inform the development of an effective management plan for the species. Most strategies tested failed to achieve positive population growth (>1) over a 50-year period, highlighting the limitations of isolated measures in securing long-term population viability. This highlights the challenges associated with little bustard conservation in Extremadura and across its broader range.

Furthermore, our simulations indicate alarming extinction risks, with near-extinction scenarios within 30 years and effective extinction projected within a 40–50 years horizon under certain conditions (see Figure S9.2 in Appendix A). These findings underscore the urgent need for targeted conservation measures and the importance of formulating long-term, comprehensive management strategies that address key ecological constraints. Such strategies must prioritize immediate actions to halt the severe population decline observed in recent decades (García de la Morena et al., 2006, 2018), followed by sustained efforts to

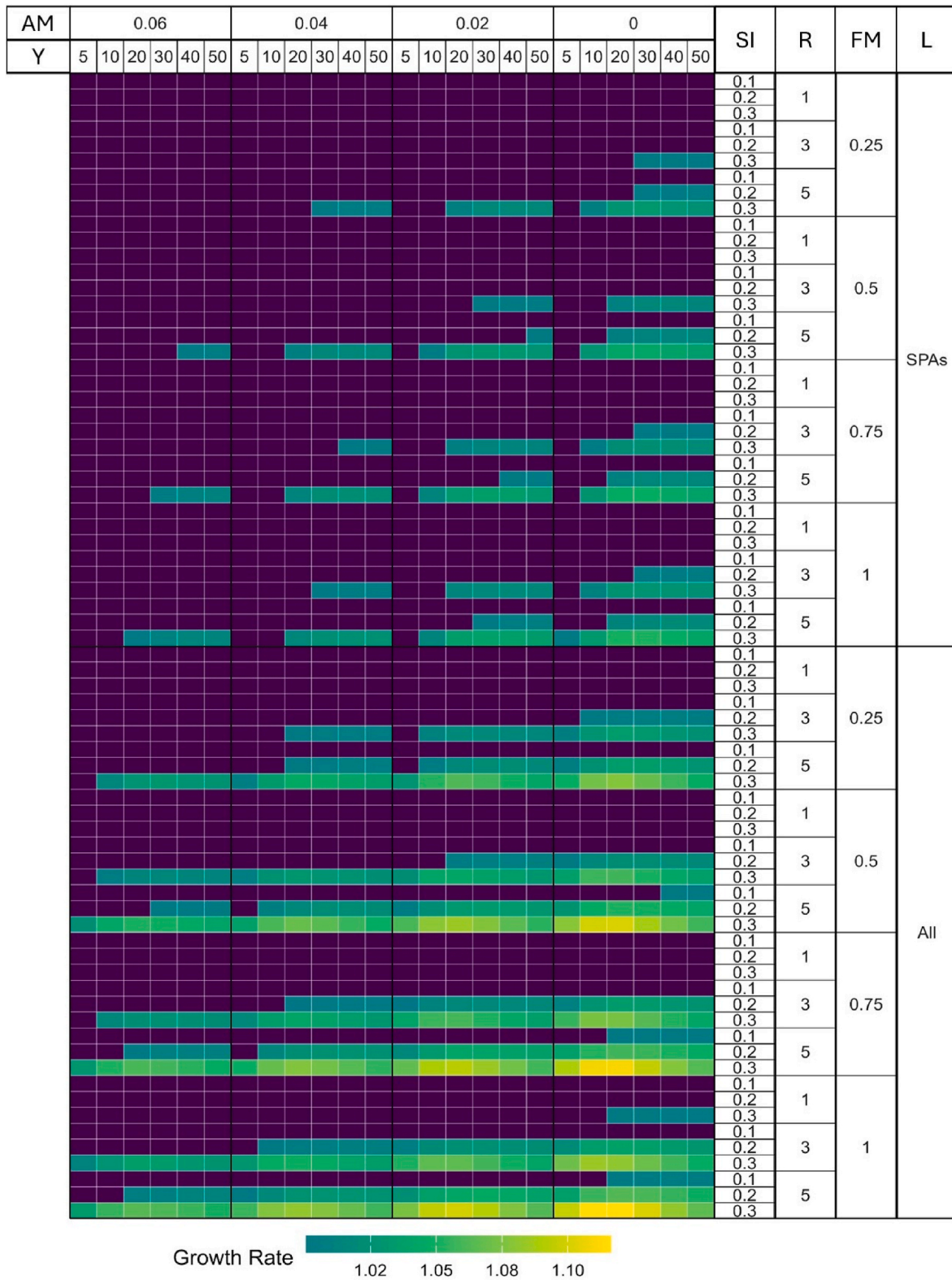


Fig. 3. Annual growth rate (λ) over a 50-year period under different simulated management strategies. The figure includes key intervention parameters: AM – Annual anthropogenic mortality probability; Y - Years post-intervention; L – Location; FM – Fraction of males; R – Radius of intervention (in habitat cells); and SI – Increase in habitat suitability. Strategies indicated in purple had population growth rates <1.

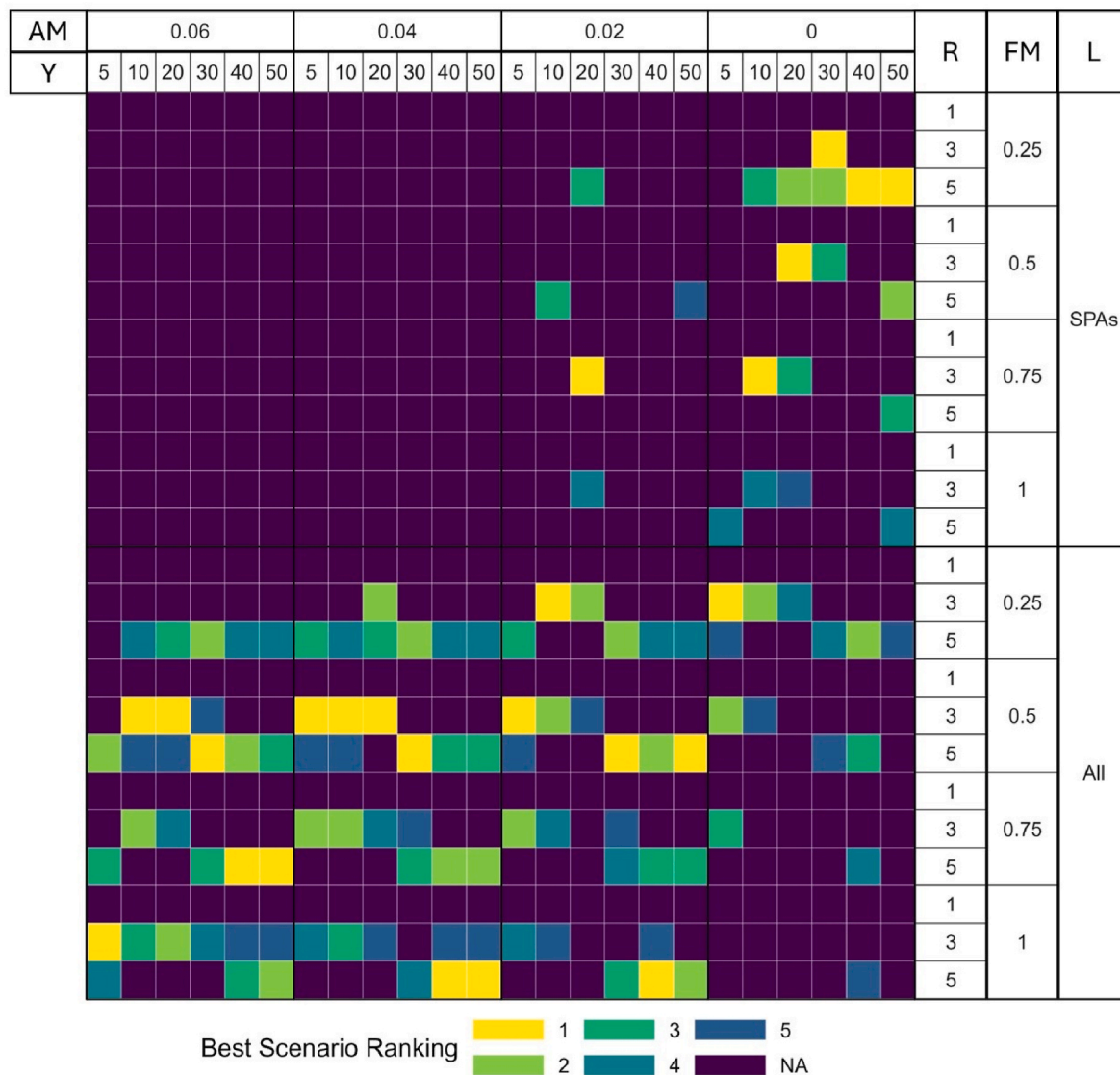


Fig. 4. Ranking of the most effective management strategies simulated for each year with available data and across different anthropogenic mortality scenarios. The ranking was determined based on the ratio between the observed annual population growth rate (λ) and the total intervention area allocated to enhancing habitat suitability. The figure includes key intervention parameters: AM – Annual anthropogenic mortality probability; Y - Years post-intervention; L – Location; FM – Fraction of males; R – Radius of intervention (in habitat cells).

facilitate the recovery of viable population levels.

4.1.1. Manage just SPAs or the species' entire range?

Although Extremadura hosts one of Spain's most important breeding populations of little bustards within Special Protection Areas (SPAs), comprising approximately 65% of the regional population (Traba et al., 2022), our analysis indicates that focusing conservation efforts exclusively within SPAs, without addressing anthropogenic mortality, is unlikely to be an effective strategy. The results strongly suggest that reducing anthropogenic mortality is a critical prerequisite for any conservation plan to be successful. Even when both habitat improvement and anthropogenic mortality reduction measures are implemented within SPAs, achieving sustained population growth rates (>1) over 50 years remains highly dependent on the intensity of interventions. In contrast, strategies without spatial restrictions on habitat improvement consistently yield higher growth rates and require less intensive efforts to achieve positive population trends.

However, an important consideration is that male breeding sites outside SPAs tend to exhibit lower habitat suitability (Crispim-Mendes

et al., 2024), suggesting that intervention costs may be higher in these areas than within SPAs. Consequently, selecting intervention sites for habitat improvement should account for both habitat suitability and the need for mortality mitigation, particularly within SPAs, where a large portion of the population congregates during the breeding season and where conservation actions may be more cost-effective. Nevertheless, better outcomes are expected when interventions extend beyond SPAs, particularly in areas with higher species densities, where targeted conservation efforts could maximize population recovery across the species' range.

4.1.2. How much habitat should be managed?

In selecting intervention sites for habitat suitability improvement, our simulations prioritized breeding male locations during the breeding season (namely, leks) under the assumption that these areas host higher numbers of breeding females (Morales et al., 2014; Silva et al., 2014; Tarjuelo et al., 2013). Maintaining high habitat quality and stability in these locations over the years is expected to increase local densities (Silva et al., 2017) and enhance reproductive success (Morales et al.,

2013). However, the male-skewed sex ratio and the low survival rate of breeding females emphasize the importance of also including female settlement areas in conservation interventions. Defining an optimal intervention radius around male locations is therefore crucial for an effective management strategy.

Our results indicate that effective conservation strategies for the little bustard require relatively large intervention buffers. Strategies employing a single habitat cell buffer (250m radius) around male locations were less effective than those using 3- or 5-cell buffers (750m and 1250m radii, respectively). Notably, the 250m buffer strategies only resulted in population growth rates >1 when coupled with the complete elimination of anthropogenic mortality.

Cost-effectiveness analysis revealed that while 3-cell buffers (750m) are occasionally top-ranked for short to medium-term interventions (5–30 years), 5-cell buffers (1250m) provide better results in medium-to long-term scenarios (30–50 years). Larger intervention areas tend to increase overall habitat suitability, but they also entail higher intervention costs due to the decreasing suitability of areas farther from male home range centroids.

A more cost-effective strategy could involve a phased approach, initially implementing a 750m buffer and expanding it to 1250m as the population grows. This adaptive management approach would allow for lower initial costs while providing flexibility for future adjustments based on population response. Additionally, implementing habitat improvements at the management unit level (land parcels) is crucial to ensuring precise and feasible interventions, while also facilitating long-term agreements with landowners.

Regarding lek interventions, targeting 50% of leks generally yields the most efficient outcomes. However, in scenarios where anthropogenic mortality is fully eliminated, intervening in only 25% of leks within SPAs is optimal. These decisions should be carefully integrated into the broader conservation strategy, considering factors such as buffer size, spatial constraints, and intervention timelines.

4.1.3. How does the habitat suitability need to be improved?

Our methodology evaluated three levels of suitability increase (0.1, 0.2, and 0.3) in the habitat suitability index, applying these increments uniformly across all intervention sites, regardless of their initial suitability. However, in a realistic conservation scenario, most habitat management interventions would prioritize medium-to low-suitability areas, aiming to maximize the effectiveness of management actions and achieve the highest possible gains in habitat quality. While our approach is primarily conceptual, it allows us to quantify the population-level impacts of different intervention intensities.

Our results indicate that marginal and intermediate suitability increases (0.1 and 0.2) are insufficient to reverse the population decline unless interventions target the majority of lek sites and include substantial reductions in anthropogenic mortality. Even under these conditions, growth rates remain significantly lower than those observed in scenarios with a suitability increase of 0.3. These findings highlight the critical importance of maximizing breeding habitat quality, rather than relying on partial improvements, when designing agri-environmental measures (Morales et al., 2013; Traba et al., 2022).

Although our model assumes similar habitat preferences for males and females at the model scale (Crispim-Mendes et al., 2024), it's important to acknowledge that they differ at finer scales (Morales et al., 2008; Silva et al., 2014). As we move towards higher resolution models, it becomes imperative to incorporate detailed information on female habitat preferences. Therefore, when designing habitat management strategies aimed at improving suitability, it's essential to account for both male and female habitat preferences.

4.1.4. Anthropogenic mortality

A key finding of our study is that a management strategy focused solely on enhancing breeding habitat suitability, without addressing anthropogenic mortality, is unlikely to produce sustainable population

growth. Similar conclusions were reached by Mañosa and Bota (2023) in a study conducted in Catalonia, Spain, which emphasized that to guarantee the long-term viability of the little bustard and to secure a reasonable share of conservation effort from stakeholders, it is critical to reduce both natural and anthropogenic mortality.

In our analysis, anthropogenic mortality reduction was modelled as a uniform probability applied across the entire study area, ranging from no reduction to complete elimination. While this approach provides valuable insights into the importance of mitigating anthropogenic threats, a more realistic approach would involve explicitly identifying and spatially representing the main sources of anthropogenic mortality. In this context, one crucial improvement to our model would be the integration of the electrical grid within the study area, incorporating species-specific collision probabilities for different powerline types. This enhancement would allow for testing targeted mitigation strategies, such as line marking or burial, which have been implemented with varying levels of effectiveness and cost efficiency across different regions (Silva et al., 2023).

By refining our approach to account for spatial variation in anthropogenic threats, future conservation planning could prioritize mitigation actions in high-risk areas, ultimately enhancing the effectiveness of management strategies for species recovery.

4.1.5. What is the best conservation strategy?

Prioritizing interventions that maximize conservation impact while considering financial constraints is crucial to ensure that conservation efforts are both effective and sustainable in the long term (Tallis et al., 2021).

The analysis of the top-rated simulated conservation strategies offers valuable insights for managing the little bustard population in Extremadura. In the absence of substantial reductions in anthropogenic mortality, effective strategies should focus on targeting 25% of male locations for habitat improvement within a 5-cell buffer, covering approximately 127,000 ha. Alternatively, interventions targeting 50% of male locations within a 3-cell buffer for 20 years, followed by an expansion to a 5-cell buffer over a total area of 216,000 ha, could also yield positive results. In scenarios where anthropogenic mortality is reduced, the most promising strategy involves intervening within a 3-cell buffer at 25% of male locations for 20 years, followed by an expansion to a 5-cell buffer. However, targeting 50% of male locations is generally more effective in ensuring long-term population stability and growth.

If anthropogenic mortality is fully mitigated, the optimal strategy would be targeting 25% of male locations within SPAs, using a 5-cell buffer covering approximately 41,000 ha. However, it is essential to evaluate strategies not only based on efficiency but also in terms of their expected outcomes. Some strategies that appear efficient on paper may still fail to achieve the desired population growth rates.

Cost considerations are crucial in strategy design, requiring a balance between the one-time costs of reducing anthropogenic mortality and the ongoing costs associated with habitat improvement. Realistic cost estimates and clear conservation objectives, including target population sizes, should guide the design of these strategies. Furthermore, less ambitious strategies could delay or significantly hinder population recovery, underlining the need for adaptive management. Regular monitoring is essential to adjust interventions and ensure long-term effectiveness (Zurell et al., 2022).

4.2. Final considerations and future prospects

The IBM developed in this study represents a significant advancement in conservation planning by integrating ecological complexity and species-specific behavioural variability into population forecasts, while enabling evidence-based decision-making. By accounting for multiple interacting variables, such as various levels of anthropogenic mortality and habitat improvement across specific areas, our approach provides a

robust framework for predicting the outcomes of different conservation strategies and refining restoration efforts as results emerge. Such a targeted approach is more effective than broad, non-specific measures, ensuring a more efficient allocation of time and resources.

The model results have provided new insights into the need for integrated strategies that focus on both increasing habitat suitability and reducing mortality to reverse the declining population trend of the little bustard in Extremadura. Results also indicated that habitat improvement actions must extend beyond the boundaries of the SPAs to achieve substantial recovery. Furthermore, the model advanced our understanding of the biology and population dynamics of the species, particularly the correlation between the survival probability of different life stages and habitat suitability. The model also revealed that the species faces a regional extinction risk within the next 30–50 years if the necessary conservation actions are not taken.

While some aspects of the model require further validation and refinement, this tool currently offers the most comprehensive framework available for supporting the conservation of the species. This highlights the immense potential of IBMs in supporting the management of complex ecological processes (Stillman et al., 2015). Key improvements should focus on enhancing the model's predictive accuracy by incorporating detailed migration and dispersal data, as well as micro-habitat suitability maps for females, which would allow for a more refined approach to habitat management. The integration of future climate change projections would improve long-term conservation planning, while the inclusion of spatially explicit representations of anthropogenic mortality sources, such as power lines, and more detailed management units would refine the implementation of conservation measures. Additionally, incorporating financial cost assessments would enable more thorough cost-benefit analyses, guiding conservation efforts towards economically viable and sustainable strategies. The model should also be designed to allow for adaptive management, ensuring that conservation interventions can be adjusted over time based on population responses, thus increasing their effectiveness.

Future research should address the broader challenges in steppe bird conservation (Pérez-Granados et al., 2025), with emphasis on understanding the impact of land-use changes, which is crucial for developing effective mitigation strategies, particularly in the context of the expanding renewable energy infrastructure. Additionally, investigating the role of agri-environmental policies in shaping habitat quality and population trends will provide valuable insights for optimizing conservation measures and incentives. Importantly, interventions designed to reduce anthropogenic mortality and enhance breeding habitat suitability for the little bustard are likely to benefit other steppe species with similar ecological needs, such as the great bustard (*Otis tarda*) and pin-tailed sandgrouse (*Pterocles alchata*). This highlights the importance of exploring multispecies conservation approaches, including the potential of the little bustard as an umbrella species to support broader conservation efforts across cereal and grassland landscapes (Morales et al., 2023).

In summary, the model developed in this study represents a significant step in advancing the tools available for designing effective management strategies for the little bustard and other grassland birds in Extremadura and beyond. It also provides a valuable means to assess the impact of anthropogenic threats such as power lines and habitat loss driven by the expansion of solar farms across the Iberian Peninsula.

CRediT authorship contribution statement

Tiago Crispim-Mendes: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ana Teresa Marques:** Writing – review & editing, Conceptualization. **Francesco Valerio:** Writing – review & editing, Conceptualization. **Sérgio Godinho:** Writing – review & editing, Conceptualization. **Ricardo Pita:** Writing – review & editing, Conceptualization. **João Paulo Silva:** Writing – review & editing,

Supervision, Investigation, Funding acquisition, Conceptualization.

Funding

TCM was funded by National Funds through FCT - Foundation for Science and Technology under a doctoral grant (SFRH/BD/145,156/2019). ATM was funded by the project NORTE-01-0246-FEDER-000063, supported by Norte Portugal Regional Operational Programme (NORTE2020), under the Portugal 2020 Partnership Agreement, through the European Regional Development Fund (ERDF). JPS was supported by an FCT contract (DL57/2019/CP1440/CT0021). RP was supported by the FCT through a research contract under the CEEC research contract 2022.02878.CEECIND. SG was funded by the FUEL-SAT project “Integration of multi-source satellite data for wildland fuel mapping: the role of remote sensing for an effective wildfire fuel management” from the Foundation for Science and Technology (PCIF/GRF/0116/2019), and by National Funds through FCT under the Project UIDB/05183/2020.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Tiago Crispim-Mendes reports financial support was provided by FCT - Foundation for Science and Technology. Joao Paulo Silva reports financial support was provided by FCT - Foundation for Science and Technology. Ricardo Pita reports financial support was provided by FCT - Foundation for Science and Technology. Sergio Godinho reports financial support was provided by FCT - Foundation for Science and Technology. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Special thanks go to Maria de Jesús Palacios and Ángel Sánchez (Dirección General de Sostenibilidad, Consejería de Agricultura de la Junta de Extremadura) for their support and encouragement in carrying out this work. We are grateful to Nuno Queiroz, Marisa Vedor, and Ivo Costa for providing assistance and a server to run the models. We also thank SEO- BirdLife for providing the data from the 2022 Little bustard census in Extremadura, conducted under the project LIFE20 NAT/ES/001477 *Agrostepas Ibéricas Enfoques agrarios sostenibles para la conservación de especies y hábitats agrosteparios en Red Natura 2000*.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2025.124790>.

Data availability

Data will be made available on request.

References

- Alonso, H., Correia, R.A., Marques, A.T., Palmeirim, J.M., Moreira, F., Silva, J.P., 2019. Male post-breeding movements and stopover habitat selection of an endangered short-distance migrant, the Little Bustard *Tetrax tetrax*. *Ibis* 162, 279–292. <https://doi.org/10.1111/ibi.12706>.
- An, L., Grimm, V., Sullivan, A., TurnerII, B.L., Malleon, N., Heppenstall, A., Vincenot, C., Robinson, D., Ye, X., Liu, J., Lindkvist, E., Tang, W., 2021. Challenges, tasks, and opportunities in modeling agent-based complex systems. *Ecol Modell* 457. <https://doi.org/10.1016/j.ecolmodel.2021.109685>.
- Augusiak, J., Van den Brink, P.J., Grimm, V., 2014. Merging validation and evaluation of ecological models to “evaluation”: a review of terminology and a practical approach. *Ecol Modell* 280, 117–128. <https://doi.org/10.1016/j.ecolmodel.2013.11.009>.

- Ayllón, D., Railsback, S.F., Vincenzi, S., Groeneveld, J., Almodóvar, A., 2016. InSTREAM-Gen: modelling eco-evolutionary dynamics of trout populations under anthropogenic environmental change. *Ecol Modell* 326, 36–53. <https://doi.org/10.1016/j.ecolmodel.2015.07.026>.
- Beaumont, M.A., 2010. Approximate bayesian computation in evolution and ecology. *Annu. Rev. Ecol. Evol. Syst.* 41, 379–406. <https://doi.org/10.1146/annurev-ecolsys-102209-144621>.
- Beaumont, M.A., Zhang, W., Balding, D.J., 2002. Approximate Bayesian computation in population genetics. *Genetics* 162, 2025–2035. <https://doi.org/10.1093/genetics/162.4.2025>.
- Berthet, E.T.A., Bretagnolle, V., Segrestin, B., 2012. Analyzing the design process of farming practices ensuring little bustard conservation: lessons for collective landscape management. *J. Sustain. Agric.* 36, 319–336. <https://doi.org/10.1080/10440046.2011.627988>.
- BirdLife International, 2022. *State of the World's Birds 2022: Insights and Solutions for the Biodiversity Crisis*. Cambridge, UK: BirdLife International, Cambridge, UK. BirdLife International.
- BirdLife International, 2021. *European Red List of Birds*. Publications Office of the European Union, Luxembourg. <https://doi.org/10.2779/959320>.
- Boult, V.L., Quaipe, T., Fishlock, V., Moss, C.J., Lee, P.C., Sibly, R.M., 2018. Individual-based modelling of elephant population dynamics using remote sensing to estimate food availability. *Ecol Modell* 387, 187–195. <https://doi.org/10.1016/j.ecolmodel.2018.09.010>.
- Bravo, C., Cuscó, F., Morales, M.B., Mañosa, S., 2017. Diet composition of a declining steppe bird the Little Bustard (*Tetrax tetrax*) in relation to farming practices. *Avian Conserv. Ecol.* 12 (1). <https://doi.org/10.5751/ACE-00938-120103>.
- Bretagnolle, V., Denonfoux, L., Villers, A., 2018. Are farming and birds irreconcilable? A 21-year study of bustard nesting ecology in intensive agroecosystems. *Biol. Conserv.* 228, 27–35. <https://doi.org/10.1016/j.biocon.2018.09.031>.
- Bretagnolle, V., Inchausti, P., 2005. Modelling population reinforcement at a large spatial scale as a conservation strategy for the declining little bustard (*Tetrax tetrax*) in agricultural habitats. *Anim. Conserv.* 8, 59–68. <https://doi.org/10.1017/S1367943004001866>.
- Bretagnolle, V., Mañosa, S., Morales, M.B., 2022. Natural history of the little bustard: morphology, biometry, diet, sexual dimorphism, and social and breeding behaviour. In: Bretagnolle, V., Traba, J., Morales, M.B. (Eds.), *Little Bustard: Ecology and Conservation*. Springer Nature, Switzerland, pp. 29–56.
- Bretagnolle, V., Villers, A., Denonfoux, L., Cornulier, T., Inchausti, P., Badenhausser, I., 2011. Rapid recovery of a depleted population of Little Bustards *Tetrax tetrax* following provision of alfalfa through an agri-environment scheme. *Ibis* 153, 4–13. <https://doi.org/10.1111/j.1474-919X.2010.01092.x>.
- Campolongo, F., Cariboni, J., Saltelli, A., 2007. An effective screening design for sensitivity analysis of large models. *Environ. Model. Software* 22, 1509–1518. <https://doi.org/10.1016/j.envsoft.2006.10.004>.
- Cook, C.N., Hockings, M., Carter, R.W., 2010. Conservation in the dark? The information used to support management decisions. *Front. Ecol. Environ.* 8, 181–188. <https://doi.org/10.1890/090020>.
- Crispim-Mendes, T., Valerio, F., Marques, A.T., Pita, R., Godinho, S., Silva, J.P., 2024. High-resolution species distribution modelling reveals spatio-temporal variability of habitat suitability in a declining grassland bird. *Landsc. Ecol.* 39, 49. <https://doi.org/10.1007/s10980-024-01848-6>.
- Cuscó, F., Bota, G., Llovet, A., Mañosa, S., 2021. Nesting and incubation behaviour of the little bustard *tetrax tetrax* and its relation to hatching success. *ARDEOLA* 68, 95–122. <https://doi.org/10.13157/arla.68.1.2021.ra6>.
- DeAngelis, D.L., Diaz, S.G., 2019. Decision-making in agent-based modeling: a current review and future prospectus. *Front Ecol Evol* 6, 237. <https://doi.org/10.3389/fevo.2018.00237>.
- Delgado, M.P., Traba, J., García de la Morena, E., Morales, M.B., 2010. Habitat selection and density-dependent relationships in spatial occupancy by male little bustards *tetrax tetrax*. *Ardea* 98, 185–194. <https://doi.org/10.5253/078.098.0208>.
- Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneith, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Lucas, A.G., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razaque, J., Reyers, B., Chowdhury, R.R., Shin, Y.J., Visseren-Hamakers, I., Willis, K.J., Zayas, C.N., 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science* 366. <https://doi.org/10.1126/science.aax3100>, 1979.
- Drenske, S., Radchuk, V., Scherer, C., Esterer, C., Kowarik, I., Fritz, J., Kramer-Schadt, S., 2023. On the road to self-sustainability: reintroduced migratory European northern bald ibises *Geronticus eremita* still need management interventions for population viability. *Oryx* 57, 637–648. <https://doi.org/10.1017/S0030605322000540>.
- Faria, N., Silva, J.P., 2010. Habitat selection of the little bustard during the beginning of an agricultural year. *ARDEOLA* 57, 363–373.
- Galic, N., Schmolke, A., Bartel, S., Roy, C., Brain, R., 2023. Applying a hybrid model to support management of the endangered Topeka shiner in oxbow habitats. *Front Ecol Evol* 10, 1–13. <https://doi.org/10.3389/fevo.2022.1075244>.
- Gann, G.D., McDonald, T., Walder, B., Aronson, J., Nelson, C.R., Jonson, J., Hallett, J.G., Eisenberg, C., Guariguata, M.R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decler, K., Dixon, K.W., 2019. International principles and standards for the practice of ecological restoration. In: *Restor Ecol*, second ed., vol. 27, pp. S1–S46. <https://doi.org/10.1111/rec.13035>.
- García de la Morena, E., Bota, G., Mañosa, S., Morales, M., 2018. *El Sisón Común en España. II Censo Nacional. SEO/BirdLife, Madrid, Madrid*.
- García de la Morena, E., Bota, G., Ponjoan, A., Morales, M., 2006. *El Sisón Común. I Censo Nacional 2005. SEO/BirdLife, Madrid*.
- García de la Morena, E., Morales, M.B., Bota, G., Silva, J.P., Ponjoan, A., Suárez, F., Mañosa, S., Juana, E. De, 2015. Migration patterns of iberian little bustards *tetrax tetrax*. *ARDEOLA* 62, 95–112. <https://doi.org/10.13157/arla.62.1.2015.95>.
- Gray, C., Rothman, D.S., Peters-Burton, E., Smith, C., Parsons, E.C.M., 2023. Individual-based model use in marine policy. *J. Integr. Environ. Sci.* 20, 2271550. <https://doi.org/10.1080/1943815X.2023.2271550>.
- Grimm, V., Augustiak, J., Focks, A., Frank, B.M., Gabsi, F., Johnston, A.S.A., Liu, C., Martin, B.T., Meli, M., Radchuk, V., Thorbek, P., Railsback, S.F., 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecol Modell* 280, 129–139. <https://doi.org/10.1016/j.ecolmodel.2014.01.018>.
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huht, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Plo, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüter, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. *Ecol Modell* 198, 115–126. <https://doi.org/10.1016/j.ecolmodel.2006.04.023>.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. *Ecol Modell* 221, 2760–2768. <https://doi.org/10.1016/j.ecolmodel.2010.08.019>.
- Grimm, V., Railsback, S.F., 2005. *Individual-based Modeling and Ecology*. Princeton University Press, Princeton, New Jersey. <https://doi.org/10.1515/9781400850624>.
- Grimm, V., Railsback, S.F., Vincenot, C.E., Berger, U., Gallagher, C., DeAngelis, D.L., Edmonds, B., Ge, J., Giske, J., Groeneveld, J., Johnston, A.S.A., Milles, A., Nabe-Nielsen, J., Polhill, J.G., Radchuk, V., Rohwäder, M.-S., Stillman, R.A., Thiele, J.C., Ayllón, D., 2020. The ODD protocol for describing agent-based and other simulation models: a second update to improve clarity, replication, and structural realism. *J. Artif. Soc. Soc. Simulat.* 23. <https://doi.org/10.18564/jasss.4259>.
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., Mcdonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H. P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. *Ecol. Lett.* 16, 1424–1435. <https://doi.org/10.1111/ele.12189>.
- Heinrichs, J.A., Aldridge, C.L., Gummer, D.L., Monroe, A.P., Schumaker, N.H., 2018. Prioritizing actions for the recovery of endangered species: emergent insights from Greater Sage-grouse simulation modeling. *Biol. Conserv.* 218, 134–143. <https://doi.org/10.1016/j.biocon.2017.11.022>.
- Hradsky, B.A., Kelly, L.T., Robley, A., Wintle, B.A., 2019. FoxNet: an individual-based model framework to support management of an invasive predator, the red fox. *J. Appl. Ecol.* 56, 1460–1470. <https://doi.org/10.1111/1365-2664.13374>.
- Inchausti, P., Bretagnolle, V., 2005. Predicting short-term extinction risk for the declining Little Bustard (*Tetrax tetrax*) in intensive agricultural habitats. *Biol. Conserv.* 122, 375–384. <https://doi.org/10.1016/j.biocon.2004.08.001>.
- Jiguet, F., Arroyo, B., Bretagnolle, V., 2000. Lek mating systems: a case study in the Little Bustard *Tetrax tetrax*. *Behav. Process.* 51, 63–82. [https://doi.org/10.1016/S0376-6357\(00\)00119-4](https://doi.org/10.1016/S0376-6357(00)00119-4).
- Jiguet, F., Bretagnolle, V., 2014. Sexy males and choosy females on exploded leks: correlates of male attractiveness in the Little Bustard. *Behav. Process.* 103, 246–255. <https://doi.org/10.1016/j.beproc.2014.01.008>.
- Lapiedra, O., Ponjoan, A., Gamero, A., Bota, G., Mañosa, S., 2011. Brood ranging behaviour and breeding success of the threatened little bustard in an intensified cereal farmland area. *Biol. Conserv.* 144, 2882–2890. <https://doi.org/10.1016/j.biocon.2011.08.005>.
- Lees, A.C., Haskell, L., Allinson, T., Bezeng, S.B., Burfield, I.J., Renjifo, L.M., Rosenberg, K.V., Viswanathan, A., Butchart, S.H.M., 2022. State of the world's birds. *Annu. Rev. Environ. Resour.* 47, 231–260. <https://doi.org/10.1146/annurev-environ-112420-014642>.
- Mañosa, S., Bota, G., 2023. Modelling the effectivity of a land sparing strategy to preserve an endangered steppe-land bird population in cereal farmland: scopes and limits. *Biol. Conserv.* 288, 110386. <https://doi.org/10.1016/j.biocon.2023.110386>.
- Mañosa, S., Bota, G., Villers, A., Bretagnolle, V., Morales, M.B., 2022. Breeding biology and demographic traits: population parameters, reproduction and survival. In: Bretagnolle, V., Traba, J., Morales, M.B. (Eds.), *Little Bustard: Ecology and Conservation*. Springer Nature, Switzerland, pp. 81–100. <https://doi.org/10.1007/978-3-030-84902-3>.
- Marcelino, J., Moreira, F., Mañosa, S., Cuscó, F., Morales, M.B., García de la Morena, E., Bota, G., Palmeirim, J.M., Silva, J.P., 2018. Tracking data of the Little Bustard *Tetrax tetrax* in Iberia shows high anthropogenic mortality. *Bird. Conserv. Int.* 28, 509–520. <https://doi.org/10.1017/S095927091700051X>.
- McCarthy, D.P., Donald, P.F., Scharlemann, J.P.W., Buchanan, G.M., Balmford, A., Green, J.M.H., Bennun, L.A., Burgess, N.D., Fishpool, L.D.C., Garnett, S.T., Leonard, D.L., Maloney, R.F., Morling, P., Schaefer, H.M., Symes, A., Wiedenfeld, D. A., Butchart, S.H.M., 2012. Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. *Science* 338, 946–949. <https://doi.org/10.1126/science.1229803>, 1979.
- McLane, A.J., Semeniuk, C., McDermid, G.J., Marceau, D.J., 2011. The role of agent-based models in wildlife ecology and management. *Ecol Modell* 222, 1544–1556. <https://doi.org/10.1016/j.ecolmodel.2011.01.020>.
- Morales, M.B., Bretagnolle, V., 2022. The little bustard around the world: distribution, global conservation status, threats and population trends. In: Bretagnolle, V., Traba, J., Morales, M.B. (Eds.), *Little Bustard: Ecology and Conservation*. Springer Nature, Switzerland, pp. 57–80. <https://doi.org/10.1007/978-3-030-84902-3>.

- Morales, M.B., Bretagnolle, V., Arroyo, B., 2005a. Viability of the endangered little bustard *Tetrax tetrax* population of western France. *Biodivers. Conserv.* 14, 3135–3150. <https://doi.org/10.1007/s10531-004-0382-z>.
- Morales, M.B., Casas, F., García de la Morena, E., Ponjoan, A., Calabuig, G., Martínez-Padilla, J., García, J.T., Mañosa, S., Viñuela, J., Bota, G., 2014. Density dependence and habitat quality modulate the intensity of display territory defence in an exploded lekking species. *Behav. Ecol. Sociobiol.* 68, 1493–1504. <https://doi.org/10.1007/s00265-014-1758-z>.
- Morales, M.B., García, J.T., Arroyo, B., 2005b. Can landscape composition changes predict spatial and annual variation of little bustard male abundance? *Anim. Conserv.* 8, 167–174. <https://doi.org/10.1017/S1367943005001988>.
- Morales, M.B., Mañosa, S., Villers, A., García de la Morena, E., Bretagnolle, V., 2022. Migration, movements, and non-breeding ecology. In: Bretagnolle, V., Traba, J., Morales, M.B. (Eds.), *Little Bustard: Ecology and Conservation*. Springer Nature, Switzerland, pp. 123–150. <https://doi.org/10.1007/978-3-030-84902-3>.
- Morales, M.B., Merencio, A., García de la Morena, E., 2023. Evaluation of a potential umbrella species using favourability models: the case of the endangered little bustard (*Tetrax tetrax*) and steppe birds. *Biodivers. Conserv.* 32, 3307–3327. <https://doi.org/10.1007/s10531-023-02655-2>.
- Morales, M.B., Traba, J., Carriles, E., Delgado, M.P., de la Morena, E.L.G., 2008. Sexual differences in microhabitat selection of breeding little bustards *Tetrax tetrax*: ecological segregation based on vegetation structure. *Acta Oecol.* 34, 345–353. <https://doi.org/10.1016/j.actao.2008.06.009>.
- Morales, M.B., Traba, J., Delgado, M.P., García de la Morena, E., 2013. The use of fallows by nesting little bustard *Tetrax tetrax* females: implications for conservation in mosaic cereal farmland. *ARDEOLA* 60, 85–97. <https://doi.org/10.13157/arla.60.1.2012.85>.
- Morris, M.D., 1991. Factorial sampling plans for preliminary computational experiments. *Technometrics* 33, 161–174. <https://doi.org/10.1080/00401706.1991.10484804>.
- Pérez-Granados, C., Benítez-López, A., Díaz, M., Gameiro, J., Lenzner, B., Roura-Pascual, N., Gómez-Catasús, J., Tarjuelo, R., Barrero, A., Bolonio, L., Bota, G., Brambilla, M., Bravo, C., Brotons, L., la Rosa, D.B., Cabodevilla, X., Búrdalo, A.C., Carricondo, A., Casas, F., Concepción, E.D., Constán-Nava, S., Crispim-Mendes, T., Giral, D., Golivets, M., Latombe, G., Leiva, A., López-Iborra, G.M., López-Poveda, G., Mañosa, S., Martín, C.A., Morales, M.B., Moreira, F., Mougeot, F., Nikolov, B., Olea, P.P., Onrubia, A., Reverter, M., Revilla-Martín, N., Rigal, S., Jiménez, G.R., Sáez-Gómez, P., Sálek, M., Salgado, I., Santangeli, A., Santos, C., Sanz-Pérez, A., Serrano, D., Silva, J.P., Torrijo, A., Traba, J., Tryjanowski, P., Václav, R., Valera, F., Vögeli, M., Zurdo, J., Marques, A.T., 2025. Key conservation actions for European steppes in the context of the post-2020 global biodiversity framework. *Sustain. Sci.* <https://doi.org/10.1007/s11625-024-01602-6>, 2020.
- Pollock, L.J., O'Connor, L.M.J., Mokany, K., Rosauer, D.F., Talluto, M.V., Thuiller, W., 2020. Protecting biodiversity (in all its complexity): new models and methods. *Trends Ecol. Evol.* 35, 1119–1128. <https://doi.org/10.1016/j.tree.2020.08.015>.
- Powers, R.P., Jetz, W., 2019. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nat. Clim. Chang* 9, 323–329. <https://doi.org/10.1038/s41558-019-0406-z>.
- R Core Team, 2021. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.
- Railsback, S.F., Grimm, V., 2019. *Agent-based and Individual-Based Modeling: a Practical Introduction, second ed.* Princeton University Press, New Jersey, United States of America.
- Regos, A., Gonçalves, J., Arenas-Castro, S., Alcaraz-Segura, D., Guisan, A., Honrado, J.P., 2022. Mainstreaming remotely sensed ecosystem functioning in ecological niche models. *Remote Sens. Ecol. Conserv.* 8, 431–447. <https://doi.org/10.1002/rse2.255>.
- Rivas-Martínez, S., Díaz González, T.E., Fernández-González, F., Izco, J., Loidi, J., Lousã, M., Penas, A., 2002. *Vascular plant communities of Spain and Portugal. Itinera Geobot.* 15, 5–432.
- Salecker, J., Sciaini, M., Meyer, K.M., Wiegand, K., 2019. The <sc>nlrx r</sc> package: a next-generation framework for reproducible NetLogo model analyses. *Methods Ecol. Evol.* 10, 1854–1863. <https://doi.org/10.1111/2041-210X.13286>.
- Schmolke, A., Thorbek, P., DeAngelis, D.L., Grimm, V., 2010. Ecological models supporting environmental decision making: a strategy for the future. *Trends Ecol. Evol.* 25, 479–486. <https://doi.org/10.1016/j.TREE.2010.05.001>.
- Seaborn, T., Day, C.C., Galla, S.J., Höök, T.O., Jossie, E., Landguth, E.L., Liu, R., Simmons, R.K., 2023. Individual-based models for incorporating landscape processes in the conservation and management of aquatic systems. *Current Landscape Ecology Reports* 8, 119–135. <https://doi.org/10.1007/s40823-023-00089-8>.
- Serrano-Davies, E., Traba, J., Arroyo, B., Mougeot, F., Cuscó, F., Mañosa, S., Bota, G., Faria, N., Villers, A., Casas, F., Attie, C., Devoucoux, P., Bretagnolle, V., Morales, M.B., 2023. Biased adult sex ratios in Western Europe populations of Little Bustard *Tetrax tetrax* as a potential warning signal of unbalanced mortalities. *Bird. Conserv. Int.* 33, e40. <https://doi.org/10.1017/S0959270922000430>.
- Silva, J.P., Estanque, B., Moreira, F., Palmeirim, J.M., 2014. Population density and use of grasslands by female Little Bustards during lek attendance, nesting and brood-rearing. *J. Ornithol.* 155, 53–63. <https://doi.org/10.1007/s10336-013-0986-8>.
- Silva, J.P., Faria, N., Catry, T., 2007. Summer habitat selection and abundance of the threatened little bustard in Iberian agricultural landscapes. *Biol. Conserv.* 139, 186–194. <https://doi.org/10.1016/j.biocon.2007.06.013>.
- Silva, J.P., Marques, A.T., Bernardino, J., Allinson, T., Andryushchenko, Y., Dutta, S., Kessler, M., Martins, R.C., Moreira, F., Pallett, J., Pretorius, M.D., Scott, H.A., Shaw, J.M., Collar, N.J., 2023. The effects of powerlines on bustards: how best to mitigate, how best to monitor? *Bird. Conserv. Int.* 33. <https://doi.org/10.1017/S0959270922000314>.
- Silva, J.P., Moreira, F., Palmeirim, J.M., 2017. Spatial and temporal dynamics of lekking behaviour revealed by high-resolution GPS tracking. *Anim. Behav.* 129, 197–204. <https://doi.org/10.1016/j.anbehav.2017.05.016>.
- Silva, J.P., Pinto, M., Palmeirim, J.M., 2004. Managing landscapes for the little bustard *Tetrax tetrax*: lessons from the study of winter habitat selection. *Biol. Conserv.* 117, 521–528. <https://doi.org/10.1016/j.biocon.2003.09.001>.
- Silva, J.P., Soares, F.C., Guzmán, J.M., Marques, A.T., García de la Morena, E., Juhlin, C.M., Guisado, R.R., Cendrero, J., Crispim-Mendes, T., Valerio, F., Gameiro, J., Correia, R., Godinho, S., García-Baltasar, S., Abad-Gómez, J.M., Moreira, F., Pacheco, J., 2024. El sisón común (*Tetrax tetrax*) en Extremadura: Población y Ecología. Serie Monografías de la Dirección General de Sostenibilidad: Especies Protegidas. Junta de Extremadura, Mérida, España.
- Stillman, R.A., Railsback, S.F., Giske, J., Berger, U., Grimm, V., 2015. Making predictions in a changing world: the benefits of individual-based ecology. *Bioscience* 65, 140–150. <https://doi.org/10.1093/biosci/biu192>.
- Synes, N.W., Ponchon, A., Palmer, S.C.F., Osborne, P.E., Bocedi, G., Travis, J.M.J., Watts, K., 2020. Prioritizing conservation actions for biodiversity: lessening the impact from habitat fragmentation and climate change. *Biol. Conserv.* 252, 108819. <https://doi.org/10.1016/j.biocon.2020.108819>.
- Tallis, H., Fargione, J., Game, E., McDonald, R., Baumgarten, L., Bhagabati, N., Cortez, R., Griscom, B., Higgins, J., Kennedy, C.M., Kiesecker, J., Kroeger, T., Leberer, T., McGowan, J., Mandle, L., Masuda, Y.J., Morrison, S.A., Palmer, S., Shirer, R., Shyamsundar, P., Wolff, N.H., Possingham, H.P., 2021. Prioritizing actions: spatial action maps for conservation. *Ann. N. Y. Acad. Sci.* 1505, 118–141. <https://doi.org/10.1111/nyas.14651>.
- Tarjuelo, R., Delgado, M.P., Bota, G., Morales, M.B., Traba, J., Ponjoan, A., Hervás, I., Mañosa, S., 2013. Not only habitat but also sex: factors affecting spatial distribution of little bustard *Tetrax tetrax* families. *Acta Ornithol* 48, 119–128. <https://doi.org/10.3161/000164513x670070>.
- Thiele, J.C., Kurth, W., Grimm, V., 2014. Facilitating parameter estimation and sensitivity analysis of agent-based models: a cookbook using NetLogo and “R”. *J. Artif. Soc. Soc. Simulat.* 17. <https://doi.org/10.18564/jasss.2503>.
- Tisue, S., Wilensky, U., 2004. Netlogo: a simple environment for modeling complexity. In: *International Conference on Complex Systems*, pp. 16–21.
- Traba, J., Morales, M.B., 2019. The decline of farmland birds in Spain is strongly associated to the loss of fallowland. *Sci. Rep.* 9, 1–6. <https://doi.org/10.1038/s41598-019-45854-0>.
- Traba, J., Morales, M.B., Silva, J.P., Bretagnolle, V., Devoucoux, P., 2022. Habitat selection and space use. In: Bretagnolle, V., Traba, J., Morales, M.B. (Eds.), *Little Bustard: Ecology and Conservation*. Springer Nature, Switzerland, pp. 101–122. <https://doi.org/10.1007/978-3-030-84902-3>.
- Travers, H., Selinske, M., Nuno, A., Serban, A., Mancini, F., Barychka, T., Bush, E., Rasolofson, R.A., Watson, J.E.M., Milner-Gulland, E.J., 2019. A manifesto for predictive conservation. *Biol. Conserv.* 237, 12–18. <https://doi.org/10.1016/j.biocon.2019.05.059>.
- Ustin, S.L., Middleton, E.M., 2021. Current and near-term advances in Earth observation for ecological applications. *Ecol. Process* 10, 1–57. <https://doi.org/10.1186/s13717-020-00255-4>.
- Valjarević, A., 2024. GIS and remote sensing methods in predicting the dissipation time of rural settlements under the influence of climate change in the Republic of Serbia. *Journal of Urban Management*. <https://doi.org/10.1016/j.jum.2024.12.002>.
- van der Vaart, E., Beaumont, M.A., Johnston, A.S.A., Sibby, R.M., 2015. Calibration and evaluation of individual-based models using Approximate Bayesian Computation. *Ecol. Modell.* 312, 182–190. <https://doi.org/10.1016/j.ecolmodel.2015.05.020>.
- Vedder, D., Ankenbrand, M., Sarmento Cabral, J., 2021. Dealing with software complexity in individual-based models. *Methods Ecol. Evol.* 12, 2324–2333. <https://doi.org/10.1111/2041-210X.13716>.
- Wilensky, U., 1999. *NetLogo*. Evanston, IL: Center for Connected Learning and Computer-Based Modeling. Northwestern University.
- Wintle, B.A., Bekessy, S.A., Keith, D.A., Van Wilgen, B.W., Cabeza, M., Schröder, B., Carvalho, S.B., Falcucci, A., Maiorano, L., Regan, T.J., Rondinini, C., Boitani, L., Possingham, H.P., 2011. Ecological-economic optimization of biodiversity conservation under climate change. *Nat. Clim. Chang* 1, 355–359. <https://doi.org/10.1038/nclimate1227>.
- Zurell, D., König, C., Malchow, A.K., Kapitzka, S., Bocedi, G., Travis, J., Fandos, G., 2022. Spatially explicit models for decision-making in animal conservation and restoration. *Ecography* 1–16. <https://doi.org/10.1111/ecog.05787>, 2022.