Universidade de Évora - Instituto de Investigação e Formação Avançada

Programa de Doutoramento em Biologia

Tese de Doutoramento

Conservation Planning using Individual-Based Modeling: Assessing Anthropogenic Impacts on Endangered Species

Tiago Filipe Crispim Mendes

Orientador(es) | Ricardo Pita
Sérgio Rui Godinho
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Author statement

This PhD thesis was prepared as a compilation of scientific articles published or submitted for publication in journals registered in the Web of Science (WoS) that integrate some of the central chapters. These articles were carried out in collaboration with other authors. However, the candidate clarifies that he led all phases of the work of each article, including its conception, experimental design, data analysis, and writing.

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Oliveira, A., Medinas, D., Craveiro, J., Milhinhas, C., Sabino-Marques, H., **Mendes, T.**, Spadoni, G., Oliveira, A., Guilherme Sousa, L., Tapisso, J. T., Santos, S., Lopes-Fernandes, M., da Luz Mathias, M., Mira, A., & Pita, R. (2023). Large-scale grid-based detection in occupancy surveys of a threatened small mammal: A comparison of two non-invasive methods. *Journal for Nature Conservation*, *72*, 126362. https://doi.org/10.1016/j.jnc.2023.126362

Peralta, D., Vaz, T., Clara, F., **Mendes, T.**, Mira, A., Santos, S., Alves, P. C., Lambin, X., Beja, P., Paupério, J., & Pita, R. (2023). From species detection to population size indexing: the use of sign surveys for monitoring a rare and otherwise elusive small mammal. *European Journal of Wildlife Research*, *69*(9), 1–14. https://doi.org/10.1007/s10344-022-01634-2

Valerio, F., Godinho, S., Marques, A. T., **Crispim-Mendes, T.,** Pita, R., & Silva, J. P. (2024). GEE_xtract: High-quality remote sensing data preparation and extraction for multiple spatio-temporal ecological scaling. *Ecological Informatics*, *80*(January), 102502. https://doi.org/10.1016/j.ecoinf.2024.102502

Perez-granados, C., Benítez-lópez, A., Diaz, M., Marques, A., Gómez-catasús, J., …, **Crispim-Mendes, T.,**…, & Zurdo, J. (2023). A strategic European roadmap for the effective implementation of the post-2020 Global Biodiversity Framework in steppe ecosystems. PREPRINT (Version 1) available at Research Square https://doi.org/10.21203/rs.3.rs-3677639/v1

Books and book sections

Santos, S., Cerveira, A., & **Mendes, T.** (2023). *Microtus duodecimcostatus* rato-toupeira-mediterrânico. In M. Mathias, C. Fonseca, L. Rodrigues, C. Grilo, M. Lopes-Fernandes, J. Palmeirim, M. Santos-Reis, P. Alves, J. Cabral, M. Ferreira, A. Mira, C. Eira, N. Negrões, J. Paupério, R. Pita, A. Rainho, L. Rosalino, J. Tapisso, & J. Vingada (Eds.), *Livro Vermelho dos Mamíferos de Portugal Continental* (pp. 160–161). FCiências.ID, ICNF, Lisboa.

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. (In Press). El sisón común (*Tetrax tetrax*) en Extremadura: Población y Ecología. Serie Monografías de la Dirección General de Sostenibilidad: Especies Protegidas.

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Abstract

Human activities have historically influenced wildlife in multifaceted ways. However, the relentless expansion of human populations and changing consumption patterns have led to unprecedented habitat conversion and degradation, coupled with the proliferation of anthropogenic infrastructures. These changes result in significant spatio-temporal landscape alterations leading to habitat degradation and exposure to additional mortality factors, significantly impacting the survival of numerous species, and posing threats to ecosystems and biodiversity.

To safeguard ecosystem functioning and ensure species survival, robust conservation strategies and tools are essential to guide conservation policies based on cost-effective management aimed at sustainable development. Swift and well-informed actions are crucial in urgent conservation scenarios, supported by a comprehensive understanding of wildlife responses to anthropogenic threats and management efforts. This underscores the growing importance of predictive ecology in optimizing biodiversity conservation outcomes.

This thesis combined several technological, methodological, and scientific advancements to assess how endangered vertebrate species respond to various anthropogenic impacts, with the goal of informing management actions and supporting conservation planning. In this context Individual-based models (IBMs) stand as a promising tool, given their process-based nature and bottom-up approach, which allow for the representation of intraspecific and environmental variability. Focusing on three distinct species of conservation concern, native to the Mediterranean region, this research employed IBMs to examine the demographic effects of pressing anthropogenic impacts, such as human-induced spatio-temporal habitat changes and anthropogenic mortality associated with energy infrastructure.

Overall, results highlighted the influence of interactions between patch spatial and temporal attributes on post-colonization demography within dynamic environments and how environmental changes across space and time affect long-term population trends. Results also demonstrated the significant impact that anthropogenic mortality due to power lines can have on wildlife populations. Notably, this thesis provided compelling evidence of the potential of IBMs as a tool to support the management and conservation of endangered species.

Keywords: Modelling; Management; Demography; Anthropogenic Pressure; Habitat Loss

Planeamento de Conservação utilizando Individual-Based Models: Avaliando Impactos Antropogénicos em Espécies Ameaçadas

Resumo

O crescimento e expansão das populações humanas e as mudanças nos padrões de consumo tem levado a uma conversão e degradação de habitats sem precedentes, juntamente com a proliferação de infraestruturas antropogénicas. Estas alterações resultam em modificações espácio-temporais muito significativas na paisagem e expõem a vida selvagem a fatores adicionais de mortalidade, ameaçando a sobrevivência de numerosas espécies e impactando ecossistemas e biodiversidade.

Para salvaguardar o funcionamento dos ecossistemas e a sobrevivência das espécies, são essenciais estratégias e ferramentas de conservação robustas para orientar políticas de gestão custo-efetivas visando um desenvolvimento sustentável. Ações rápidas e bem informadas são cruciais em cenários de conservação urgentes, suportadas por uma compreensão abrangente das respostas das populações às ameaças antropogénicas e aos esforços de conservação. Isto sublinha a crescente importância da ecologia preditiva na otimização de ações de conservação.

Esta tese combinou diferentes avanços tecnológicos, metodológicos e científicos para avaliar a resposta de espécies de vertebrados ameaçadas por vários impactos antropogénicos, com o objetivo de informar ações de gestão e apoiar o planeamento da conservação. Neste contexto, os *Individual-Based Models* (IBMs) destacam-se como uma ferramenta promissora, dada a sua natureza baseada em processos, que permite representar a heterogeneidade individual e ambiental. Focando-se em três espécies ameaçadas, nativas da região Mediterrânica, esta investigação utilizou IBMs para examinar os efeitos demográficos de impactos antropogénicos, como alterações espácio-temporais e a mortalidade associada a infraestruturas.

No geral, os resultados destacaram a influência de interações entre atributos espaciais do habitat na demografia pós-colonização em ambientes dinâmicos, e como as mudanças ambientais no tempo e do espaço afetam as tendências populacionais a longo prazo. Foi também demonstrado o impacto significativo que a mortalidade causada por linhas elétricas pode ter nas populações, assim como o potencial da utilização de IBMs como ferramentas de apoio à gestão e conservação de espécies ameaçadas.

Palavras-chave: Modelação; Gestão; Demografia; Pressão Antropogénica; Perda de habitat

Chapter 1

General Introduction

Chapter 1 – General Introduction

1.1 Conservation challenges in a changing world

Anthropogenic impacts on the environment have led to the conversion and degradation of natural habitats, resulting in severe consequences for biodiversity (Powers and Jetz, 2019; Tilman et al., 2017). The ongoing growth of human populations, coupled with increasing per capita consumption rates, has catalysed profound transformations in global agricultural practices, leading to the adoption of more efficient systems for food, fuel, or fibre production (Wilting et al., 2017). According to the Food and Agriculture Organization (FAO, 2017), agricultural production more than tripled between 1960 and 2015. Projections suggest that by 2050, the global population will reach approximately 10 billion, potentially increasing agricultural demand by 50% compared to 2013 levels, primarily due to rising incomes in low- and middle-income countries. This anticipated shift in consumption patterns towards higher demand for meat, fruit, and vegetables relative to cereals will escalate pressure on natural resources, leading to increased deforestation, land degradation, and greenhouse gas emissions (FAO, 2017).

The rise in global living standards and socio-economic status in recent decades has driven a parallel increase in electricity demand and consumption. This trend is fuelled by expanding electrification, industrialization, urbanization, economic growth, and technological advancements (Atanane et al., 2023). Projections from the International Energy Agency (IEA, 2019) indicate that the world's electricity demand is expected to continue its upward trajectory, nearly doubling by 2050. However, this expansion comes at a cost, as the growing demand for renewable energy and the proliferation of new power lines pose a significant threat to wildlife, resulting in an additional source of mortality for multiple taxa, including birds (Bernardino et al., 2018), bats (Richardson et al., 2021), insects (Grodsky et al., 2021), fish, and other aquatic species (Copping et al., 2021; He et al., 2021).

Reconciling human development with biodiversity conservation has thus become a major global challenge. Throughout this thesis, I will delve into the potential of various technological, methodological, and scientific advancements in assessing the response of endangered species to different anthropogenic impacts. Additionally, I will explore how these advancements can aid in the development of improved management and conservation planning.

1.2 Anthropogenization of European landscapes

Currently, 90% of European land is covered by rural areas, with agriculture and forestry being the predominant land uses (Ellis and Ramankutty, 2008; Pašakarnis et al., 2013). European farmland areas traditionally support high biodiversity levels, resulting from the rich diversity of cultural landscapes that have prevailed during many centuries in many areas (Plieninger et al., 2006). This is most noticeable in Mediterranean peninsulas, considered as biodiversity hotspots in the European context (Hewitt, 2011).

The Mediterranean region stands as a testament to millennia of human presence and its profound impact on the natural environment. Over the course of 10,000 years, human interaction with the Mediterranean environment has been exceptionally long-standing and diverse (Blondel, 2006; Blondel et al., 2010). This extended history has left a significant imprint, particularly through a huge and progressive process of deforestation spanning the past millennium, which has profoundly transformed the Mediterranean landscape (Blondel and Aronson, 1999). This transformation led to the extinction of top predators and large herbivores, allowing the remaining taxa to explore and take advantage of these new landscapes with low-impact practices (Blondel, 2006). As a result, high levels of biodiversity have emerged in these anthropogenic landscapes, with species adapted to open habitats, such as grasslands and steppes, becoming particularly reliant on these anthropogenic and semi-natural environments (Blondel, 2006; Blondel and Aronson, 1999; Wright et al., 2012).

However, over the last decades, European agricultural landscapes have undergone profound transformations. The creation of the Common Agricultural Policy (CAP), aimed at enhancing food self-sufficiency, incentivized farmers to adopt new technologies and methods, expand average farm size, specialize in certain crops, and increase yields, primarily cereals and fodder for livestock production (meat and milk) (Reif and Vermouzek, 2019; van Vliet et al., 2015). These incentives have resulted in the conversion of natural habitats into agricultural land (i.e. habitat fragmentation *sensu lato*), the intensification of crop and livestock production in areas already under agricultural use (i.e. habitat degradation), or both processes together, resulting in temporal and spatial environmental homogenization (Benton et al., 2003). Conversely, there has been an increase in the abandonment of marginal lands, further reducing habitat complexity (Martínez-Abraín et al., 2020; Sirami et al., 2008). These shifts in agricultural practices are known to negatively impact farmland biodiversity, with detrimental effects on overall ecosystem functioning and human well-being (McMichael et al., 2007).

In line with global trends, Europe has been witnessing a rise in its electricity demand, while concurrently transforming its energy infrastructure towards a more sustainable, greener energy matrix (Agora Energiewende, 2019). In recent years, renewable energy technologies like solar photovoltaics and wind power have seen significant technological advancements and cost reductions. These developments are expected to facilitate the transition to green energy at the required scale and magnitude (Elia et al., 2021). This transition is expected to result in reduced reliance on fossil fuels and mitigating the impacts of climate change (IEA, 2019). However, while this transition presents promising opportunities for wildlife conservation, it also presents significant challenges, particularly for volant vertebrate taxa (Lees et al., 2022). In particular, some green energy infrastructure, such as wind turbines, can pose significant collision hazards for certain bird species, especially larger-bodied and soaring species (Thaxter et al., 2017). Despite this, before being distributed to final consumers, electricity produced at power plants must travel long distances on high-voltage transmission lines to substations, where the voltage is changed from high to median and low tension (Bernardino, 2021). Regardless of the technology used to generate power, the electricity grid is expanding at a rate of around 5% per year (Lees et al., 2022). This expansion leads to a proliferation of new overhead power lines, which constitute a significant source of mortality for birds due to electrocutions and collisions with wires, resulting in the deaths of hundreds of thousands to millions of birds annually (Bernardino et al., 2018).

All these anthropogenic pressures often lead to the alteration of ecological processes and the depletion of ecosystem services, and in some cases, can even result in species extinction (Haddad et al., 2015; Mitchell et al., 2015). Despite repeated policy commitments to reduce the rate of biodiversity loss (Mace et al., 2018), the relentless impact of human activities has led to dramatic and widespread declines in wildlife populations, evocative of past mass extinctions (Dirzo et al., 2014). In response to these challenges, the United Nations (UN) has launched the UN Decade on Ecosystem Restoration 2021–2030, aiming to protect and revive ecosystems worldwide and safeguard the integrity and resilience of our biosphere. More recently, the EU Environmental Council approved the Nature Restoration Law, further emphasizing the commitment to ecological restoration and conservation efforts. Habitat restoration, as a conservation approach, aims to rehabilitate both abiotic and biotic elements of habitats to support the recovery of target species or communities (Volis, 2019). However, the implementation of conservation and restoration initiatives is frequently hindered by their high cost and the scarcity of time and financial resources (McCarthy et al., 2012). In this context, accurately predicting how species respond to specific anthropogenic impacts and conservation interventions is crucial for devising efficient and cost-effective conservation management strategies.

1.3 Technological advancements in conservation science

To halt the alarming trend of biodiversity decline, conservation efforts must be grounded in robust data and leverage cutting-edge technological and methodological tools. Recent advancements in technology across various research disciplines have provided a diverse array of essential tools that have significantly impacted conservation science, improving the effectiveness and efficiency of efforts to preserve biodiversity and manage natural resources. These advancements include the sampling of behavioural and demographic traits of animal populations, the use of detailed environmental data from remote sensing, and ongoing improvements in the computational power and simulation modelling software (e.g. Gorelick et al., 2017; Ma et al., 2015; Regos et al., 2022; Ustin and Middleton, 2021). Together, these advancements offer promising opportunities for developing accurate ecological models capable of predicting population dynamics under scenarios of environmental change.

The increased understanding of behavioural and demographic processes has been greatly facilitated by advancements in animal tracking techniques. These techniques now enable the collection of large volumes of high-resolution movement data for animals of various sizes and ecologies (Kays et al., 2015). This field has experienced significant evolution in recent years, largely due to technological progress in battery production, resulting in smaller and more affordable batteries, as well as the development of energy-efficient microprocessors. Moreover, advancements in global positioning systems, cellular networks, and satellite technology have enabled widespread adoption of GPS tracking for medium- to large-sized vertebrates (Kays et al., 2015; Nathan et al., 2008). These developments have provided access to high-resolution spatio-temporal data on animal movement, further enhanced by the integration of on-animal sensors such as accelerometers and temperature gauges. Coupled with the rapidly increasing computational power, these advancements have propelled this field into the realm of big data (Kays et al., 2015).

Concurrently, recent advancements in satellite remote sensing offer a cost-effective means to monitor environmental changes at fine spatial and temporal scales, with the potential to correlate these changes with various population processes (Neumann et al., 2015). Currently, remote sensing techniques provide access to topographical data (e.g. SRTM: Shuttle Radar Topography Mission), land cover information (e.g. GlobCover, MODIS: Moderate Resolution

Imaging Spectroradiometer, Landsat), and climatic conditions (via modelled data) with resolutions ranging from several kilometres down to 10 meters (Kays et al., 2015; Kearney et al., 2020).

These type of data and resolution, coupled with detailed animal movement data, enables an unprecedented understanding of the dynamic interactions between animal behaviour, ecological process, and environmental conditions in both space and time Gaillard et al., 2010; Kays et al., 2015; Valerio et al., 2024). Consequently, such data enable the development of models capable of predicting movements while accounting for the internal and external factors that animals experience (Nathan et al., 2008). These models in turn will facilitate the identification and prediction of critical habitat patches, the comprehension of fragmentation and barrier effects on movement patterns, and the identification of wildlife corridors to promote connectivity (Kays et al., 2015).

Lastly, advancements in computational resources, such as the rapid increase in computing power and improved software accessibility, have facilitated the development and utilization of more sophisticated ecological models. This democratization of modelling efforts enables researchers to delve deeper into ecological phenomena, pushing the boundaries of ecological understanding and conservation practice.

1.4 The role of predictive ecology in conservation science

The escalating anthropogenic pressures on ecosystems and the resulting alarming rate of biodiversity loss highlight the urgent need for conservation efforts to evolve in complexity and efficacy, transitioning from reactive to proactive approaches (Travers et al., 2019). In response, there is a growing recognition of the pivotal role of predictive ecology in informing conservation strategies (Mouquet et al., 2015; Pennekamp et al., 2017). Predictive ecology is a branch of ecology that uses ecological models to predict the outcomes of various ecological processes and interactions (Mouquet et al., 2015; Travers et al., 2019). This approach enables conservationists to make informed decisions, assess risks, allocate resources efficiently, and plan for future scenarios, particularly in the face of uncertainty and rapid environmental changes (Travers et al., 2019).

Ecological models are cost-effective and valuable tools for encapsulating our current knowledge of biological phenomena and complex ecosystem processes (Guisan et al., 2013). They encompass a spectrum of methodologies, from correlative to process-based approaches, each providing unique insights into ecological processes and offering guidance for effective conservation strategies (Briscoe et al., 2019; Dormann et al., 2012). Correlative models, or phenomenological models, establish statistical relationships between environmental variables and biodiversity patterns (Dormann et al., 2012). While valuable for species-environment relationships, these models may lack mechanistic detail and struggle with extrapolation beyond observed data ranges. In contrast, process-based models aim to establish causal links between ecological variables, explicitly representing underlying processes such as physiology, demographics, and evolution (Zurell et al., 2022). By simulating the underlying processes driving ecological phenomena, mechanistic models offer a grounded understanding of ecosystem functioning, enabling robust predictions under novel environmental conditions and facilitating scenario testing for conservation impacts (Briscoe et al., 2023).

Furthermore, ecological models can be categorized based on their temporal dimension into static and dynamic models. Static models predict equilibrium states or snapshot distributions of species or habitats, providing valuable insights into spatial patterns and site selection for conservation actions (Kearney and Porter, 2009; Zurell et al., 2022). Dynamic models, on the other hand, simulate time-dependent changes in ecosystem states, capturing transient dynamics and temporal trajectories, crucial for predicting population viability, community dynamics, and ecosystem resilience under changing conditions (Zurell et al., 2022, 2016).

In practice, the choice between correlative and process-based models, as well as between static and dynamic representations of the environment, depends on the specific conservation objectives and the available data (Briscoe et al., 2019; Dormann et al., 2012). Correlative models may suffice for predicting species distributions and identifying suitable conservation sites, while process-based models are essential for understanding the underlying mechanisms driving ecosystem dynamics and predicting responses to management interventions. Dynamic models are indispensable for capturing temporal changes and guiding adaptive management strategies (Zurell et al., 2022).

Effective conservation planning requires a comprehensive grasp of spatio-temporal dynamics in biodiversity and ecosystems, encompassing species distributions, population trends, habitat suitability, and community responses to anthropogenic pressures and conservation actions. Predictive ecology offers valuable tools for achieving this understanding, by providing insights into both explanatory and anticipatory predictions (Mouquet et al., 2015).

However, integrating data from diverse sources remains a major challenge in predictive ecology, underscoring the need for enhanced collaboration and data accessibility across disciplines (Zurell et al., 2022). Individual-Based Models (IBMs), due to their process-based nature and flexible temporal and spatial representation, can play a crucial role in integrating data from various sources (Seaborn et al., 2023). This makes IBMs a particularly valuable tool in predictive ecology and conservation science, offering a new approach to address complex ecological questions and to develop effective management strategies (Stillman et al., 2015).

Ultimately, predictive ecology embodies a proactive approach to conservation, leveraging advanced modelling techniques to anticipate future ecological trajectories and inform conservation strategies under environmental uncertainty. By combining explanatory and anticipatory predictions, predictive ecology enhances our ability to conserve biodiversity and maintain ecosystem resilience in a rapidly changing world (Mouquet et al., 2015).

1.5 Individual-Based Models

IBMs, also known as Agent-Based Models, stand as a pivotal milestone in the advancement of simulation modelling across environmental, social, and computational sciences. These models represent a transformative approach, particularly in scenarios involving adaptive agents such as organisms, people, or institutions, and their intricate behaviour and interactions (An et al., 2021; Grimm and Railsback, 2005). Over the past two decades, IBMs have undergone a remarkable evolution, transitioning from rudimentary toy models to sophisticated frameworks capable of addressing multifaceted issues in the management of social-ecological systems (Berger et al., 2024). This evolution reflects a shift from opaque, ad hoc designs towards theory- and data-grounded designs, enhancing the transparency and coherence of these models, thereby fostering greater confidence in their predictive abilities (DeAngelis and Grimm, 2014; Grimm, 1999; Schlüter et al., 2017).

The surge in the use of IBMs is driven by a growing recognition of the inadequacies of traditional ecological models in capturing the intricacies of ecological interactions. Ecosystems exhibit non-linear dynamics and heterogeneity across spatial and temporal scales, posing challenges to conventional modelling approaches (Seaborn et al., 2023). IBMs offer a flexible framework for modelling these complexities, allowing researchers to explore emergent patterns and dynamics from complex systems with unprecedented detail and accuracy (Grimm and Railsback, 2005; Seaborn et al., 2023).

One of the defining features of IBMs is their ability to explicitly incorporate processes across multiple scales, enabling system-level behaviours to emerge from the interactions between individual agents and their environment (Grimm and Railsback, 2012; Lippe et al., 2019). This bottom-up approach surpasses the limitations of traditional population-level models, offering insights into phenomena that arise from fine-scale interactions occurring at the individual level (Seaborn et al., 2023). IBMs have been widely adopted across various research domains, ranging from simple, abstract models for testing theories to empirically based models with intricate submodels and parameters for understanding and solving real-world problems (An et al., 2021; Macal, 2016). In particular, by allowing the integration of spatially explicit environmental data, IBMs can offer unique insights into ecosystem dynamics and species behaviour. Leveraging geographic information systems (GIS) and remote sensing technologies, researchers can parameterize IBMs with real-world environmental data, enhancing the model's fidelity to ecological reality (Bithell et al., 2008; Seaborn et al., 2023). This spatially explicit approach enables IBMs to investigate landscape-scale phenomena, such as habitat fragmentation, species dispersal, and the effects of environmental change on biodiversity patterns (Gray et al., 2023; Heinrichs et al., 2018).

While IBMs have undoubtedly advanced our modelling capabilities, it's crucial to recognize their limitations and challenges. These models often require extensive computational resources and can be complex to develop and interpret (An et al., 2021). Moreover, ensuring the reliability and validity of IBM outcomes remains a persistent challenge, with models involving a rigorous and technically demanding development process (DeAngelis and Grimm, 2014; Grimm et al., 2014; Salecker et al., 2019; Schmolke et al., 2010).

The development and validation of IBMs require a thorough and iterative process, encompassing model design, parameterization, validation, and sensitivity analysis (Figure 1.1) (Augusiak et al., 2014; Seaborn et al., 2023). Collaboration with stakeholders and interdisciplinary teams is often essential to ensure the model's relevance and applicability to real-world scenarios (Grimm et al., 2014; McLane et al., 2011). As IBMs continue to evolve, there has been a growing emphasis on establishing standards for documenting model development and ensuring reproducibility in scientific research. Initiatives such as the Overview, Design concepts, and Details (ODD) protocol (Grimm et al., 2020, 2010) and the TRAnsparent and Comprehensive Ecological modelling documentation (TRACE) framework provide guidelines for documenting IBMs in a consistent and transparent manner (Grimm et al., 2014). Furthermore, the use of specialized software environments and programming languages tailored for IBMs has streamlined the development process and facilitated the dissemination of modelling techniques within the scientific community (Abar et al., 2017). Tools for designing simulation experiments and conducting sensitivity analyses have also played a crucial role in improving the reliability and robustness of model outcomes (e.g. Salecker et al., 2019).

The practical implications of IBMs in conservation science extend far beyond academic research, influencing management strategies and policy decisions (Gray et al., 2023; Malchow et al., 2024). By incorporating heterogeneous individual characteristics and environmental factors, IBMs offer a nuanced understanding of ecosystem dynamics, informing targeted conservation interventions and adaptive management strategies (Seaborn et al., 2023). Moreover, spatially explicit IBMs can play a crucial role in recovery planning for endangered species, facilitating data integration, threat prioritization, and action planning to meet conservation goals (e.g. Carter et al., 2015; Heinrichs et al., 2018; Zhang et al., 2017). Additionally, the scalability of IBMs allows for the exploration of alternative management scenarios and the assessment of their potential outcomes under different environmental contexts (Stillman et al., 2015).

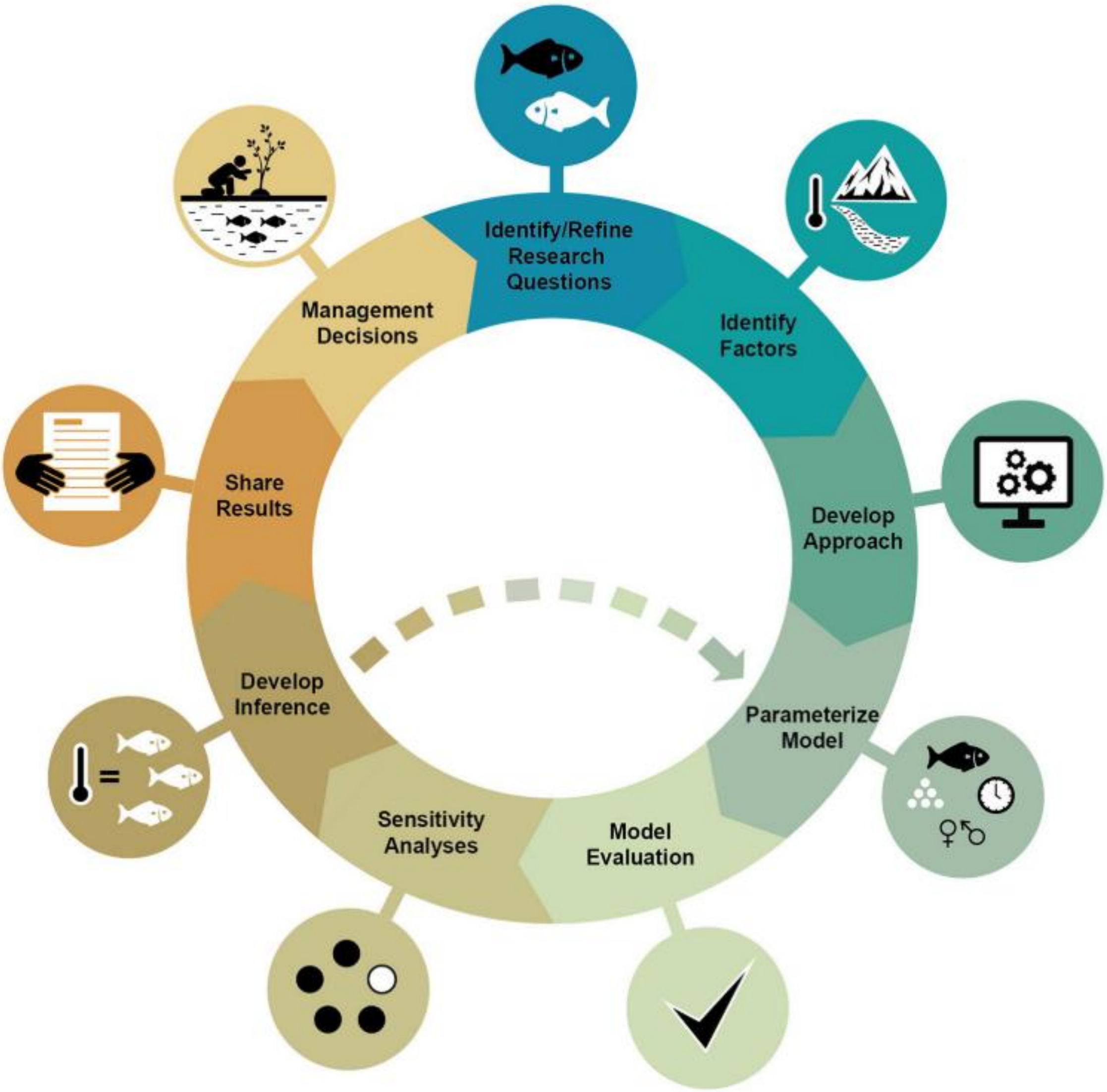

Figure 1.1 Iterative model process (adapted from Seaborn et al., 2023).

As we look to the future, IBMs hold immense potential for advancing scientific understanding and informing decision-making. However, achieving this potential requires continuous collaboration, innovation, and critical reflection to address the methodological and practical challenges inherent in IBM research.

1.6 Thesis aims

This thesis was motivated by the crucial need to gather and synthesize the vast amount of dispersed information available on a set of endangered vertebrate species with different life history attributes in order to improve their conservation planning in human-dominated Mediterranean areas. This integration is essential for developing more effective and cohesive conservation strategies grounded in comprehensive knowledge about the species. In response to this challenge, IBMs were assumed as a promising tool, due to their process-based nature and bottom-up approach, enabling the representation of heterogeneity among individuals and environmental attributes. IBMs, by incorporating detailed behaviours and explicit spatio-temporal representation of their environment across multiple scales, offer the flexibility to integrate diverse data from various sources and types. These characteristics allow for a more nuanced and comprehensive understanding of conservation challenges than traditional methodologies. Thus, IBMs represent a significant advancement for conservation planning by providing a comprehensive framework to address complex ecological interactions and inform targeted conservation efforts effectively.

The overall aim of this thesis is to leverage advanced technological tools to assess the impacts of anthropogenic environmental changes, particularly those linked to the agriculture and energy sectors, on vertebrate endangered species in Mediterranean ecosystems, in order to provide insights for enhanced management and conservation planning.

Specifically, this thesis has three main research goals:

1. Examine the demographic effects of human-induced spatio-temporal habitat changes on threatened species;
2. Investigate population-level impacts of anthropogenic mortality associated to the increase in energy infrastructures;
3. Highlight the high potential of IBMs as tools for supporting conservation management planning.

These research goals were explored from different perspectives, both independently and integratively throughout the thesis, using case studies of distinct species facing specific conservation challenges. Each study employed advanced modelling techniques to evaluate anthropogenic impacts on a chosen model species. Individual-Based Modelling techniques were used, with models developed at varying levels of complexity tailored to each case study's objectives. Additionally, the development of these models integrated additional technological resources, including animal tracking and remote sensing data, as well as machine learning algorithms to create predictive models at high spatio-temporal resolution.

1.7 Model species

Three species native to the Mediterranean region and occurring in the Iberian Peninsula were selected as case studies: the Cabrera vole (*Microtus cabrerae*), the Bonelli's eagle (*Aquila fasciata*), and the Little Bustard (*Tetrax tetrax*). These species have been extensively studied, yielding abundant behavioural and demographic data. Currently, they are classified as threatened on the Iberian Peninsula. Despite their taxonomic differences, including variations in body size, diet, habitat, behaviour, and overall ecological requirements, they collectively illustrate the common challenges shared by various ecological and functional guilds in response to human activities.

1.7.1 Cabrera vole

The Cabrera vole is a small mammal endemic to the Iberian Peninsula, which is typically spatially structured in small population units or subpopulations (colonies) connected by dispersal, thus presenting a metapopulation-like structure and dynamics crucial for its persistence at the landscape and regional scales (Pita et al., 2014). This species typically inhabits wet grassland patches, often smaller than 2000m^2, commonly associated to small streams, soil depressions, and temporarily flooded areas, often alongside agricultural fields, ditches, and road verges (Pita et al., 2011, 2006).

Currently, the Cabrera vole is globally classified as "Near-Threatened" by the IUCN, and as "Vulnerable" in both Portugal (Barbosa et al., 2023) and Spain (Palomo et al., 2007), primarily due to threats posed by human activities such as agricultural intensification, overgrazing, urbanization, and road construction. These activities result in habitat destruction, fragmentation, and degradation (Pita et al., 2007, 2006).

Small mammals like the Cabrera vole are valuable model systems for studying ecological processes in natural populations due to their capacity to respond swiftly to environmental changes (Barrett and Peles, 1999). In Mediterranean regions, several small mammal species, including the Cabrera vole, have experienced notable population declines linked to agricultural intensification (e.g. Mathias et al., 2023; Peralta et al., 2016; Pita et al., 2007).

1.7.2 Bonelli's eagle

The Bonelli's eagle is a long-lived territorial raptor with a wide geographic distribution, ranging from the Mediterranean coast across the Iberian Peninsula, Maghreb, and the Middle East, extending further into the Arabian Peninsula and southern Asia, covering territories from Iran to eastern China (Orta et al., 2020). This species undergoes distinct phases throughout its life cycle. Initially, after the post-fledging dependence period, individuals enter a nomadic and transient stage until territorial recruitment, dispersing over vast distances spanning hundreds or even thousands of kilometres (Balbontíin and Ferrer, 2009; Real and Mañosa, 2001). Following this phase, there is a territorial and monogamous period where individuals establish breeding pairs and exhibit fidelity to specific home ranges, displaying strong pair bonding within and between breeding seasons (Bosch et al., 2010).

Despite its expansive range, the Bonelli's eagle confronts significant conservation challenges, particularly in Portugal and Spain, where it is classified as “Vulnerable” (Almeida et al., 2022). This category of threat is largely due to anthropogenic factors, with electrocution at power lines and direct persecution identified as major causes of mortality for the species (Hernández-Matías et al., 2015; Real and Mañosa, 2001).

This model system was chosen because previous research has shown that even minor levels of mortality from electrocution can jeopardize local populations (Hernández-Matías et al., 2015). The plight of the Bonelli's eagle exemplifies the significant challenges posed by human-induced threats related to energy infrastructures. Studying this species provides critical insights into the conservation strategies needed not only for its survival but also for the broader preservation of similar long-lived territorial species facing comparable anthropogenic pressures.

1.7.3 Little Bustard

The little bustard is a medium-sized bird of the Bustard family (Otididae) that inhabits open dry grasslands and extensive agricultural landscapes (Iñigo and Barov, 2010). It is known as a migratory or partially migratory species, with the majority of individuals exhibiting migratory behaviour and seasonal variation in habitat preferences (García de la Morena et al., 2015; Silva et al., 2010, 2007). With a fragmented Palaearctic distribution (BirdLife International, 2018), it currently has two widely separated breeding populations, one in Southern Eurasia, mainly in Russia and Kazakhstan, and the other in Western Europe, mainly in the Iberian Peninsula and

France, with the Iberian population standing out as a global stronghold for the species (Iñigo and Barov, 2010).

Despite the Iberian Peninsula's importance for the species, it is classified as “Critically endangered” in Portugal (Almeida et al., 2022) and as “Endangered” in Spain (López-Jiménez et al., 2021), having experienced marked declines in this region over recent decades (García de la Morena et al., 2018; Silva et al., 2024, 2023). Primary threats include habitat loss and degradation due to agricultural intensification (Silva et al., 2022; Traba and Morales, 2019), as well as anthropogenic mortality, particularly from collisions with power lines (Marcelino et al., 2017; Moreira et al., 2012).

This species serves as an iconic and outstanding representative of steppe birds, a group intricately linked with Mediterranean agricultural ecosystems, yet facing significant global declines due to habitat conversion and intensified grazing practices (BirdLife International, 2022).

1.8 Thesis outline

The thesis is structured into six main chapters, consisting of a general introduction; four scientific papers, either published (Chapters 3 and 4), submitted for publication (Chapter 2), or in preparation for publication (Chapter 5) in international peer-reviewed journals; and a final chapter synthetizing the main conclusions. Specifically:

The present **Chapter 1** provides the general introduction which includes the thesis overall context, its main objectives, the thesis structure, and also a brief background for the most important topics addressed in this research.

Chapter 2 delves into the demography of local populations under frequent natural and anthropogenic disturbances, aiming to identify the specific characteristics of local habitat patches that enhance their potential to become temporary sources, hence contributing to metapopulation persistence in highly dynamic environments. Evidence suggests that species inhabiting networks of ephemeral patches frequently display source-sink dynamics, in which some local populations serve as temporary sources at some point between initial colonization and the disappearance of the patch. For effective local (site-based) conservation management in environments characterized by spatial and temporal heterogeneity, an understanding of the demography of these populations is essential to promote their long-term persistence.

We developed an IBM for simulating post-colonization demography within a single short-lived habitat patch amid a hostile matrix, considering different patch spatial attributes (size, habitat quality and connectivity) and times to disturbance (i.e. patch lifespan), using the Cabrera vole in highly dynamic agricultural systems as case study. The IBM encompasses individual-level patterns and behaviours, including voles spatial organization, breeding behaviour, parental care, migration, and survival. Our primary objective was to investigate the overarching hypothesis that the emergence of a source local population within an ephemeral habitat patch is primarily driven by the patch's spatial attributes and the time to disturbance. The insights gained from our findings offer valuable guidance for refining conservation management strategies in networks of short-lived habitat patches affected by disturbance.

> **Paper #1 – Crispim-Mendes T.**, Roos D., Ferreira C.M., Paupério P., Silva J.P., Godinho S., Alves P.C., Mira A., Beja P., Lambin X. & Pita R. (Under revision) Patch spatial attributes and time to disturbance affect the emergence of source local populations within ephemeral habitats. Ecological Modelling

Chapter 3 investigates the impact of additional mortality from anthropogenic sources on population dynamics in long-lived top predators. Given their relatively low intrinsic population growth rates, large home ranges, small population sizes, and low carrying capacity, it is anticipated that long-lived top predators are highly susceptible to additional mortality. Understanding how the magnitude of population impacts varies with the spatial distribution of mortality risk across territories and the exposure of different life stages (i.e., territorial, and non-territorial individuals) is essential for designing cost-effective conservation strategies to prevent and mitigate these impacts.

We developed an IBM to assess how exposure to additional anthropogenic mortality affects long-lived raptor species exhibiting territorial behaviour, using the Bonelli's eagle under variable risks of electrocution at power lines as case study. The model integrates individual-level patterns and behaviours related to mortality, age structure, reproduction, dispersion, and territoriality. Our primary objective was to estimate changes in population growth rates resulting from variations in mortality risks among different life stages (i.e., territorial versus non-territorial individuals) and across different sets of territories (i.e., few versus multiple territories).

> **Paper #2 –** Marques A.T.*, **Crispim-Mendes T.***, Palma L., Pita R., Moreira F. & Beja P. (2024) Using individual-based demographic modelling to estimate the impacts of anthropogenic mortality on territorial predators. Ecological Modelling 493, 110752. https://doi.org/10.1016/j.ecolmodel.2024.110752
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> *Joint first authors

Chapter 4 investigates how environmental changes across space and time impact long-term population trends, focusing on endangered species with distinct phenological phases. For these species, it is imperative to gain a thorough understanding of the key ecological traits shaping their distribution during each phenological phase. This understanding is crucial for accurately discerning their long-term declining trends and identifying crucial conservation areas throughout the phenological cycle. Additionally, the reconstruction of a species' historical distribution range emerges as a valuable tool for comprehending the impact of interannual environmental and climatic fluctuations.

We built high-resolution Species Distribution Models (SDMs) for the key phenological phases of the little bustard. The SDMs were developed using a machine learning algorithm (Random Forests), which integrated remotely sensed metrics at high temporal resolution with long-term GPS telemetry data. Our specific objectives included characterizing the drivers of the species' distribution across its winter, breeding, and post-breeding phases, as well as determining the variation in habitat suitability for the little bustard both spatially, across phenological phases (seasonal SDMs), and temporally, over the years (2005–2021).

> **Paper #3 – 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. Landscape Ecology 39, 49. https://doi.org/10.1007/s10980-024-01848-6

Chapter 5 explores the potential of utilizing IBMs as management support tools to aid in the conservation of endangered species. Conservation and restoration efforts are frequently hampered by limited time and financial resources, which are often in short supply. However, especially for endangered species, it is crucial to employ targeted, precise, and well-founded management strategies to ensure the effectiveness of conservation measures and maximize cost-effectiveness. In this context, having access to a tool that enables the prediction of the population impact of implementing different management strategies, as well as the assessment of their implementation costs, allows for a cost-effectiveness analysis and the selection of the best management strategies according to different conservation objectives and available budget. This capability can provide an invaluable asset for guiding conservation efforts toward optimal outcomes.

We developed a high-resolution, spatially explicit IBM to support the conservation efforts for the little bustard across its whole area of occurrence in Extremadura, Spain. The model leverages the SDMs developed in Chapter 4 to provide a comprehensive understanding of the species' distribution and population dynamics throughout the yearly cycle. To accurately simulate the species' demographic trends, the model incorporates patterns of phenology and age structure, along with individual-level processes such as survival, reproduction, spatial organization, migration, and dispersion. Our primary objectives included calibrating and validating the model and conducting a preliminary theoretical exercise to assess its potential and usefulness. We aimed to gain a broad understanding of how a cost-effective conservation plan for the species could be implemented in the study area, with a particular focus on mitigating anthropogenic mortality and enhancing habitat suitability in selected locations.

> **Paper #4 –** **Crispim-Mendes, T.**, Marques, A.T., Valerio, F., Godinho, S., Pita, R., Silva, J.P. (In prep.) Spatially explicit individual-based models as tools to address pressing conservation decisions: A case study with the little bustard.

Chapter 6 delves into the main findings of the preceding chapters and the significance of the current research for conservation planning. Additionally, it provides a synthesis on the potential of Individual-Based Models in examining the effects of anthropogenic activities on endangered species and their utility as tools for conservation management (Figure 1.2). The chapter concludes with a glimpse into potential directions for future research and offers some concluding remarks.

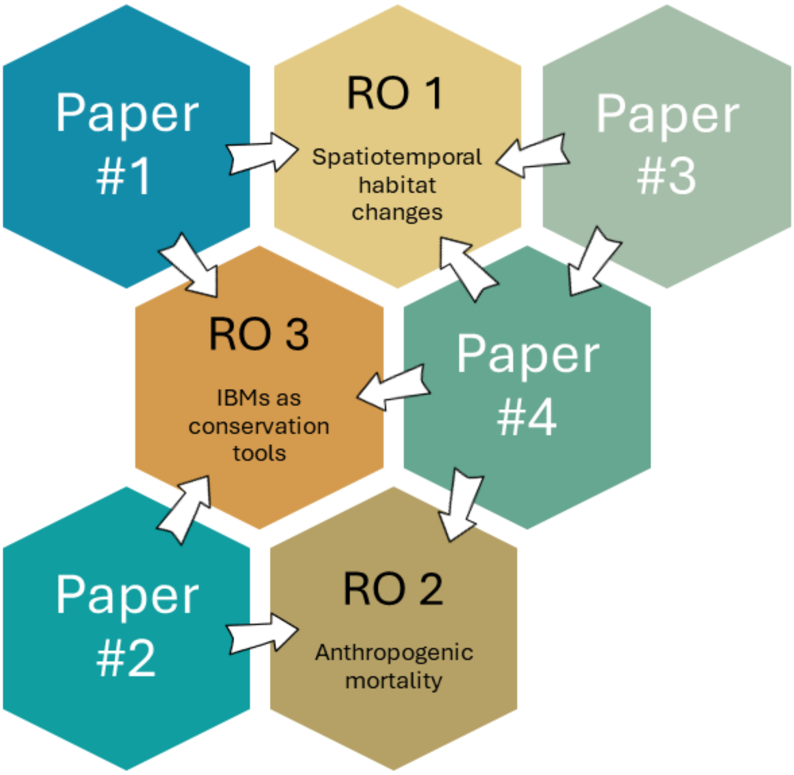

Figure 1.2 Relationship between the research papers and the three main research objectives (RO 1-3) of the thesis.

1.9 References

Abar, S., Theodoropoulos, G.K., Lemarinier, P., O'Hare, G.M.P., O'Hare, G.M.P., 2017. Agent Based Modelling and Simulation tools: A review of the state-of-art software. Comput Sci Rev 24, 13–33. https://doi.org/10.1016/j.cosrev.2017.03.001

Agora Energiewende, 2019. European Energy Transition 2030: The Big Picture. Ten Priorities for the next European Commission to meet the EU's 2030 targets and accelerate towards 2050, Agora Energiewende.

Almeida, J., Godinho, C., Leitão, D., Lopes, R., 2022. Lista Vermelha das Aves de Portugal Continental, Centro Nacional de Conservação da Flora. SPEA, ICNF, LabOR/UÉ, CIBIO/BIOPOLIS, Portugal.

An, L., Grimm, V., Sullivan, A., TurnerII, B.L., Malleson, 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

Atanane, A., Benabbou, L., El Ouafi, A., 2023. Electricity demand Forecasting: A systematic literature review, in: 2023 14th International Conference on Intelligent Systems: Theories and Applications (SITA). IEEE, pp. 1–8. https://doi.org/10.1109/SITA60746.2023.10373741

Augusiak, J., Van den Brink, P.J., Grimm, V., 2014. Merging validation and evaluation of ecological models to "evaludation": A review of terminology and a practical approach. Ecol Modell 280, 117–128. https://doi.org/10.1016/j.ecolmodel.2013.11.009

Balbontíin, J., Ferrer, M., 2009. Movements of juvenile Bonelli's eagles *Aquila fasciata* during dispersal. Bird Study 56, 86–95. https://doi.org/10.1080/00063650802648374

Barbosa, S., Mestre, F., Pita, R., 2023. *Microtus cabrerae* rato-de-cabrera, in: Mathias ML (coord.), Fonseca C, Rodrigues L, Grilo C, Lopes-Fernandes M, Palmeirim JM, Santos-Reis M, Alves PC, Cabral JA, Ferreira M, Mira A, Eira C, Negrões N, Paupério J, Pita R, Rainho A, Rosalino LM, T.J.& V.J. (Ed.), Livro Vermelho Dos Mamíferos de Portugal Continental. Lisboa.

Barrett, G.W., Peles, J.D., 1999. Landscape Ecology of Small Mammals. Springer- Verlag, New York.

Benton, T., Vickery, J., Wilson, J., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol Evol 18, 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9

Berger, U., Bell, A., Barton, C.M., Chappin, E., Dreßler, G., Filatova, T., Fronville, T., Lee, A., van Loon, E., Lorscheid, I., Meyer, M., Müller, B., Piou, C., Radchuk, V., Roxburgh, N., Schüler, L., Troost, C., Wijermans, N., Williams, T.G., Wimmler, M.C., Grimm, V., 2024. Towards reusable building blocks for agent-based modelling and theory development. Environmental Modelling & Software 175, 106003. https://doi.org/10.1016/j.envsoft.2024.106003

Bernardino, J., 2021. Improving impact monitoring and mitigation of bird collisions with power lines (Ph.D. Thesis). Faculdade de Ciências da Universidade do Porto, Portugal.

Bernardino, J., Bevanger, K., Barrientos, R., Dwyer, J.F., Marques, A.T., Martins, R.C., Shaw, J.M., Silva, J.P., Moreira, F., 2018. Bird collisions with power lines: State of the art and priority areas for research. Biol Conserv 222, 1–13. https://doi.org/10.1016/j.biocon.2018.02.029

BirdLife International, 2022. State of the World's Birds 2022: Insights and solutions for the biodiversity crisis. Cambridge, UK: BirdLife Internationa, Cambridge, UK. BirdLife International.

BirdLife International, 2018. State of the world's birds: taking the pulse of the planet. BirdLife International, Cambridge, UK.

Bithell, M., Brasington, J., Richards, K., 2008. Discrete-element, individual-based and agent-based models: Tools for interdisciplinary enquiry in geography? Geoforum 39, 625–642. https://doi.org/10.1016/j.geoforum.2006.10.014

Blondel, J., 2006. The "design" of Mediterranean landscapes: A millennial story of humans and ecological systems during the historic period. Hum Ecol 34, 713–729. https://doi.org/10.1007/s10745-006-9030-4

Blondel, J., Aronson, J., 1999. Biology and Wildlife of the Mediterranean Region. Oxford University Press, Oxford.

Blondel, J., Aronson, J., Bodiou, J.Y., Boeuf, G., 2010. The Mediterranean Region: Biological Diversity in Space and Time, The Quarterly Review of Biology. Oxford University Press, New York.

Bosch, R., Real, J., Tintó, A., Zozaya, E.L., Castell, C., 2010. Home-ranges and patterns of spatial use in territorial Bonelli's Eagles *Aquila fasciata*. Ibis 152, 105–117. https://doi.org/10.1111/j.1474-919X.2009.00985.x

Briscoe, N.J., Elith, J., Salguero-Gómez, R., Lahoz-Monfort, J.J., Camac, J.S., Giljohann, K.M., Holden, M.H., Hradsky, B.A., Kearney, M.R., McMahon, S.M., Phillips, B.L., Regan, T.J., Rhodes, J.R., Vesk, P.A., Wintle, B.A., Yen, J.D.L., Guillera-Arroita, G., 2019. Forecasting species range dynamics with process-explicit models: matching methods to applications. Ecol Lett 22, 1940–1956. https://doi.org/10.1111/ele.13348

Briscoe, N.J., Morris, S.D., Mathewson, P.D., Buckley, L.B., Jusup, M., Levy, O., Maclean, I.M.D., Pincebourde, S., Riddell, E.A., Roberts, J.A., Schouten, R., Sears, M.W., Kearney, M.R., 2023. Mechanistic forecasts of species responses to climate change: The promise of biophysical ecology. Glob Chang Biol 29, 1451–1470. https://doi.org/10.1111/gcb.16557

Carter, N., Levin, S., Barlow, A., Grimm, V., 2015. Modeling tiger population and territory dynamics using an agent-based approach. Ecol Modell 312, 347–362. https://doi.org/10.1016/j.ecolmodel.2015.06.008

Copping, A.E., Hemery, L.G., Viehman, H., Seitz, A.C., Staines, G.J., Hasselman, D.J., 2021. Are fish in danger? A review of environmental effects of marine renewable energy on fishes. Biol Conserv 262, 109297. https://doi.org/10.1016/j.biocon.2021.109297

DeAngelis, D.L., Grimm, V., 2014. Individual-based models in ecology after four decades. F1000Prime Rep 6. https://doi.org/10.12703/P6-39

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science (1979) 345, 401–406. https://doi.org/10.1126/science.1251817

Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B., Singer, A., 2012. Correlation and process in species distribution models: Bridging a dichotomy. J Biogeogr 39, 2119–2131. https://doi.org/10.1111/j.1365-2699.2011.02659.x

Elia, A., Kamidelivand, M., Rogan, F., Ó Gallachóir, B., 2021. Impacts of innovation on renewable energy technology cost reductions. Renewable and Sustainable Energy Reviews 138. https://doi.org/10.1016/j.rser.2020.110488

Ellis, E.C., Ramankutty, N., 2008. Putting people in the map: Anthropogenic biomes of the world. Front Ecol Environ 6, 439–447. https://doi.org/10.1890/070062

FAO, 2017. The future of food and agriculture – Trends and challenges. FAO - Food and Agriculture Organization of the United Nations, Rome.

Gaillard, J.M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., Van Moorter, B., 2010. Habitat-performance relationships: Finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 2255–2265. https://doi.org/10.1098/rstb.2010.0085

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., 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

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sens Environ 202, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Gray, C., Rothman, D.S., Peters-Burton, E., Smith, C., Parsons, E.C.M., 2023. Individual-Based Model use in Marine Policy. Journal of Integrative Environmental Sciences 20, 2271550. https://doi.org/10.1080/1943815X.2023.2271550

Grimm, V., 1999. Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? Ecol Modell 115, 129–148. https://doi.org/10.1016/S0304-3800(98)00188-4

Grimm, V., Augusiak, 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., 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., 2012. Pattern-oriented modelling: A “multi-scope” for predictive systems ecology. Philosophical Transactions of the Royal Society B: Biological Sciences 367, 298–310. https://doi.org/10.1098/rstb.2011.0180

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, StevenF., 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. Jasss 23. https://doi.org/10.18564/jasss.4259

Grodsky, S.M., Campbell, J.W., Hernandez, R.R., 2021. Solar energy development impacts flower-visiting beetles and flies in the Mojave Desert. Biol Conserv 263, 109336. https://doi.org/10.1016/j.biocon.2021.109336

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

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1, e1500052. https://doi.org/10.1126/sciadv.1500052

He, F., Thieme, M., Zarfl, C., Grill, G., Lehner, B., Hogan, Z., Tockner, K., Jähnig, S.C., 2021. Impacts of loss of free-flowing rivers on global freshwater megafauna. Biol Conserv 263, 109335. https://doi.org/10.1016/j.biocon.2021.109335

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

Hernández-Matías, A., Real, J., Parés, F., Pradel, R., 2015. Electrocution threatens the viability of populations of the endangered Bonelli's eagle (*Aquila fasciata*) in Southern Europe. Biol Conserv 191, 110–116. https://doi.org/10.1016/j.biocon.2015.06.028

Hewitt, G.M., 2011. Mediterranean Peninsulas: The Evolution of Hotspots, Biodiversity Hotspots. Springer Berlin Heidelberg, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-20992-5_7

IEA, 2019. World Energy Outlook 2019, IEA. Paris.

Iñigo, A., Barov, B., 2010. Action plan for the little bustard *Tetrax tetrax* in the European Union, SEO|BirdLife and BirdLife International for the European Commission.

Kays, R., Crofoot, M.C., Jetz, W., Wikelski, M., 2015. Terrestrial animal tracking as an eye on life and planet. Science (1979) 348, aaa2478. https://doi.org/10.1126/science.aaa2478

Kearney, M., Porter, W., 2009. Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. Ecol Lett 12, 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x

Kearney, M.R., Gillingham, P.K., Bramer, I., Duffy, J.P., Maclean, I.M.D., 2020. A method for computing hourly, historical, terrain-corrected microclimate anywhere on earth. Methods Ecol Evol 11, 38–43. https://doi.org/10.1111/2041-210X.13330

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

Lippe, M., Bithell, M., Gotts, N., Natalini, D., Barbrook-Johnson, P., Giupponi, C., Hallier, M., Hofstede, G.J., Le Page, C., Matthews, R.B., Schlüter, M., Smith, P., Teglio, A., Thellmann, K., 2019. Using agent-based modelling to simulate social-ecological systems across scales. Geoinformatica 23, 269–298. https://doi.org/10.1007/s10707-018-00337-8

López-Jiménez, Nicolás, García de la Morena, E., Bota, G., Mañosa, S., Morales, M.B., Traba, J., 2021. Sisón Comun, *Tetrax tetrax*, in: López-Jiménez, N. (Ed.), Libro Rojo de Las Aves de España. SEO/BirdLife, Madrid, pp. 521–527.

Ma, Y., Wu, H., Wang, L., Huang, B., Ranjan, R., Zomaya, A., Jie, W., 2015. Remote sensing big data computing: Challenges and opportunities. Future Generation Computer Systems 51, 47–60. https://doi.org/10.1016/j.future.2014.10.029

Macal, C.M., 2016. Everything you need to know about agent-based modelling and simulation. Journal of Simulation 10, 144–156. https://doi.org/10.1057/jos.2016.7

Mace, G.M., Barrett, M., Burgess, N.D., Cornell, S.E., Freeman, R., Grooten, M., Purvis, A., 2018. Aiming higher to bend the curve of biodiversity loss. Nat Sustain 1, 448–451. https://doi.org/10.1038/s41893-018-0130-0

Malchow, A., Fandos, G., Kormann, U.G., Grüebler, M.U., Kéry, M., Hartig, F., Zurell, D., 2024. Fitting individual-based models of spatial population dynamics to long-term monitoring data. Ecological Applications. https://doi.org/10.1002/eap.2966

Marcelino, J., Moreira, F., Mañosa, S., Cuscó, F., Morales, M.B., García de la Morena, E., Bota, G., Palmeirim, J.M., Silva, J.P., 2017. 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

Martínez-Abraín, A., Jiménez, J., Jiménez, I., Ferrer, X., Llaneza, L., Ferrer, M., Palomero, G., Ballesteros, F., Galán, P., Oro, D., 2020. Ecological consequences of human depopulation of rural areas on wildlife: A unifying perspective. Biol Conserv 252. https://doi.org/10.1016/j.biocon.2020.108860

Mathias, M., Fonseca, C., Rodrigues, L., Grilo, C., Lopes-Fernandes, M., Palmeirim, J., Santos-Reis, M., Alves, P., Cabral, J., Ferreira, M., Mira, A., Eira, C., Negrões, N., Paupério, J., Pita, R., Rainho, A., Rosalino, L., Tapisso, J., Vingada, J., 2023. Livro Vermelho dos Mamíferos de Portugal Continental. FCiências.ID, ICNF, Lisboa.

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 (1979) 338, 946–949. https://doi.org/10.1126/science.1229803

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

McMichael, A.J., Powles, J.W., Butler, C.D., Uauy, R., 2007. Food, livestock production, energy, climate change, and health. The Lancet 370, 1253–1263. https://doi.org/10.1016/S0140-6736(07)61256-2

Mitchell, M.G.E., Suarez-Castro, A.F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K.J., Johansen, K., Rhodes, J.R., 2015. Reframing landscape fragmentation's effects on ecosystem services. Trends Ecol Evol 30, 190–198. https://doi.org/10.1016/j.tree.2015.01.011

Moreira, F., Silva, J.P., Alcazar, R., Palmeirim, J.M., 2012. Movimentos locais e regionais do sisão (*Tetrax tetrax*): aplicação ao desenvolvimento de uma carta de risco de colisão com linhas aéreas de distribuição de energia. Fundo EDP para a Biodiversidade.

Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., Faure, D., Garnier, E., Gimenez, O., Huneman, P., Jabot, F., Jarne, P., Joly, D., Julliard, R., Kéfi, S., Kergoat, G.J., Lavorel, S., Le Gall, L., Meslin, L., Morand, S., Morin, X., Morlon, H., Pinay, G., Pradel, R., Schurr, F.M., Thuiller, W., Loreau, M., 2015. Predictive ecology in a changing world. Journal of Applied Ecology 52, 1293–1310. https://doi.org/10.1111/1365-2664.12482

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences 105, 19052–19059. https://doi.org/10.1073/pnas.0800375105

Neumann, W., Martinuzzi, S., Estes, A.B., Pidgeon, A.M., Dettki, H., Ericsson, G., Radeloff, V.C., 2015. Opportunities for the application of advanced remotely-sensed data in ecological studies of terrestrial animal movement. Mov Ecol 3, 8. https://doi.org/10.1186/s40462-015-0036-7

Orta, J., Kirwan, G.M., Christie, D., Boesman, P.F.D., Marks, J.S., Garcia, E., 2020. Bonelli's Eagle (*Aquila fasciata*), in: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D., de Juana, E. (Eds.), Birds of the World. Cornell Lab of Ornithology, pp. 573–574. https://doi.org/10.2173/bow.boneag2.01

Palomo, L., Gisbert, J., Blanco, J., 2007. Atlas y Libro Rojo de los Mamíferos Terrestres de España. SECEM, SECEMU, Madrid, Spain: Dirección General de Conservación de la Naturaleza.

Pašakarnis, G., Morley, D., Maliene, V., 2013. Rural development and challenges establishing sustainable land use in Eastern European countries. Land use policy 30, 703–710. https://doi.org/10.1016/j.landusepol.2012.05.011

Pennekamp, F., Adamson, M.W., Petchey, O.L., Poggiale, J.C., Aguiar, M., Kooi, B.W., Botkin, D.B., DeAngelis, D.L., 2017. The practice of prediction: What can ecologists learn from applied, ecology-related fields? Ecological Complexity 32, 156–167. https://doi.org/10.1016/j.ecocom.2016.12.005

Peralta, D., Leitão, I., Ferreira, A., Mira, A., Beja, P., Pita, R., 2016. Factors affecting southern water vole (*Arvicola sapidus*) detection and occupancy probabilities in Mediterranean farmland. Mammalian Biology 81, 123–129. https://doi.org/10.1016/j.mambio.2015.10.006

Pita, R., Beja, P., Mira, A., 2007. Spatial population structure of the Cabrera vole in Mediterranean farmland: The relative role of patch and matrix effects. Biol Conserv 134, 383–392. https://doi.org/10.1016/j.biocon.2006.08.026

Pita, R., Mira, A., Beja, P., 2014. *Microtus cabrerae* (Rodentia: Cricetidae). Mammalian Species 46, 48–70. https://doi.org/10.1644/912.1

Pita, R., Mira, A., Beja, P., 2011. Assessing habitat differentiation between coexisting species: The role of spatial scale. Acta Oecologica 37, 124–132. https://doi.org/10.1016/j.actao.2011.01.006

Pita, R., Mira, A., Beja, P., 2006. Conserving the Cabrera vole, *Microtus cabrerae*, in intensively used Mediterranean landscapes. Agric Ecosyst Environ 115, 1–5. https://doi.org/10.1016/j.agee.2005.12.002

Plieninger, T., Höchtl, F., Spek, T., 2006. Traditional land-use and nature conservation in European rural landscapes. Environ Sci Policy 9, 317–321. https://doi.org/10.1016/j.envsci.2006.03.001

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

Real, J., Mañosa, S., 2001. Dispersal of juvenile and immature Bonelli's eagles in northeastern Spain. Journal of Raptor Research 35, 9–14.

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

Reif, J., Vermouzek, Z., 2019. Collapse of farmland bird populations in an Eastern European country following its EU accession. Conserv Lett 12, 1–8. https://doi.org/10.1111/conl.12585

Richardson, S.M., Lintott, P.R., Hosken, D.J., Economou, T., Mathews, F., 2021. Peaks in bat activity at turbines and the implications for mitigating the impact of wind energy developments on bats. Sci Rep 11, 1–6. https://doi.org/10.1038/s41598-021-82014-9

Salecker, J., Sciaini, M., Meyer, K.M., Wiegand, K., 2019. The NLRX R package: A next-generation framework for reproducible NetLogo model analyses. Methods Ecol Evol 10, 1854–1863. https://doi.org/10.1111/2041-210X.13286

Schlüter, M., Baeza, A., Dressler, G., Frank, K., Groeneveld, J., Jager, W., Janssen, M.A., McAllister, R.R.J., Müller, B., Orach, K., Schwarz, N., Wijermans, N., 2017. A framework for mapping and comparing behavioural theories in models of social-ecological systems. Ecological Economics 131, 21–35. https://doi.org/10.1016/j.ecolecon.2016.08.008

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

Silva, J.P., Arroyo, B., Marques, A.T., Morales, M.B., Devoucoux, P., Mougeot, F., 2022. Threats Affecting Little Bustards: Human Impacts, in: Bretagnolle, V., Traba, J., Morales, M.B. (Eds.), Little Bustard: Ecology and Conservation. Springer Nature, Switzerland, pp. 243–272. https://doi.org/10.1007/978-3-030-84902-3

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., Gameiro, J., Valerio, F., Marques, A.T., 2024. Portugal's farmland bird crisis requires action. Science (1979) 383, 157–157. https://doi.org/10.1126/science.adn1390

Silva, J.P., Marques, A.T., Carrapato, C., Machado, R., Alcazar, R., Delgado, A., Godinho, C., Elias, G., Gameiro, J., 2023. A nationwide collapse of a priority grassland bird related to livestock conversion and intensification. Sci Rep 13, 10005. https://doi.org/10.1038/s41598-023-36751-8

Silva, J.P., Palmeirim, J.M., Moreira, F., 2010. Higher breeding densities of the threatened little bustard *Tetrax tetrax* occur in larger grassland fields: Implications for conservation. Biol Conserv 143, 2553–2558. https://doi.org/10.1016/j.biocon.2010.06.023

Sirami, C., Brotons, L., Burfield, I., Fonderflick, J., Martin, J.L., 2008. Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean. Biol Conserv 141, 450–459. https://doi.org/10.1016/j.biocon.2007.10.015

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

Thaxter, C.B., Buchanan, G.M., Carr, J., Butchart, S.H.M., Newbold, T., Green, R.E., Tobias, J.A., Foden, W.B., O'Brien, S., Pearce-Higgins, J.W., 2017. Bird and bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment. Proceedings of the Royal Society B: Biological Sciences 284. https://doi.org/10.1098/rspb.2017.0829

Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., Packer, C., 2017. Future threats to biodiversity and pathways to their prevention. Nature 546, 73–81. https://doi.org/10.1038/nature22900

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

Travers, H., Selinske, M., Nuno, A., Serban, A., Mancini, F., Barychka, T., Bush, E., Rasolofoson, 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

Valerio, F., Godinho, S., Marques, A.T., Crispim-Mendes, T., Pita, R., Silva, J.P., 2024. GEE_xtract: High-quality remote sensing data preparation and extraction for multiple spatio-temporal ecological scaling. Ecol Inform 80, 102502. https://doi.org/10.1016/j.ecoinf.2024.102502 van Vliet, J., de Groot, H.L.F., Rietveld, P., Verburg, P.H., 2015. Manifestations and underlying drivers of agricultural land use change in Europe. Landsc Urban Plan 133, 24–36. https://doi.org/10.1016/j.landurbplan.2014.09.001

Volis, S., 2019. Conservation-oriented restoration – a two for one method to restore both threatened species and their habitats. Plant Divers 41, 50–58. https://doi.org/10.1016/j.pld.2019.01.002

Wilting, H.C., Schipper, A.M., Bakkenes, M., Meijer, J.R., Huijbregts, M.A.J., 2017. Quantifying Biodiversity Losses Due to Human Consumption: A Global-Scale Footprint Analysis. Environ Sci Technol 51, 3298–3306. https://doi.org/10.1021/acs.est.6b05296

Wright, H.L., Lake, I.R., Dolman, P.M., 2012. Agriculture-a key element for conservation in the developing world. Conserv Lett 5, 11–19. https://doi.org/10.1111/j.1755-263X.2011.00208.x

Zhang, J., Dennis, T.E., Landers, T.J., Bell, E., Perry, G.L.W., 2017. Linking individual-based and statistical inferential models in movement ecology: A case study with black petrels (*Procellaria parkinsoni*). Ecol Modell 360, 425–436. https://doi.org/10.1016/j.ecolmodel.2017.07.017

Zurell, D., König, C., Malchow, A.K., Kapitza, S., Bocedi, G., Travis, J., Fandos, G., 2022. Spatially explicit models for decision-making in animal conservation and restoration. Ecography 2022, 1–16. https://doi.org/10.1111/ecog.05787

Zurell, D., Thuiller, W., Pagel, J., Cabral, J.S., Münkemüller, T., Gravel, D., Dullinger, S., Normand, S., Schiffers, K.H., Moore, K.A., Zimmermann, N.E., 2016. Benchmarking novel approaches for modelling species range dynamics. Glob Chang Biol 22, 2651–2664. https://doi.org/10.1111/gcb.13251

Chapter 2

Patch spatial attributes and time to disturbance affect the emergence of source local populations within ephemeral habitats

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Chapter 2 – Patch spatial attributes and time to disturbance affect the emergence of source local populations within ephemeral habitats

Abstract

Understanding the demography of local populations within ephemeral habitat patches is crucial for effective local (site-based) conservation management in spatially and temporally heterogeneous environments. Evidence suggests that species persisting in networks of ephemeral patches often exhibit source-sink dynamics, where certain local populations act as temporary sources at some time between initial colonization and patch disappearance due to disturbance. Here we present an individual-based demographic model inspired by Cabrera voles (*Microtus cabrerae*) in dynamic agricultural mosaics to test the hypothesis that the emergence of a source local population within an ephemeral habitat patch is largely driven by the combined effects of the patch spatial attributes (size, internal quality and connectivity to other hypothetical patches) and the time to disturbance (i.e. the patch lifespan). We focused on two key emergent demographic metrics quantifying the source-sink status of local populations based on their self-sustainability and potential contribution to other patches. We used sensitivity analyses to estimate the strength of linear associations between these metrics and the patch spatial attributes, and to quantify the main and interaction effects across different patch lifespans since initial colonization. Our model revealed that considerable spatial and temporal variation may emerge in local populations' source-sink status based on differences in patch size, internal quality, connectivity, and lifespan. According to predictions, patch internal quality correlated positively with local population self-sustainability and potential contribution to other patches, though the strength of these relationships was mostly relevant only after about three vole generation times (ca. one year) since initial colonization, and only in combination with the positive effects of patch size and connectivity. Accordingly, results also supported the prediction that the emergence of a temporary source local population is conditional to the longevity of the habitat patch, with short patch lifespans (less than about three vole generation times) greatly limiting local population self-sustainability and potential contribution to other patches. While empirical testing is needed to confirm these findings, our study strengthens the view that local management efforts focusing on reducing or mitigating disturbance (e.g. severe droughts, human farming activities) at large and well-connected high-quality patches will likely promote the occurrence of temporary source local populations, which should be crucial for long-term species persistence over larger spatial scales.

Keywords

Demography, Individual-based model, Metapopulation, Source-sink dynamics, Cabrera vole

2.1 Introduction

All environments vary in space and time, and many species have adapted to persist in dynamic ecosystems where suitable habitat is patchily distributed and exposed to natural and anthropogenic disturbance (e.g. Amarasekare and Possingham, 2001; Freemark et al., 2002; Keymer et al., 2000; Reigada et al., 2015; Van Teeffelen et al., 2012). Illustrative examples include fire-prone ecosystems (e.g. forests, savannas), areas affected by severe water imbalances (e.g. grasslands in arid and semi-arid environments), or by repeated drought or flood events (intermittent wetlands), as well as agricultural areas impacted by harvesting, grazing and mowing, all contributing to create spatial and temporal patterns in habitat structure and composition. Disturbance-driven variation in the amount, location and configuration of suitable habitat critically affects species that persist via extinction-colonization dynamics, altering population states and trajectories from the local (patch-level) to the landscape scale (e.g. Amarasekare and Nisbet, 2001; Butterworth et al., 2023; Heinrichs et al., 2016; Johnson, 2004; Reigada et al., 2015). Empirical and modelling studies indicate that species inhabiting networks of short-lived habitat patches (e.g. early successional grasslands created and destroyed through disturbance) often persist through source-sink dynamics, whereby local populations with net demographic deficits are supported by immigration from local populations with net demographic excess (e.g. Frouz and Kindlmann, 2015; Reigada et al., 2015). This suggests that the long-term persistence of such species may critically depend on the continued (though possibly fluctuating) availability of patches that, once colonized, can potentially behave as temporary demographic sources. Identifying the specific attributes of local habitat patches that enhance their potential to become temporary sources within a few generations of being colonized is therefore important to improve conservation management in dynamic environments (e.g. Furrer and Pasinelli, 2016; Sample et al., 2019). This is, however, hindered by the difficulty of identifying the source-sink status of local populations subjected to short-term (transient) dynamics, in which sharp temporal changes in key demographic parameters may occur over time between initial colonization and patch disappearance due to disturbance (e.g. Johnson, 2004; Paquet et al., 2020).

Two major demographic properties are commonly used to identify the source and sink status of local populations: self-sustainability (i.e. the ability to persist through local recruitment from births), and demographic contribution to other patches (i.e. the disproportionate production of propagules beyond patch boundaries relative to those absorbed) (Loreau et al., 2013; Pulliam, 1988; Runge et al., 2006). Evaluating the self-sustainability of persisting local populations at any given time involves examining the imbalance between births and immigration. When local recruitment from births (internal recruitment) is too low to surpass mortality or emigration, then population persistence will be highly dependent on immigration (external recruitment), otherwise it will face local extinction (Hanski and Gaggiotti, 2004; Millon et al., 2019). Evaluating the demographic contribution of a local population to other patches requires assessing the asymmetries in directional flow between immigration and emigration (Loreau et al., 2013; Runge et al., 2006). If the flux of individuals favours immigration over emigration, then the local population may be considered a sink. Conversely, if local population persistence is guaranteed by internal recruitment through births, and the outflow of emigrants outweighs the influx of immigrants, then the local population will qualify as a source (e.g. Altermatt and Ebert, 2010). While the determination of the source-sink status of occupied habitat patches is usually made under the assumption of long-term equilibrium dynamics (but see Sample et al., 2020), efforts to measure the short-term (transient) self-sustainability and potential demographic contribution of newly established local populations in ephemeral patches remains elusive (e.g. Caswell, 2007; Heinrichs et al., 2019). However, given that many species live in dynamic environments characterized by transient short-lived habitat patches where local populations frequently operate below equilibrium, understanding how patch spatial attributes and time to disturbance influence the emergence of a temporary source is important for ecological and conservation research (Caswell, 2007; Ezard et al., 2010; Iles et al., 2018).

Variation in habitat quality has been at the core of source-sink dynamics since the concept was first introduced, wherein high-quality habitats function as sources, while low-quality habitats function as sinks (Pulliam, 1988). However, there is still limited understanding of whether variation in other local patch attributes (e.g. size, connectivity) also shapes the emergence of sources and sinks, and how patch lifespan impacts post-colonization sink-to-source transition potential (e.g. Altermatt and Ebert, 2010; Heinrichs et al., 2016; Pasinelli et al., 2011). Notably, it is still largely uncertain how variations in patch size, intrinsic quality, and connectivity interact in determining the potential of local populations to, at least temporarily, become self-sustainable and able to positively contribute to an overall metapopulation before facing local extinction due to disturbance. This is probably related to the difficulty of tracking the required amount of detailed demographic and individual level data spanning the patches' lifespan since initial colonization, particularly when considering the large number of suitably different patches which would be required to gain inference into such processes (e.g. Heinrichs et al., 2019, 2016; Runge et al., 2006).

Because local demography emerges from a complex interaction between individuals within patches of varying characteristics, process-based approaches incorporating complex biological data are increasingly recommended and used to generate new insights and predictions on the way complex systems may respond to environmental change (e.g. Pilowsky et al., 2022; Poniatowski et al., 2018). In particular, Individual-Based-Models (IBMs, Grimm and Railsback, 2005) have an enormous potential for recreating the demographic dynamics of small, recently formed local populations, and the appearance of complex responses to patch size, quality and connectivity (DeAngelis and Grimm, 2014; Grimm et al., 2017). IBMs have at times been deemed over-parameterized compared to more simplified/cruder caricature models (Kaul and Ventikos, 2013). However, where sufficient biological knowledge is available to motivate the inclusion of processes in a model caricature, and sufficient data is available to parameterise functional relationships, IBMs allow for a highly suited synthesis of a broad range of knowledge that can result in emergent properties that are difficult to identify in nature (Kaul and Ventikos, 2013; Railsback and Grimm, 2019; Wilensky and Rand, 2015).

Here, we developed an in silico IBM approach inspired by the near-threatened, but data-rich, Iberian endemic Cabrera vole (*Microtus cabrerae*) in Mediterranean farmland, to test the general hypothesis that the emergence of a source local population within an ephemeral habitat patch is largely driven by the combined effects of patch spatial attributes (including its size, internal quality and connectivity) and the time to disturbance (i.e. the patch lifespan) (e.g. Fahrig, 1992). Based on simulations quantifying local population internal recruitment from births, immigration inflow, and emigration outflow at different times since initial colonization, we explore how patch characteristics affected emergent demographic imbalances determining the source-sink status of local populations. We predict that internal patch quality should be the most critical spatial attribute driving local population self-sustainability and demographic contribution beyond patch boundaries, due to its general positive association to reproduction and local recruitment (e.g. Griffen and Norelli, 2015). However, complex synergistic interactions among patch spatial attributes may come into play, in response to the temporal changes in local population density over time since colonization (Hatton, 2020; Santoro et al., 2016). For instance, as density increases over time within large and well-connected patches, and local living space becomes limited, the relevance of immigration should gradually decrease relative to internal recruitment from births and to the outflow of emigrants, potentially involving a transition of the local population from sink to source (Pulliam and Danielson, 1991). Therefore, we also predict that, in general, shorter patch lifespans (e.g. due to increased habitat turnover or frequency of disturbance) should weaken the emergence of source local populations, as there may be limited time to approach local carrying capacity or near-equilibrium density (Heinrichs et al., 2016; Van Teeffelen et al., 2012).

2.2 Methods

2.2.1 Model species

Cabrera voles are considered habitat specialists occurring in wet grassland habitat patches that are typically scattered across Mediterranean agricultural landscapes, and are often associated to small streams, soil depressions, temporally flooded or waterlogged areas, or wet meadows along the margins of agricultural fields and roads (Pita et al., 2014). Within these patches, Cabrera voles are typically organised in small family groups consisting of a monogamous breeding pair and their offspring (Pita et al., 2010), preferring microhabitats that offer dense cover by sedges and rushes, which provide food and protection against predators and extreme temperatures (e.g. Luque-Larena and López, 2007; Pita et al., 2011, 2006). Mean generation time is estimated at ca. 4 months, corresponding to around 3 generations per year (Mathias et al., 2023). In intensive Mediterranean farmland, suitable habitat patches rarely exceed 2000m2 and are subjected to frequent turnover due to human activities (e.g. ploughing, overgrazing) with many patches often lasting no more than about two years, eventually recovering some time after the disturbance (Pita et al., 2007). Because the species seems to be relatively well-adapted to such habitat dynamism, it is likely that some patches may behave as temporary sources along their relatively short lifetime, making the identification of the factors determining the occurrence of such sources an important goal in local conservation management. At present, the species is threatened by changes in land-uses associated to agriculture intensification, and abandonment of traditional agricultural practices, which result in the loss, fragmentation and degradation of suitable habitats (Pita et al., 2014; Mathias et al., 2023). These threats, together with climate change, have been identified as the main factors responsible for the predicted population declines of Cabrera vole (meta)populations in many areas across its distribution range (Garrido-García et al., 2018; Mestre et al., 2015). The species thus provides a suitable model for other species with both metapopulation dynamics and small group sizes constrained by short-lived habitat patches.

2.2.2 Model description

We developed an individual-based modelling (IBM) framework implemented in NetLogo (version 6.2.1, Wilensky, 1999) to simulate the post-colonization demography of the Cabrera vole within a single short-lived habitat patch amid a hostile matrix. The model consisted in repeated simulations considering different combinations of patch size, internal quality and connectivity to other hypothetical patches (not explicitly represented) in order to uncover the site-specific spatial attributes under which a local population in a newly colonized habitat patch may, at least temporarily, transition from sink to source. Below, we provide a general overview of the model's overall structure and processes involved, following the ODD protocol (Overview, Design concepts, Details) as recommended by Grimm et al. (2020). For a full ODD model description (Grimm et al., 2020, 2010, 2006); see Appendix A – ODD protocol). All simulation runs for testing and analysing the model, were performed using the "*NLRX*" package (version 0.4.3, Salecker et al., 2019) for program R (version 4.1.1, R Core Team, 2021). The full model code is available at:

https://github.com/TCrispimMendes/IBM_Emergence_Of_Source_Local_Populations_Within_Ephemeral_Habitats

The overall purpose of our model was to simulate individual-level processes and to assess the role of patch spatial attributes and time to disturbance in emergent demographic parameters and metrics quantifying local population self-sustainability and contribution to other patches. For this, the model systematically considered multiple combinations of patch size, internal quality, and connectivity values, with corresponding patch attributes defined for each simulated population during model initialization and remaining constant throughout the simulation. Patch size varied from 500 m2 to 5000 m2, reflecting the typical range of patch sizes occupied by the species in fragmented landscapes (Pita et al., 2014). Patch internal quality and connectivity were formulated as single synthetic measures ranging from 0 (minimum) to 1 (maximum), implicitly reflecting different biotic and abiotic conditions affecting habitat suitability at the patch (e.g. vegetation and soil properties) and landscape scales (e.g. proximity to surrounding habitat patches and degree of matrix hostility).

We adopted a pattern-oriented modelling (POM) strategy (Grimm, 2005; Grimm and Railsback, 2012) in order to align model outcomes to empirical data on individual-level patterns and behaviours, including spatial organization, breeding behaviour, parental care, migration, and survival. The model processes and sequence of events are illustrated in Figure 2.1.

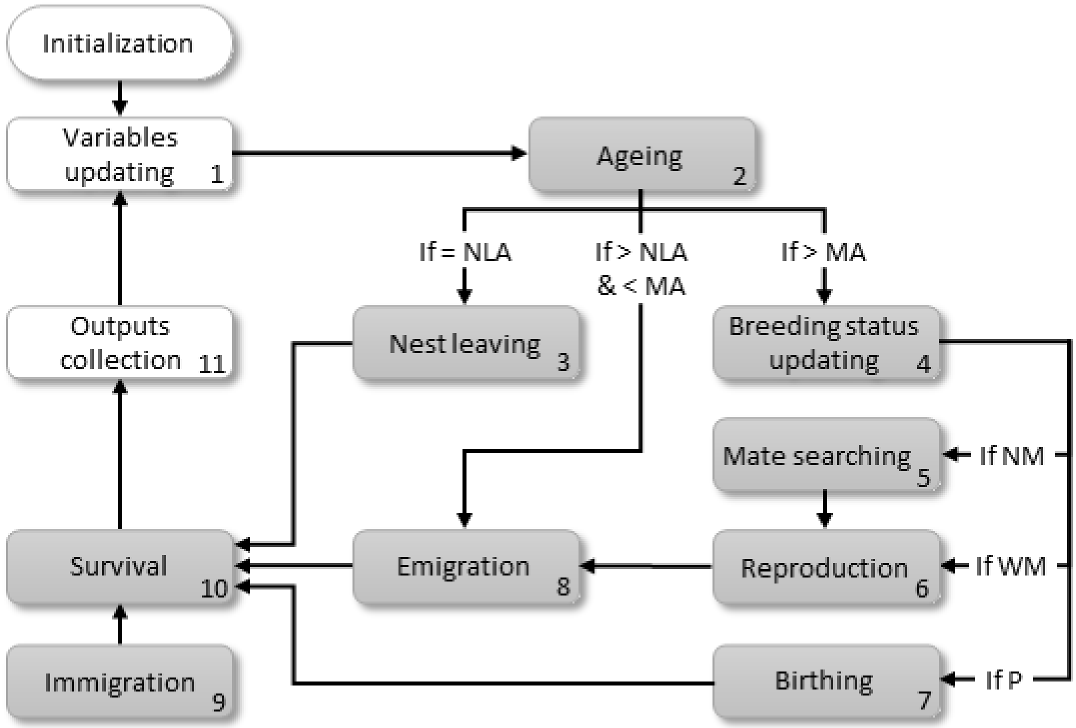

Figure 2.1 Conceptual diagram of the model to simulate post-colonization demography of Cabrera voles within a short-lived habitat patch amid a hostile matrix, considering different combinations of patch size, internal quality and connectivity. White boxes correspond to processes at the system level (i.e. the environment and data collection) and grey boxes correspond to processes at agent level (i.e. the voles). The numbers in the lower right corner of the boxes refer to the submodel corresponding to the respective process (see Appendix A – ODD protocol). Some processes are dependent on the age of the individuals: maternal nest leaving age (NLA) and maturation age (MA); or breeding status: no mate (NM), with mate (WM) and pregnant (P).

The model includes the following entities: habitat cells (1x1m^2), Cabrera vole individuals (*agents*), and the global environment (*observer*; the only entity at the system level, controlling the sub-models [see Appendix A – ODD protocol] and defining the simulation date). The state variables characterizing these entities are listed in Table 2.1. Habitat cells are arranged in a circular pattern around the centre of the model world, forming a single habitat patch, varying in size according to the number of cells included in the simulation, which determine patch carrying capacity. Each Cabrera vole individual (except nestling pups) is represented by a circular home range, with size randomly generated according to a normal distribution $N(X, \sigma)$

of $N(535.64, 327.29)$ for males, and $N(355.45, 271.39)$ for females, following Pita et al. (2010). The spatial arrangement of individuals within the patch followed the prevailing monogamous mating system of the species, adhering to home-range overlapping rules based on individuals' sex, relationship type (e.g. mates vs. non-mates), kinship, and current breeding status (Pita et al., 2010) (see Appendix A - ODD protocol, Table A.4).

Each simulation was conducted over a period of two years (approximately six vole generation times), with a single time step in the model representing one week. This weekly time scale is adequate for accurately capturing individual behaviours and post-colonization demography of the species, while the two-year duration corresponds to the typical lifespan of patches found in highly managed farmland areas (e.g. Pita et al., 2007). Simulations were initiated at the beginning of October, coinciding with the period of increased reproductive investment (Pita et al., 2014; Ventura et al., 1998). Each simulation initiated with one male and one female founding voles, representing a recent colonization event in the patch.

Table 2.1 List of agents intervening in the model, with their state variables and corresponding status or measure unit. * indicates female-specific state variables

State Variable	Variable type (possible values)
Habitat cells	
Cell location	Numeric (spatial coordinates)
Habitat type	Categorical ("favourable"; "matrix")
Cabrera voles	
Unique identification code	Numeric (-)
Location in patch	Numeric (spatial coordinates)
Sex	Categorical ("F"; "M")
Age	Numeric (weeks)
Residence time in the patch	Numeric (weeks)
Home-range size	Numeric (m^2)
Breeding status	Categorical (Mate's ID; "no-mate"; "helper")
Parent's identification codes	Categorical (Parent's ID; "founder"; "immigrant")
Time step of last reproduction*	Numeric (-)
Female is pregnant	Boolean
Litter's father identification code*	Numeric (-)
Time step to give birth*	Numeric (-)
Global environment	
Date at the end of the current time step	Date (day/month/year)

At each time step, relevant processes included maternal nest leaving and territory searching (at 6 weeks of age), reproductive maturation (at 8 weeks of age), and mate searching (for adults without a defined mate, and excluding parents and full siblings to avoid inbreeding, e.g. Lambin, 1994). In addition, individual probabilities of survival, reproduction, emigration and immigration were determined according to empirical information on species biology and ecology (Fernández-Salvador et al., 2005a, 2001; Pita et al., 2010; Proença-Ferreira et al., 2019). Specifically, weekly probability of mortality was generated for each animal at each time step based on Bernoulli trials with probability of 0.12 for juveniles and 0.02 for adults (estimated from Fernández-Salvador et al., 2005b; Radchuk et al., 2016; Topping et al., 2012) (see Appendix A – ODD protocol, subsection 5 and 7.10).

Regarding reproduction probability, although Cabrera voles can mate throughout the year, the probability of successful breeding typically fluctuates according to seasonal variations in local habitat quality (Fernández-Salvador et al., 2005b, 2005a; Rosário, 2012; Ventura et al., 1998) Therefore, weekly probability of reproduction were generated for each individual by Bernoulli trials with probabilities randomly taken from the range of variation identified by empirical observations across different months of the year (between 0 and 100%, estimated from Fernández-Salvador et al. 2005b; Rosário 2012), weighted by the patch internal quality (e.g. Griffen and Norelli, 2015) (see Appendix A – ODD protocol, subsection 5 and 7.6). As for inter-birth intervals, while postpartum mating behaviour of Cabrera voles remains undocumented, females were allowed to give birth only once the previous litter had vacated the nest. Although most vole species can mate and give birth within less than ca. 30 days postpartum (Gilbert, 1984), we assumed limited female receptivity during lactation, beginning at postpartum oestrus, given the Cabrera vole is considered a less prolific, slow-reproducing species, with k-strategic life-history characteristics (investment in offspring via parental care) (Fernández-Salvador et al., 2005b). This conservative assumption was also supported by the association of the species to small patches of scarce habitats, which may also delay postpartum mating, owing to resource shortage, as found in other *Microtus* species (e.g. Sabau and Ferkin, 2013).

The weekly probability of emigration of lactating females or pair-bounded breeding animals was set at 0%, while individuals unable to establish a home-range due to space limitations had an emigration probability of 100%. Remaining animals were assigned a probability of emigration based on Bernoulli trials with probability taken from the range of empirical values found in natural populations (between 7.5 and 17.7%, estimated from Fernández-Salvador et al. 2005b; Proença-Ferreira et al. 2019), weighted by the patch connectivity value (see Appendix A – ODD protocol, subsection 7.1). These rules were implemented to reflect the individuals' propensity to emigrate, while considering the socio-ecological context and the proximity to putative neighbouring patches, in line with empirical data and general ecological theory (e.g. Hanski and Gaggiotti, 2004), thus providing realism to our model. The overall emigration probability at each time step thus emerged from individuals' responses to competition for space and for mates, both largely regulated by density-regulated stochastic process.

The weekly probability of immigration of a new individual into the focal patch was generated based on Bernoulli trials with probability randomly taken from the range of variation identified in empirical observations across the annual cycle (between 5.0 and 37.6%, estimated from Pita et al. 2017, Proença-Ferreira et al. 2019), weighted by the patch connectivity value (e.g. Hanski and Gaggiotti, 2004) (see Appendix A – ODD protocol, subsections 6 and 7). However, successful settlement of immigrants ultimately depended on space availability for establishing a home range while adhering to the spatial overlapping rules considered (see Appendix A – ODD protocol, subsections 7.3).

Overall, the fundamental concepts underlying the design of the model thus support the main requirements that i) Cabrera's vole populations are patchily distributed, with individuals typically grouped into distinct local populations restricted to small habitat patches (Pita et al., 2006; Rosário and Mathias, 2007); ii) reproduction follows a *k*-selection strategy (Fernández-Salvador et al., 2001), where monogamy stands as the prevailing social and mating system, even though eventual deviations to facultative polygyny were also deemed possible (Pita et al., 2014); iii) breeding activity follows an opportunistic strategy linked to variations in local habitat quality (Fernández-Salvador et al., 2005b); and iv) migration occurs in response to competition for mates and space. These principles are represented in the model through the different submodels for reproduction, socio-spatial overlapping rules among individuals, and migration (see Appendix A – ODD protocol).

2.2.3 Model outputs

The model was designed to collect demographic data at three months intervals, roughly corresponding to the end of the four main seasons in the Mediterranean basin (autumn, from October to December; winter, from January to March; spring, from April to June; and summer, from July to September). This allowed us not only to capture eventual transitions in population source-sink behaviour over time, but also to infer the status of local populations at different hypothetical disturbance timings (from 3 months to two years). According to our hypothesis, the primary outputs emerging from our model focused on metrics describing the strength of local populations' self-sustainability and potential contribution to other patches. Several metrics with varying emphasis on self-sustainability and demographic contribution, have been suggested to differentiate sources and sinks or to rank the relative importance of local populations based on various key demographic parameters (e.g. births, mortality, immigration and emigration rates) (e.g. Pulliam, 1988; Runge et al., 2006; Sample et al., 2019). However, these metrics have been specifically applied for populations in equilibrium, while their utility remains uncertain under transient dynamics (Sample et al., 2020). In addition, the use of single metrics that accurately reflect both self-sustainability and potential demographic contribution of local populations remains contentious (Runge et al., 2006; Sample et al., 2020), and different metrics may therefore be required for assessing the changes in source-sink status of local populations. In particular, because the source-sink status of local populations can change depending on the environmental conditions, there is little prospect of devising a single measure of the intrinsic strength of sources and sinks (Loreau et al., 2013). Therefore, here we opted to infer on the source-sink status of local populations based on two simple metrics that can be extracted for relatively short-interval time periods along transient population dynamics. Specifically, we measured the imbalance between births and immigration (hereafter, B-I index) in persisting local populations (i.e. where overall recruitment apparently compensates deaths) calculated as the difference between net births and net immigration divided by the total number of recruits every three months (see Table 2.2). This index measures the role of births and immigration in overall local population growth, varying between -1 and 1. Positive values in the B-I index indicate a higher proportion of births over immigration (i.e., self-sustaining through reproduction), with negative values indicating the opposite pattern (i.e. persistence via immigration). We also quantified the imbalance between immigration and emigration (hereafter I-E index) as the difference between the number of immigrants and the number of emigrants divided by the total number of migrants every three months (e.g. Christensen and Walters, 2004; Stoffels et al., 2016), see Table 2.2). This index considers the number of emigrants leaving the patch independently of their survival and ability to reach and establish in a new patch, varying also between -1 and 1, with positive values indicating higher net immigration (hence limited demographic contribution to other patches) and negative values indicating higher net emigration (i.e. increased demographic contribution). In addition, we also investigated other emergent demographic parameters (densities, sex-ratios, extinction rates) for model validation purposes (Table 2.2).

Table 2.2 List of emergent demographic outputs extracted from the model every 3 month-intervals, roughly corresponding to 4 main seasons in the Mediterranean basin (autumn, winter, spring, and summer).

Output	Description
Inference	
B-I index	Net balance between local recruitment and immigration, calculated as: $(\mathrm{N_{Births}} - \mathrm{N_{Immigrants}})/(\mathrm{N_{Births}} + \mathrm{N_{Immigrants}})$
I-E index	Net balance between immigration and emigration, calculated as: $(\mathrm{N_{Immigrants}} - \mathrm{N_{Emigrants}})/(\mathrm{N_{Immigrants}} + \mathrm{N_{Emigrants}})$
Validation	
Extinction	Whether the local population extinction occurred (1) or not (0)
Density	Snapshot of local population density (individuals/ha)
Sex-ratio	Snapshot of sex-ratio (proportion of males) in the local populations, calculated as: $(\mathrm{N_{Males}})/(\mathrm{N_{Females}} + \mathrm{N_{Males}})$
Residency	Snapshot of mean individual residence times in the local populations (in weeks)

2.2.4 Model validation

Model verification and quality assurance were carried out at different levels. First, while writing the code, the syntax was checked using the NetLogo's built-in debugger. Then, a visual debugging of the running model was performed using the NetLogo visual interface.

To test the performance of the model, a pattern-oriented validation (Grimm, 2005; Grimm and Railsback, 2012) was conducted using patterns recorded in the literature based on real-world populations (e.g. Wang, 2013) regarding (i) extinction rates (Pita et al., 2007), (ii) density (Fernández-Salvador et al., 2005b; Landete-Castillejos et al., 2000; Peralta et al., 2023; Sabino-Marques et al., 2018), (iii) sex-ratio (Pita et al., 2014), and (iv) residence times (Fernández-Salvador et al., 2005b) (Table 2.2). We assumed that overlapping uncertainty boundaries between simulation and empirical data would provide evidence that the simulation was adequate for calculating the demographic indexes used to infer on source-sink strength of local populations. For this step of model validation, we used a Latin hypercube sample procedure, in "*NLRX*" (Salecker et al., 2019), to generate 250 parameterizations over the ranges of each input parameter (size, quality and connectivity). We then ran these parameterizations with 10 different random-seeds (making a total of 2500 runs) to account for model stochasticity.

In addition, we also assessed whether some of the validation outputs changed as predicted according to the variation in patch attributes, and considering the transient nature of local population dynamics. For this, we fitted single-variable linear regression models with Normal distributed errors, using the data derived from the Sobol estimator simulations (described below). Specifically, we checked whether, despite the considerable variability, there was a positive trend in density estimates over time in established local populations, driven by the progressive occupation of empty space (through local recruitment and immigration) since initial colonization towards carrying capacity. Similarly, we examined whether our model captured a decrease in demographic extinction rate as patch size, connectivity and habitat quality increased, and whether local density increased with habitat quality, as expected from well-established ecological theory (e.g. Hanski and Gaggiotti, 2004). While we assumed that the interactions between the patch spatial attributes would have larger effects on vole demography than the main effects (potentially leading to limited explained variance by single-variable linear regressions), this approach was mostly oriented to assess the coefficients' sign (either positive or negative), rather than their magnitude or predictive ability.

2.2.5 Sensitivity analyses of model outputs

We conducted a global sensitivity analysis to check the robustness of the IBM outputs, focusing on those parameters directly related to our main hypotheses. For this, we used two methods; one based on linear regression and another on the decomposition of functional variance of each model response for each combination of patch size, quality and connectivity values. These methods measure two different model properties. In the case of linear regression, we used the Latin hypercube sampling partial rank correlation coefficients (LHS-PRCC). This method provides a non-parametric measure of the strength, direction and statistical significance of monotonic associations between model outputs and each patch attribute, after the removal of the linear effects of the other attributes (Marino et al., 2008). The PRCC ranges from -1 to +1, where values near 0 signify the absence of linear relationships, while those closer to -1 or 1 denote perfect negative or positive linear correlations, respectively. By leveraging this method, we can effectively rank patch attributes based on their impact on each model output. For decomposing variance, we used Sobol's method, which allows the decomposition of model outputs' variance into variances attributable to each patch attribute, distinguishing and quantifying the contribution of their direct and interaction effects (Sobol, 1993). The Sobol' method does not use fitted functions, but instead decomposes the variance based directly on a sample from the parameter space (Saltelli et al., 2008). Because the method aims to quantify the output variability based on this variance decomposition, it is not intended to identify the cause of the input variability, but rather to indicate the extent of its impact on model outputs (ten Broeke et al., 2016). Sobol indices range from 0 to 1, with values nearing 0 indicating a negligible contribution of the corresponding variable to model output variability, while values close to 1 imply significant influence. When a model output is highly sensitive to a particular parameter, the parameter is considered a key-player in regulating that output.

For the implementation of the LHS-PRCC, the full ranges of each input parameter (size, quality and connectivity) were used to generate 500 parameterizations in "*NLRX*" R package (Salecker et al., 2019), which was run with two different random-seeds (making a total of 1000 runs) to account for model stochasticity. The results were then used to determine the partial-rank correlation coefficients and corresponding 95% confidence intervals (via 100 bootstrapped samples) for each parameter, using the "*sensitivity*" R package (Iooss et al., 2019). Parameters were considered influential if 95% confidence intervals of correlation coefficients did not overlap 0.

In the case of Sobol's method, we calculated two main sensitivity indices for each parameter: first-order sensitivity index (S_i), and a total-order sensitivity index (S_{Ti}). S_i estimates the effect of each input parameter on each given model output, without considering the interaction effects among parameters. Conversely, S_{Ti} measures the full contribution of a single parameter to each model output while also considering possible nonlinear interactions among input parameters (Homma and Saltelli, 1996). In order to fully understand the interactions amongst input parameters, we also calculate the second-order (S_{ij}) and third-order (S_{ijk}) Sobol's indices, which measure the interaction effect between two and among three parameter arrangements respectively, on each model output (Saltelli et al., 2008).

Sobol's sensitivity indices were computed using Monte Carlo estimation implemented in "*NLRX*" (Salecker et al., 2019). The first, second and third-order indices were computed using the original estimator of Sobol (Sobol, 1993), whereas the total-order indices were computed using the Sobol-Jansen estimator (Jansen, 1999; Saltelli et al., 2010). The computational cost of these estimators depends on the number of input parameters (p) and the size of the Monte Carlo sample matrix (*n*), at a total cost of $(p + 2) \times n$, in the case of Sobol-Jansen estimator. In the case of the original Sobol estimator, the computational cost also depends on the number of indices to estimate (*N*), at a total cost of $(N + 1) \times n$. For this analysis, we chose to use 2,000 Monte Carlo samples, corresponding to a computational cost of 20,000 runs for Sobol-Jansen estimator, and 32,000 runs in the case of original Sobol estimator. In both cases, 95% confidence intervals were generated with 100 bootstrapped replications.

2.3 Results

2.3.1 Model performance

In general, validation outputs were in agreement with field observations and empirical data from published sources, suggesting that the simulated individual behaviours and emergent demographic parameters were comparable to those of real populations. In particular, mean extinction rates predicted by the model every 3 months averaged (±SD) 8.4 ± 2.6%, ranging between 6.0-11.7%, which is in accordance with comparable empirical estimates up to 15.9% (Figure 2.2). Moreover, according to expectations, the model was able to capture the general decrease in extinction rates with increasing patch size, connectivity and habitat quality (Figure 2.3 and Appendix B - Supplementary results, Table B.1). As for density, estimates predicted by the model averaged 19.2ind./ha, ranging between 2-159.8 ind./ha, also in accordance with empirical data found in real populations (Figure 2.2).

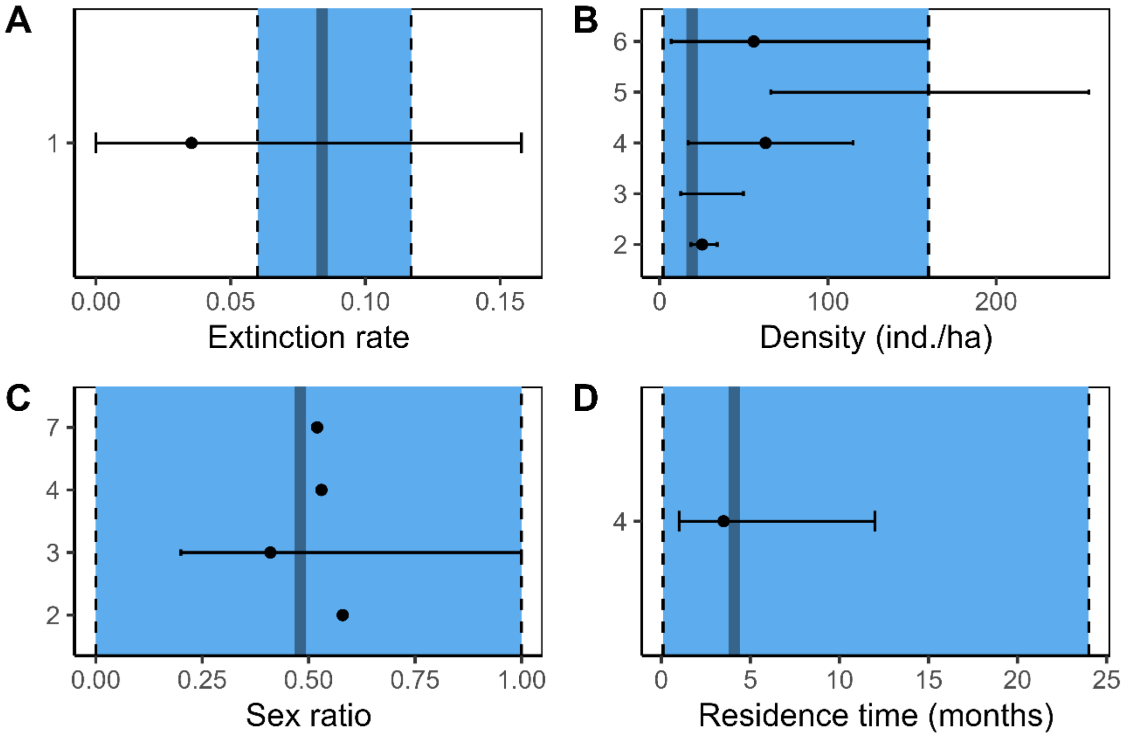

Figure 2.2 Comparison of the model's validation outputs with estimates from the empirical literature. Validation output corresponds to the mean (vertical grey line) and standard deviation (range in blue) of each parameter collected every three months of the simulations. Empirical point estimates (black points) and uncertainty (bars) are numbered as: 1 - "Pita et al. (2007)"; 2 - "Sabino-Marques et al. (2018)"; 3 - "Rosário (2012)"; 4 - "Fernández-Salvador et al. (2005b)"; 5 - "Landete-Castillejos et al. (2000)"; 6 - "Peralta et al. (2023)"; 7 - "Proença-Ferreira et al. (2019)".

Furthermore, as expected, there was an overall increasing trend in density across time and with increasing habitat quality (Figure 2.3 and Appendix B - Supplementary results, Table B.1). The average sex-ratio value recorded model outputs (0.48 ± 0.25) was in line with those registered empirically (Figure 2.2), tending towards a balance between males and females, although slightly favouring the number of females, as reported in Rosário (2012). Although the estimated mean residence time of 4.1 ± 3.0 months was slightly higher than that recorded in empirical studies (3.5 ± 2.8 months, Fernández-Salvador et al. (2005b), it was within the range of values recorded in that study (1-12 months) (Figure 2.2). It should be noted however that residence times provided in Fernández-Salvador et al. (2005b) may be underestimated, as it was based on capture recapture methods that did not allow for possible heterogeneity in individual recapture probability. Overall, therefore, our model seems to accurately recreate the post-colonization demography of voles within local population.

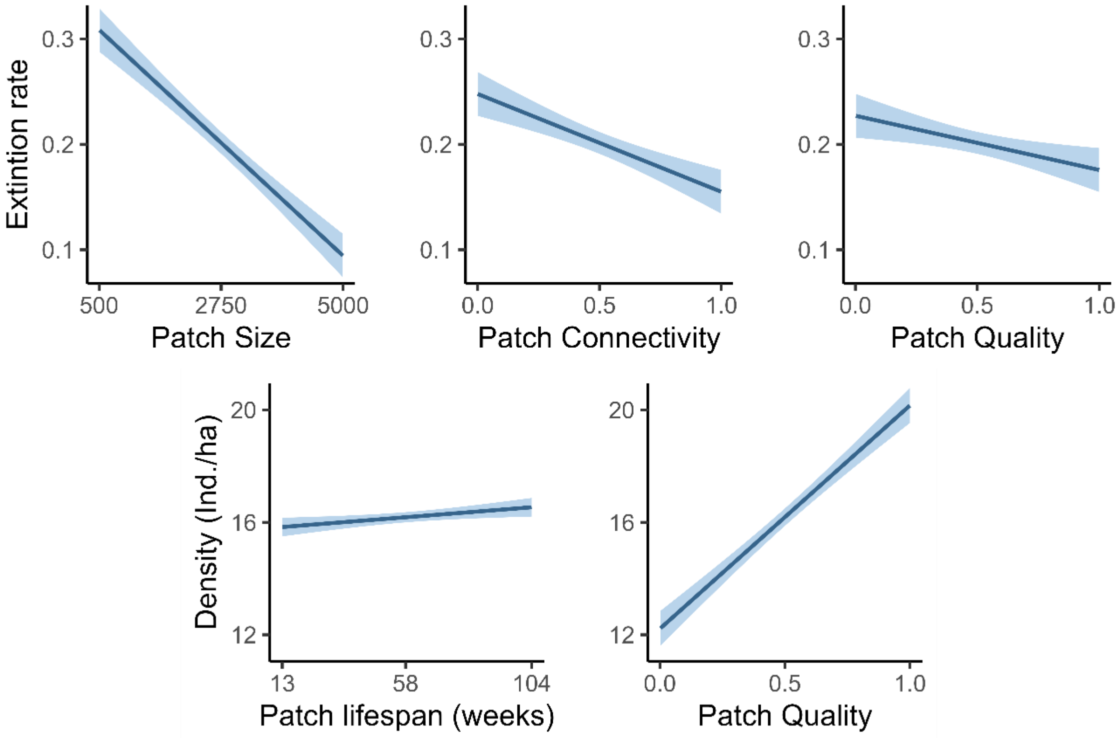

Figure 2.3 Linear regressions (lines and 95% confidence intervals) showing the general trends in validation outputs, matching expectations from general ecological theory. Data used to represent these relationships were derived from the original Sobol estimator simulations (see main text and Appendix B - Supplementary results, Table B.1).

2.3.2 Sensitivity analysis and support for main predictions

Bootstrapped estimates of LHS-PRCC between patch attributes and emergent demographic responses showed very low bias (<0.01), indicating a high stability of the estimates. However, although the results were statistically significant in most cases, correlations were generally weak (<|0.3|) (Figure 2.4).

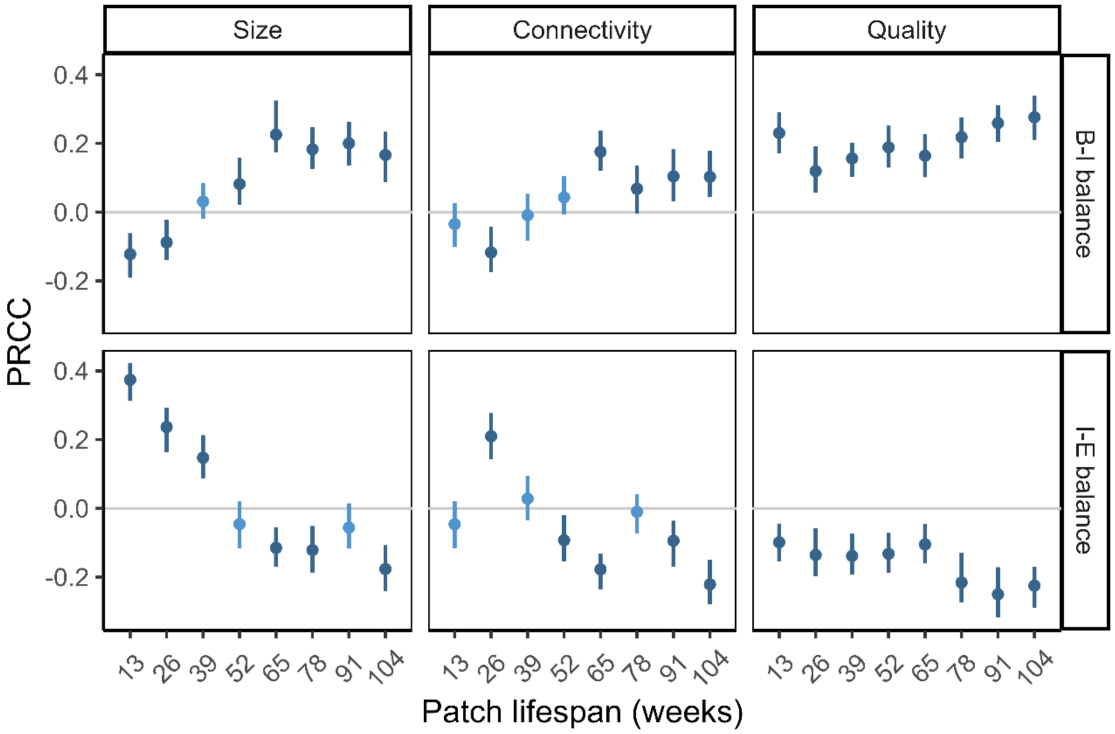

Figure 2.4 Partial rank correlation coefficients (PRCC) and 95% confidence intervals between the focal demographic indices (rows) and habitat properties (columns) over the simulation period. The lighter blue dots represent PRCC values that are not statistically significant. For a full report regarding all emergent outputs of the model (see Figure B.1 in Appendix B).

Our simulations indicated high variability in both B-I and I-E indexes (mean ± SD [range] of 0.17 ± 0.71 [-1.00 – 1.00] and -0.21 ± 0.61 [-1.00 – 1.00], respectively), suggesting high variation in both self-recruitment and contribution of local populations to other patches. As predicted, the B-I index correlated negatively with patch size and connectivity shortly after colonization, though, over time, this relation became positive (Figure 2.4 and Figure B.1 in Appendix B), concurrently with the increases also observed in density (Figure 2.3). In addition, the B-I index correlated positively with habitat quality across time (Figure 2.4 and Figure B.1 in Appendix B).

Also, according to expectations, the model predicted a positive-to-negative shift in the relationships between the I-E index and patch size and connectivity over time (Figure 2.4 and Figure B.1 in Appendix B). Furthermore, the model also supported the prediction that habitat quality negatively affects the I-E index (Figure 2.4 and Figure B.1 in Appendix B).

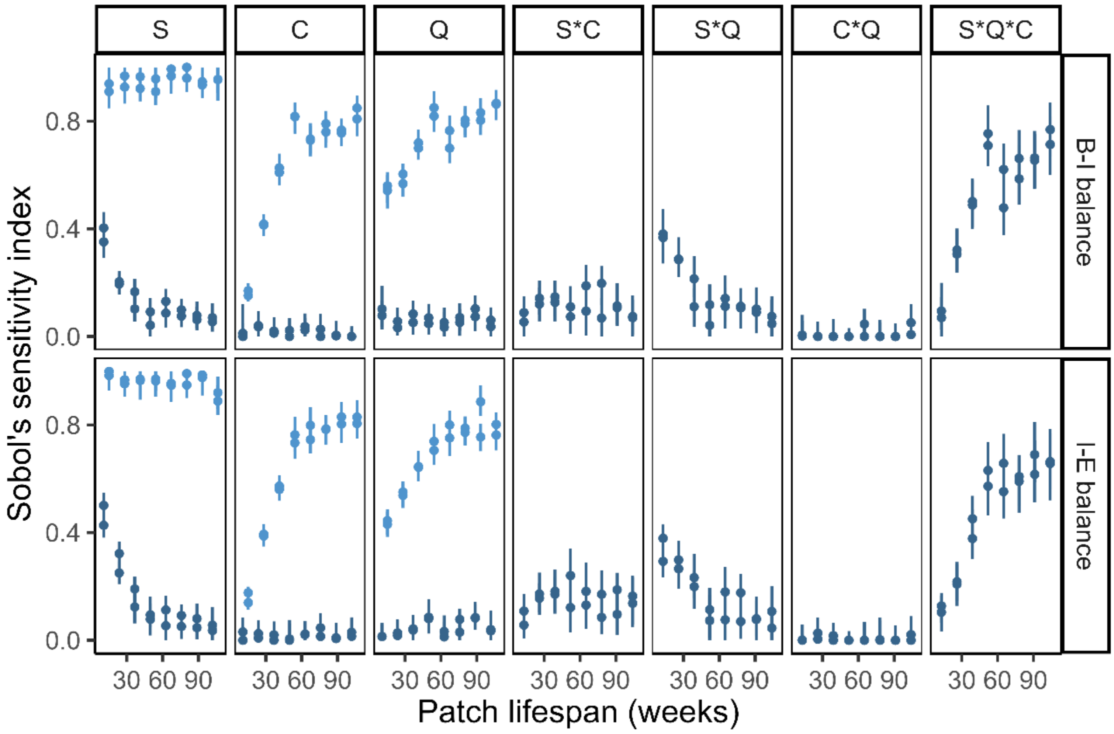

Figure 2.5 Sobol's sensitivity indices and 95% confidence intervals between the focal demographic indices (rows) and local patch attributes (columns) over the simulation period. S – patch size, C – patch connectivity, and Q - habitat quality. The first 3 columns on the left presents the estimates of the Sobol's first-order (S_i – darker blue) and a total-order (S_{Ti} - lighter blue). Columns 4 to 6 presents the estimates of the Sobol's second-order (S_{ij}), and the last column the estimates of the third-order (S_{ijk}).

When considering Sobol's indices as a whole, sensitivity patterns to patch size, quality and connectivity were broadly similar for the two focal emergent outputs along patch lifespans (Figure 2.5), supporting the prediction on the relevance of single versus interaction effects over time. Specifically, the size of the patch alone was in general the only factor exerting influence by itself (S_i), though this influence decreased over time, becoming negligible for most of the parameters by the end of the simulation. Notably, the total effect of patch size (S_{Ti}), strongly influenced model outputs throughout the whole simulation period, with sensitivity indexes always close to 1. Conversely, the total influence of patch quality and connectivity had negligible impacts shortly after colonization, though the sensitivity of model outputs to these variables greatly increased along the simulation period. In the case of patch quality, total indices generally began to show sensitivities greater than 0.5 about six months post-colonization, stabilizing after one year at ca. 0.75. In the case of connectivity, total sensitivity indexes generally only exceeded 0.5 around one year and a half after initial colonization, reaching the breakeven point after ca. one year (Figure 2.5). When comparing the first-order and total-order indices, both the B-I index and the I-E index were highly sensitive to the interaction among patch attributes rather to their main effects (i.e., very different S_i and S_{Ti} values for both parameters). In particular, the interaction among the three input factors (S_{ijk}) was of major relevance for the demographic responses considered. Indeed, despite being largely irrelevant shortly after colonization (< 6 months), the interaction among patch size, quality and connectivity became increasingly important over time, showing a stabilization trend after the first year post-colonization, with respective indices always >0.4 for both demographical indexes considered (Figure 2.5). Second-order interactions (S_{ij}) played a generally minor role, with the interaction between size and quality showing, in some cases, a moderate importance (often >0.3 and <0.4) shortly after colonization, tending to decrease along the simulation period. The interaction between size and connectivity showed a weak influence, with the 95% CI's of estimated Sobol indices mostly comprising values close to 0. Regarding the interaction between connectivity and quality, Sobol indices consistently presented values close to 0 throughout the simulation for both demographic indices considered (Figure 2.5).

2.4 Discussion

Our individual-based model inspired by the threatened Cabrera vole occurring in heterogeneous ephemeral patches provided evidence that considerable spatial and temporal variation may emerge in local populations' self-sustainability and contribution to other patches, according to variation in the size, internal quality, connectivity, and lifespan of habitat patches. This corroborated our overreaching hypothesis that patch spatial attributes and time to disturbance affect the emergence of temporary source local populations, with evidence suggesting the presence of strong interaction and synergistic effects among these factors. The idea that patch spatial attributes should not be considered alone and independently of each other when predicting the source-sink status of local populations in spatially and temporally heterogeneous environments (Heinrichs et al., 2019, 2015; Robles and Ciudad, 2012; Wright et al., 2020) is supported by our model. Importantly, the lifetime of habitat patches relative to species generation times played a critical role in post-colonization transition of local populations from sink to source, confirming the prediction that short times to disturbance should preclude the emergence of temporary source local populations (e.g. Fahrig, 1992; Van Teeffelen et al., 2012). Given the challenge of distinguishing between source and sink local populations in real ecological systems, these results are particularly relevant in highlighting that conventional and readily measurable or predictable patch-level characteristics, such as those considered here, may provide a valuable indication of the source-sink potential of local populations in ephemeral patches. While further empirical testing is needed to confirm our findings, they still strengthen the view that different conservation management strategies at local scales may be required according to the source-sink potential of target habitat patches (Furrer and Pasinelli, 2016; Heinrichs et al., 2019).

2.4.1 Emergence of source local populations of Cabrera voles in ephemeral patches

According to our model, Cabrera vole local populations occurring in large and well-connected high-quality patches may behave as temporary sources at some time after initial colonization. In line with predictions, habitat patch internal quality correlated positively with demographic metrics describing the increase in vole population self-sustainability and potential contribution to other patches throughout time since colonization by a founder breeding pair. However, the strength of these relationships was mostly relevant only after about three generation times (ca. one year) since initial colonization, and only in combination with the positive effects of patch size and connectivity. Prior to this, self-sustainability and contribution strength decreased with increasing patch size and connectivity, with patch size effects being by far the most influential. The change in the direction of these relations over time reflects the gradual filling of physical space by voles in large patches during the first generations following colonization, and, to a lesser extent, the arrival of immigrants before *in situ* growth fills the patches. Therefore, our results corroborate the idea that the source-sink potential of individual patches might not be accurately inferred from local habitat quality alone, as earlier posited (Pulliam, 1988), and that complex interactions with other sources of patch spatial variability, such as size and connectivity, may determine the emergence of sources (e.g. Nisi et al., 2023; Schumaker et al., 2014). Notably, these complex dynamics unfolded only when local populations in large and well-connected high-quality patches transition from high immigration and low emigration during the low-density phase to low immigration and high emigration as local density increases, which implies patches persisting for over one year (>3 vole generations). This highlighting the role of density-regulated processes determining the source-sink status of habitat patches from initial colonization to patch disturbance, with local populations operating below their carrying capacity having much lower chances of becoming source populations (e.g. Heinrichs et al., 2016). Therefore, based on our results and consistent with other studies, we suggest that variation in local patch attributes should provide a particularly influential context to strengthen source-sink dynamics in real landscapes.

While our model did not considered dispersal mortality of emigrants, the above influence of patch attributes on source-sink status of Cabrera vole local populations over time could potentially suggest that in real landscapes subjected to high habitat turn-over (disturbance frequency at intervals shorter than one year), the occurrence of high-quality, yet small and isolated patches would disproportionally support metapopulation persistence more significantly than their large and well-connected counterparts. Although this remains to be formally tested, such a scenario is expected to weaken the establishment of source-sink dynamics, where metapopulation persistence with high turnover of patches would require low dispersal mortality (e.g. Gundersen et al., 2001; Mestre et al., 2020). Moreover, it's important to note that, even within high-quality habitats, populations within small and poorly connected patches were generally more susceptible to stochastic extinction. This made them less prone to function as potential temporary sources, unlike local populations persisting in large, well-connected patches for over a year since colonization. These results thus support the expectation that habitat stability is important in predicting temporary source local populations in ephemeral patches (Heinrichs et al., 2016). Specifically, in the case of the Cabrera vole, eventual transitions from sink to (temporary) source seem conditional upon patches persisting for over at least one year post-initial colonization, with this broader underlying pattern apparently holding beyond the seasonal fluctuations that may occur in demographic trends within local populations. The consequences of severe synchronous adverse seasonal effects (e.g. drought) on habitat patch-network properties in real landscapes may however warrant particular attention, as these may pose a potential challenge to metapopulations responsive to ongoing climate change, as seems to be the case of the Cabrera vole (Mestre et al., 2015).

2.4.2 Model strengths and research implications

In an effort to capture the essence of Cabrera voles' local population processes within habitat patches amid a hostile matrix, we developed a stochastic individual-based model for simulating spatially explicit within-patch demography while considering implicit landscape (among patch) processes, informed by extensive empirical data. Despite the simplified nature of our model, the dimensionality of the parameter space evaluated was considerable, allowing to uncover our main predictions without resorting to complex representations of landscape realities. A further significant merit of our approach is that it focused on two simple and intuitive demographic metrics (B-I and I-E indices) as indicators of local self-sustainability and demographic contribution of temporary local populations to other patches. Although simplified, these metrics remain true to the fundamental demographic properties conventionally considered in source-sink research, while their concurrent use avoids placing particular emphasis on any of these properties, as is often the case of single-metric approaches (e.g. Furrer and Pasinelli, 2016; Sample et al., 2019). Also, according to our results, when assessed sequentially at defined time intervals, these metrics may adequately capture sharp temporal shifts in local populations' demographic trends under transient dynamics (Runge et al., 2006). Still, despite the elegance of our modelling approach, one potential criticism, we acknowledge, is that we restricted the lifespan of habitat patches to up to 2 years. While model outputs suggested considerable less variation in demographic change during latter generations relative to earlier ones, it is possible that such patch lifespan threshold may have constrained our ability to distinguish between relatively stable temporary sources and local populations that fluctuate between source and sink. However, given the relatively rapid turnover in Cabrera voles' habitat in intensively used landscapes (e.g. Pita et al., 2007), the establishment of stable sources over long time periods is mostly unlikely, making it crucial to identify the local patch attributes that most contribute to short-term sink-to-source transition in ephemeral patches, as explored here.

Although our model was effective in predicting the source-sink status of local populations based on patch spatial attributes and time to disturbance, further experimental and empirical testing of these predictions is needed to enhance the accuracy of our findings. In particular the use of fully spatially explicit landscapes and metapopulation would be crucial to infer about the scenarios under which source-sink like dynamics may occur in dynamic environments. While the use of replicated microcosms containing simplified versions of ecological systems (e.g. for small invertebrates like mites and daphnia) may help elucidate our understanding of source-sink dynamics in ephemeral habitats (Benton et al., 2007), such approaches still lack the context-specific details of complex natural systems. Conversely, empirical testing of results from simulation-based source-sink research is typically difficult to operationalize, given the costs often involved in intensive collection of demographic data (Heinrichs et al., 2016). However, by contributing to the conceptual understanding of the dynamics that may characterize post-colonization demographics within ephemeral patches, we believe our simulation results may be useful to guide and target the intensive survey efforts required to empirically assess the potential for source-sink dynamics in metapopulations (for instance, by focusing on systems with greater asymmetries in patch size, internal quality, and connectivity). Still, because the absence of empirical testing should not preclude the use of theoretical predictions on the mechanisms driving the source-sink status of local populations (particularly for species needing urgent conservation actions, as is the case of the Cabrera vole), we suggest that our results may be used to inform conservation management. Therefore, should our model insights be transferable to natural systems, it would highlight the need to prioritise the protection of large (up to 5000m2) and well-connected high-quality patches for relatively long time periods (ideally up to 2 years or more), in order to allow the establishment of local populations with some potential to function as sources, at least during some time before a new local disturbance takes place (e.g. mowing, harvesting, ploughing, burning, inundation, overgrazing, drying up), while other source populations recover, emerge, or are created in the system (e.g. Pita et al., 2007). Ensuring ongoing access to habitat patches that once colonized may function as temporary sources, should therefore enhance the likelihood of metapopulation persistence in spatially and temporally heterogeneous environments.

2.4.3 Conclusion

Landscape dynamics involving habitat turnover due to natural or human disturbances is widespread (Van Teeffelen et al., 2012), and metapopulation persistence in resulting networks of ephemeral habitats has been frequently associated to source-sink like dynamics (Reigada et al., 2015). Assessing the source-sink status of local populations is therefore important for metapopulation conservation in ephemeral patches, particularly for weighting different management options and timings under limited funding (Hastings, 2003; Keymer et al., 2000; Pasinelli et al., 2011). Our individual-based model grounded in the exceptionally well-studied biology and ecology of the Cabrera vole in Mediterranean farmland provided important insights on how patch size, internal quality and connectivity may jointly contribute to augment or diminish the likelihood of a local population to become temporary source under different patch disturbance rates. While our hypotheses were not directly formulated for real-world populations, expectations from our model should be well-suited for empirical testing, in order to more properly identify the factors potentially inciting sources-sink dynamics, and direct conservation efforts accordingly (Hastings, 2003; Keymer et al., 2000; Pasinelli et al., 2011).

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Author contributions

TCM, **PB**, **XL**, and **RP** conceived the ideas and designed methodology; **TCM** and **RP** conceived and planned the experiments; **TCM** performed the experiments; **TCM**, **DR**, **XL** and **RP** analysed the results. **TCM** and **RP** lead the writing of the manuscript, with significant contributions from **DR**, and **XL**. All authors discussed the results, commented on the manuscript, and contributed to manuscript editing and revisions.

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2.5 References

Altermatt, F., Ebert, D., 2010. Populations in small, ephemeral habitat patches may drive dynamics in a *Daphnia magna* metapopulation. Ecology 91, 2975–2982. https://doi.org/10.1890/09-2016.1

Amarasekare, P., Nisbet, R.M., 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. American Naturalist 158, 572–584. https://doi.org/10.1086/323586

Amarasekare, P., Possingham, H., 2001. Patch dynamics and metapopulation theory: The case of successional species. J Theor Biol 209, 333–344. https://doi.org/10.1006/jtbi.2001.2269

Benton, T.G., Solan, M., Travis, J.M.J., Sait, S.M., 2007. Microcosm experiments can inform global ecological problems. Trends Ecol Evol 22, 516–521. https://doi.org/10.1016/j.tree.2007.08.003

Butterworth, N.J., Benbow, M.E., Barton, P.S., 2023. The ephemeral resource patch concept. Biological Reviews 98, 697–726. https://doi.org/10.1111/brv.12926

Caswell, H., 2007. Sensitivity analysis of transient population dynamics. Ecol Lett 10, 1–15. https://doi.org/10.1111/j.1461-0248.2006.01001.x

Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: Methods, capabilities and limitations. Ecol Modell 172, 109–139. https://doi.org/10.1016/j.ecolmodel.2003.09.003

DeAngelis, D.L., Grimm, V., 2014. Individual-based models in ecology after four decades. F1000Prime Rep 6. https://doi.org/10.12703/P6-39

Ezard, T.H.G., Bullock, J.M., Dalgleish, H.J., Millon, A., Pelletier, F., Ozgul, A., Koons, D.N., 2010. Matrix models for a changeable world: The importance of transient dynamics in population management. Journal of Applied Ecology 47, 515–523. https://doi.org/10.1111/j.1365-2664.2010.01801.x

Fahrig, L., 1992. Relative importance of spatial and temporal scales in a patchy environment. Theor Popul Biol 41, 300–314. https://doi.org/10.1016/0040-5809(92)90031-N

Fernández-Salvador, R., García-Perea, R., Ventura, J., 2005a. Effect of climatic fluctuations on body mass of a Mediterranean vole, *Microtus cabrerae*. Mammalian Biology 70, 73–83. https://doi.org/10.1016/j.mambio.2004.06.002

Fernández-Salvador, R., García-Perea, R., Ventura, J., 2001. Reproduction and postnatal growth of the Cabrera vole, *Microtus cabrerae*, in captivity. Can J Zool 79, 2080–2085. https://doi.org/10.1139/cjz-79-11-2080

Fernández-Salvador, R., Ventura, J., García-Perea, R., 2005b. Breeding patterns and demography of a population of the Cabrera vole, *Microtus cabrerae*. Animal Biology 55, 147–161. https://doi.org/10.1163/1570756053993497

Freemark, K., Bert, D., Villard, M.-A., 2002. Patch-, landscape-, and regional-scale effects on biota, in: Gutzwiller, K.J. (Ed.), Applying Landscape Ecology in Biological Conservation. Springer-Verlag, New York, pp. 58–83. https://doi.org/10.1007/978-1-4613-0059-5_5

Frouz, J., Kindlmann, P., 2015. Source-sink colonization as a possible strategy of insects living in temporary habitats. PLoS One 10, 1–10. https://doi.org/10.1371/journal.pone.0127743

Furrer, R.D., Pasinelli, G., 2016. Empirical evidence for source-sink populations: a review on occurrence, assessments and implications. Biol Rev Camb Philos Soc 91, 782–795. https://doi.org/10.1111/brv.12195

Garrido-García, J.A., Nieto-Lugilde, D., Alba-Sánchez, F., Soriguer, R.C., 2018. Agricultural intensification during the Late Holocene rather than climatic aridification drives the population dynamics and the current conservation status of *Microtus cabrerae*, an endangered Mediterranean rodent. J Biogeogr 45, 448–460. https://doi.org/10.1111/jbi.13134

Gilbert, A.N., 1984. Postpartum and lactational estrus: A comparative analysis in Rodentia. J Comp Psychol 98, 232–245. https://doi.org/10.1037/0735-7036.98.3.232

Griffen, B.D., Norelli, A.P., 2015. Spatially variable habitat quality contributes to within-population variation in reproductive success. Ecol Evol 5, 1474–1483. https://doi.org/10.1002/ece3.1427

Grimm, V., 2005. Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology. Science (1979) 310, 987–991. https://doi.org/10.1126/science.1116681

Grimm, V., Ayllón, D., Railsback, S.F., 2017. Next-Generation Individual-Based Models Integrate Biodiversity and Ecosystems: Yes We Can, and Yes We Must. Ecosystems 20, 229–236. https://doi.org/10.1007/s10021-016-0071-2

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, 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., 2012. Pattern-oriented modelling: A “multi-scope” for predictive systems ecology. Philosophical Transactions of the Royal Society B: Biological Sciences 367, 298–310. https://doi.org/10.1098/rstb.2011.0180

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. Jasss 23. https://doi.org/10.18564/jasss.4259

Gundersen, G., Johannesen, E., Andreassen, H.P., Ims, R.A., 2001. Source-sink dynamics: How sinks affect demography of sources. Ecol Lett 4, 14–21. https://doi.org/10.1046/j.1461-0248.2001.00182.x

Hanski, I.A., Gaggiotti, O.E., 2004. Ecology, Genetics and Evolution of Metapopulations. Elsevier, Burlington, MA, USA.

Hastings, A., 2003. Metapopulation Persistence with Age-Dependent Disturbance or Succession. Science (1979) 301, 1525–1526. https://doi.org/10.1126/science.1087570

Hatton, I., 2020. What Regulates Growth across Levels of Organization?, in: Dobson, A., Holt, R.D., Tilman, D. (Eds.), Unsolved Problems in Ecology. Princeton University Press, pp. 203–217. https://doi.org/10.2307/j.ctvs9fh2n

Heinrichs, J.A., Bender, D.J., Gummer, D.L., Schumaker, N.H., 2015. Effects of landscape and patch-level attributes on regional population persistence. J Nat Conserv 26, 56–64. https://doi.org/10.1016/j.jnc.2015.05.002

Heinrichs, J.A., Lawler, J.J., Schumaker, N.H., 2016. Intrinsic and extrinsic drivers of source-sink dynamics. Ecol Evol 6, 892–904. https://doi.org/10.1002/ece3.2029

Heinrichs, J.A., Walker, L.E., Lawler, J.J., Schumaker, N.H., Monroe, K.C., Bleisch, A.D., 2019. Recent Advances and Current Challenges in Applying Source-Sink Theory to Species Conservation. Current Landscape Ecology Reports 4, 51–60. https://doi.org/10.1007/s40823-019-00039-3

Homma, T., Saltelli, A., 1996. Importance measures in global sensitivity analysis of nonlinear models. Reliab Eng Syst Saf 52, 1–17. https://doi.org/10.1016/0951-8320(96)00002-6

Iles, D.T., Williams, N.M., Crone, E.E., 2018. Source-sink dynamics of bumblebees in rapidly changing landscapes. Journal of Applied Ecology 55, 2802–2811. https://doi.org/10.1111/1365-2664.13175

Iooss, B., Janon, A., Pujol, G., Boumhaout, K., Da Veiga, S., Delage, T., Fruth, J., Gilquin, L., Guillaume, J., Le Gratiet, L., Lemaitre, P., Nelson, B.L., Monari, F., Oomen, R., Rakovec, O., Ramos, B., Roustant, O., Song, E., Staum, J., Sueur, R., Touati, T., Weber, F., 2019. sensitivity: Global Sensitivity Analysis of Model Outputs. R package version 1.16.3.

Jansen, M.J.W., 1999. Analysis of variance designs for model output. Comput Phys Commun 117, 35–43. https://doi.org/10.1016/S0010-4655(98)00154-4

Johnson, D.M., 2004. Source-sink dynamics in a temporally heterogeneous environment. Ecology 85, 2037–2045. https://doi.org/10.1890/03-0508

Kaul, H., Ventikos, Y., 2013. Investigating biocomplexity through the agent-based paradigm. Brief Bioinform 16, 137–152. https://doi.org/10.1093/bib/bbt077

Keymer, J.E., Marquet, P.A., Velasco-Hernandez, J.X., Levin, S.A., 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. American Naturalist 156, 478–494. https://doi.org/10.1086/303407

Landete-Castillejos, T., Andrés-Abellán, M., Argandoña, J.J., Garde, J., 2000. Distribution of the Cabrera vole (*Microtus cabrerae*) in its first reported areas reassessed by live trapping. Biol Conserv 94, 127–130. https://doi.org/10.1016/S0006-3207(99)00167-6

Loreau, M., Daufresne, T., Gonzalez, A., Gravel, D., Guichard, F., Leroux, S.J., Loeuille, N., Massol, F., Mouquet, N., 2013. Unifying sources and sinks in ecology and Earth sciences. Biological Reviews 88, 365–379. https://doi.org/10.1111/brv.12003

Luque-Larena, J.J., López, P., 2007. Microhabitat use by wild-ranging Cabrera voles *Microtus cabrerae* as revealed by live trapping. Eur J Wildl Res 53, 221–225. https://doi.org/10.1007/s10344-006-0084-9

Marino, S., Hogue, I.B., Ray, C.J., Kirschner, D.E., 2008. A methodology for performing global uncertainty and sensitivity analysis in systems biology. J Theor Biol 254, 178–196. https://doi.org/10.1016/j.jtbi.2008.04.011

Mathias ML (coord.), Fonseca, C., Rodrigues, L., Grilo, C., Lopes-Fernandes, M., Palmeirim, J., Santos-Reis, M., Alves, P., Cabral, J., Ferreira, M., Mira, A., Eira, C., Negrões, N., Paupério, J., Pita, R., Rainho, A., Rosalino, L., Tapisso, J., Vingada, J., 2023. Livro Vermelho dos Mamíferos de Portugal Continental. FCiências.ID, ICNF, Lisboa.

Mestre, F., Pita, R., Mira, A., Beja, P., 2020. Species traits, patch turnover and successional dynamics: When does intermediate disturbance favour metapopulation occupancy? BMC Ecol 20, 1–11. https://doi.org/10.1186/s12898-019-0273-5

Mestre, F., Pita, R., Paupério, J., Martins, F.M.S., Alves, P.C., Mira, A., Beja, P., 2015. Combining distribution modelling and non-invasive genetics to improve range shift forecasting. Ecol Modell 297, 171–179. https://doi.org/10.1016/j.ecolmodel.2014.11.018

Millon, A., Lambin, X., Devillard, S., Schaub, M., 2019. Quantifying the contribution of immigration to population dynamics: a review of methods, evidence and perspectives in birds and mammals. Biological Reviews 94, 2049–2067. https://doi.org/10.1111/brv.12549

Nisi, A.C., Benson, J.F., King, R., Wilmers, C.C., 2023. Habitat fragmentation reduces survival and drives source–sink dynamics for a large carnivore. Ecological Applications 33, 1–13. https://doi.org/10.1002/eap.2822

Paquet, M., Arlt, D., Knape, J., Low, M., Forslund, P., Pärt, T., 2020. Why we should care about movements: Using spatially explicit integrated population models to assess habitat source–sink dynamics, Journal of Animal Ecology. https://doi.org/10.1111/1365-2656.13357

Pasinelli, G., Runge, J.P., Schiegg, K., 2011. Source–sink status of small and large wetland fragments and growth rate of a population network, in: Sources, Sinks and Sustainability. Cambridge University Press, pp. 216–238. https://doi.org/10.1017/CBO9780511842399.012

Peralta, D., Vaz, T., Clara, F., Mendes, T., Mira, A., Santos, S., Alves, P.C., Lambin, X., Beja, P., Paupério, J., Pita, R., 2023. From species detection to population size indexing: the use of sign surveys for monitoring a rare and otherwise elusive small mammal. Eur J Wildl Res 69, 1–14. https://doi.org/10.1007/s10344-022-01634-2

Pilowsky, J.A., Colwell, R.K., Rahbek, C., Fordham, D.A., 2022. Process-explicit models reveal the structure and dynamics of biodiversity patterns. Sci Adv 8, 1–13. https://doi.org/10.1126/sciadv.abj2271

Pita, R., Beja, P., Mira, A., 2007. Spatial population structure of the Cabrera vole in Mediterranean farmland: The relative role of patch and matrix effects. Biol Conserv 134, 383–392. https://doi.org/10.1016/j.biocon.2006.08.026

Pita, R., Mira, A., Beja, P., 2014. *Microtus cabrerae* (Rodentia: Cricetidae). Mammalian Species 46, 48–70. https://doi.org/10.1644/912.1

Pita, R., Mira, A., Beja, P., 2011. Assessing habitat differentiation between coexisting species: The role of spatial scale. Acta Oecologica 37, 124–132. https://doi.org/10.1016/j.actao.2011.01.006

Pita, R., Mira, A., Beja, P., 2010. Spatial segregation of two vole species (*Arvicola sapidus* and *Microtus cabrerae*) within habitat patches in a highly fragmented farmland landscape. Eur J Wildl Res 56, 651–662. https://doi.org/10.1007/s10344-009-0360-6

Pita, R., Mira, A., Beja, P., 2006. Conserving the Cabrera vole, *Microtus cabrerae*, in intensively used Mediterranean landscapes. Agric Ecosyst Environ 115, 1–5. https://doi.org/10.1016/j.agee.2005.12.002

Poniatowski, D., Stuhldreher, G., Löffler, F., Fartmann, T., 2018. Patch occupancy of grassland specialists: Habitat quality matters more than habitat connectivity. Biol Conserv 225, 237–244. https://doi.org/10.1016/j.biocon.2018.07.018

Proença-Ferreira, A., Ferreira, C.M., Leitão, I., Paupério, J., Sabino-Marques, H., Barbosa, S., Lambin, X., Alves, P.C., Beja, P., Moreira, F., Mira, A., Pita, R., 2019. Drivers of survival in a small mammal of conservation concern: An assessment using extensive genetic non-invasive sampling in fragmented farmland. Biol Conserv 230, 131–140. https://doi.org/10.1016/j.biocon.2018.12.021

Pulliam, H.R., Danielson, B.J., 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 2, 430.

Pulliam, R., 1988. Sources, sinks, and population regulation. Am Nat 132, 652–661.

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/.

Radchuk, V., Ims, R.A., Andreassen, H.P., 2016. From individuals to population cycles: The role of extrinsic and intrinsic factors in rodent populations. Ecology 97, 720–732. https://doi.org/10.1890/15-0756.1

Railsback, S.F., Grimm, V., 2019. Agent-based and individual-based modeling: a practical introduction, Second edi. ed. Princeton University Press, New Jersey, United States of America.

Reigada, C., Schreiber, S.J., Altermatt, F., Holyoak, M., 2015. Metapopulation dynamics on ephemeral patches. American Naturalist 185, 183–195. https://doi.org/10.1086/679502

Robles, H., Ciudad, C., 2012. Influence of Habitat Quality, Population Size, Patch Size, and Connectivity on Patch-Occupancy Dynamics of the Middle Spotted Woodpecker. Conservation Biology 26, 284–293. https://doi.org/10.1111/j.1523-1739.2011.01816.x

Rosário, I.T., 2012. Towards a conservation strategy for an endangered rodent, the Cabrera vole (*Microtus cabrerae* Thomas). Insights from ecological data. PhD Thesis, University of Lisbon, Lisbon, Portugal.

Rosário, I.T., Mathias, M. da L., 2007. Post-fire recolonisation of a montado area by the endangered Cabrera vole (*Microtus cabrerae*). Int J Wildland Fire 16, 450–457. https://doi.org/10.1071/WF06096

Runge, J.P., Runge, M.C., Nichols, J.D., 2006. The role of local populations within a landscape context: Defining and classifying sources and sinks. American Naturalist 167, 925–938. https://doi.org/10.1086/503531

Sabau, R.M., Ferkin, M.H., 2013. Food deprivation and restriction during late gestation affect the sexual behavior of postpartum female meadow voles, *Microtus pennsylvanicus*. Ethology 119, 29–38. https://doi.org/10.1111/eth.12033

Sabino-Marques, H., Ferreira, C.M., Paupério, J., Costa, P., Barbosa, S., Encarnação, C., Alpizar-Jara, R., Alves, P.C., Searle, J.B., Mira, A., Beja, P., Pita, R., 2018. Combining genetic non-invasive sampling with spatially explicit capture-recapture models for density estimation of a patchily distributed small mammal. Eur J Wildl Res 64, 44. https://doi.org/10.1007/s10344-018-1206-x

Salecker, J., Sciaini, M., Meyer, K.M., Wiegand, K., 2019. The NLRX R package: A next-generation framework for reproducible NetLogo model analyses. Methods Ecol Evol 10, 1854–1863. https://doi.org/10.1111/2041-210X.13286

Saltelli, A., Annoni, P., Azzini, I., Campolongo, F., Ratto, M., Tarantola, S., 2010. Variance based sensitivity analysis of model output. Design and estimator for the total sensitivity index. Comput Phys Commun 181, 259–270. https://doi.org/10.1016/j.cpc.2009.09.018

Saltelli, A., Ratto, M., Andres, T., Campolongo, F., Cariboni, J., Gatelli, D., Saisana, M., Tarantola, S., 2008. Global Sensitivity Analysis: The Primer. John Wiley & Sons, Ltd, Chichester, UK. https://doi.org/10.1002/9780470725184

Sample, C., Bieri, J.A., Allen, B., Dementieva, Y., Carson, A., Higgins, C., Piatt, S., Qiu, S., Stafford, S., Mattsson, B.J., Semmens, D.J., Diffendorfer, J.E., Thogmartin, W.E., 2020. Quantifying the contribution of habitats and pathways to a spatially structured population facing environmental change. American Naturalist 196, 157–168. https://doi.org/10.1086/709009

Sample, C., Bieri, J.A., Allen, B., Dementieva, Y., Carson, A., Higgins, C., Piatt, S., Qiu, S., Stafford, S., Mattsson, B.J., Semmens, D.J., Thogmartin, W.E., Diffendorfer, J.E., 2019. Quantifying source and sink habitats and pathways in spatially structured populations: A generalized modelling approach. Ecol Modell 407, 108715. https://doi.org/10.1016/j.ecolmodel.2019.06.003

Santoro, S., Green, A.J., Figuerola, J., 2016. Immigration enhances fast growth of a newly established source population. Ecology 97, 1048–1057. https://doi.org/10.1890/14-2462.1

Schumaker, N.H., Brookes, A., Dunk, J.R., Woodbridge, B., Heinrichs, J.A., Lawler, J.J., Carroll, C., LaPlante, D., 2014. Mapping sources, sinks, and connectivity using a simulation model of northern spotted owls. Landsc Ecol 29, 579–592. https://doi.org/10.1007/s10980-014-0004-4

Sobol, I.M., 1993. Sensitivity analysis for non-linear mathematical models. Mathematical Modelling and Computational Experiments 1, 407–414.

Stoffels, R.J., Rehwinkel, R.A., Price, A.E., Fagan, W.F., 2016. Dynamics of fish dispersal during river-floodplain connectivity and its implications for community assembly. Aquat Sci 78, 355–365. https://doi.org/10.1007/s00027-015-0437-0

ten Broeke, G., van Voorn, G., Ligtenberg, A., 2016. Which sensitivity analysis method should I use for my agent-based model? JASSS 19. https://doi.org/10.18564/jasss.2857

Topping, C.J., Dalkvist, T., Grimm, V., 2012. Post-Hoc Pattern-Oriented Testing and Tuning of an Existing Large Model: Lessons from the Field Vole. PLoS One 7, e45872. https://doi.org/10.1371/journal.pone.0045872

Van Teeffelen, A.J.A., Vos, C.C., Opdam, P., 2012. Species in a dynamic world: Consequences of habitat network dynamics on conservation planning. Biol Conserv 153, 239–253. https://doi.org/10.1016/j.biocon.2012.05.001

Ventura, J., Lopez-Fuster, M.J., Cabrera-Millet, M., 1998. The Cabrera vole, *Microtus cabrerae*, in Spain: A biological and a morphometric approach. Netherlands Journal of Zoology 48, 83–100. https://doi.org/10.1163/156854298X00237

Wang, M., 2013. From home range dynamics to population cycles: Validation and realism of a common vole population model for pesticide risk assessment. Integr Environ Assess Manag 9, 294–307. https://doi.org/10.1002/ieam.1377

Wilensky, U., 1999. NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling. Northwestern University, Evanston, Illinois, U.S.

Wilensky, U., Rand, W., 2015. An introduction to agent-based modeling: modeling natural, social, and engineered complex systems with NetLogo. The MIT Press, Cambridge, Massachusetts. London, England.

Wright, A.D., Grant, E.H.C., Zipkin, E.F., 2020. A hierarchical analysis of habitat area, connectivity, and quality on amphibian diversity across spatial scales. Landsc Ecol 35, 529–544. https://doi.org/10.1007/s10980-019-00963-z

Chapter 3

Using individual-based demographic modelling to estimate the impacts of anthropogenic mortality on territorial predators

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Chapter 3 – Using individual-based demographic modelling to estimate the impacts of anthropogenic mortality on territorial predators

Abstract

Wildlife anthropogenic mortality is increasing worldwide, yet there is limited understanding regarding its population-level impacts. Territorial species stand out in this context, as they possess distinctive characteristics that are often overlooked but may significantly affect their vulnerability. In particular, population impacts may depend on the level and spatial distribution of additional mortality risk across territories, and on the extent to which exposure to increased mortality varies across life stages (i.e., territorial and non-territorial individuals). In this study, we developed an Individual-Based Model (IBM) to explore these issues, using the Bonelli's eagle (*Aquila fasciata*) and electrocution in powerline pylons as a model system. We used declines in annual population growth rates as a proxy for negative impacts, and conducted simulations to estimate the relative impacts of different levels of mortality risk, the spatial pattern of such risks, and the risk exposure of different life stages. Population-level impacts greatly increased with the mortality risks simulated, and they were lower when exposure to mortality risks was concentrated versus spread across territories. Impacts were highest when both territorial and non-territorial individuals were exposed to anthropogenic mortality risks, and they were higher when such exposure only affected non-territorial versus territorial individuals. Our results underscore that each breeding territory should be considered as a unit, where all existing pylons should be intervened whenever mitigation actions are put in place. Results also highlight the importance of considering both the territorial and non-territorial fractions of the population to prevent and mitigate the impacts of increased mortality. More generally, our study illustrates the value of IBM frameworks such as ours to explore population-level impacts resulting from anthropogenic mortality in territorial species, and to inform the development of conservation strategies to mitigate such impacts.

Keywords

Agent-based models, *Aquila fasciata*, electrocution, population dynamics, power lines

3.1 Introduction

Wildlife is increasingly affected by mortality from multiple anthropogenic sources (Hill et al., 2020; Loss et al., 2015), including legal harvesting (e.g. overfishing; Hill et al., 2019), direct persecution (Inskip and Zimmermann, 2009; Madden et al., 2019), bycatch (Hall et al., 2000) and interactions with infrastructures (Bernardino et al., 2018; Forman and Alexander, 1998; Marques et al., 2014). Such mortality may have far-reaching consequences on population dynamics, potentially leading to local extinctions (Diffendorfer et al., 2021; Grilo et al., 2021). In particular, long-lived top predators should be highly vulnerable to additional mortality, due to their relatively low intrinsic population growth rates, large home ranges, small population sizes, and low carrying capacity (Ripple et al., 2014). Therefore, a detailed understanding is needed on how additional mortality can affect the population dynamics of these species, providing information to design cost-effective strategies for avoiding and mitigating impacts (Chevallier et al., 2015; Loveridge et al., 2017).

Several studies have modelled the effects of anthropogenic wildlife mortality, aiming to estimate critical mortality thresholds above which population viability may be compromised, and to guide the development of measures to avoid and mitigate mortality impacts (Borda-de-Água et al., 2014; Cervantes et al., 2022; Chambert et al., 2023; Dillingham and Fletcher, 2008; Schippers et al., 2020). However, few studies have focused on long-lived, territorial species (but see Heurich et al., 2018), and most were based on overly simplistic assumptions, ignoring potentially important population processes associated with territorial behaviour. First, territorial animals live within home ranges that are often used exclusively by a breeding pair, largely excluding other breeding or non-breeding individuals (Newton, 1992). In such populations, the carrying capacity is defined by the number of territories that can be established in a given area, which thus define the upper bound for the breeding population (Newton, 1992). Second, territoriality implies that the exposure of breeding individuals to anthropogenic mortality risks may be spatially heterogeneous across the population. For instance, power lines may cross some territories but not others, and thus only some breeders and their offspring may be exposed to electrocution or collision risk. Third, in territorial species there is often a large number of non-territorial individuals (i.e., individuals not attached to a breeding territory, usually immatures but also non-breeding adults) that use areas away from breeding territories (Adams, 2001; Newton, 1992) and may thus be exposed to risks different from those of breeding adults. Finally, while most population models consider recruitment to the breeding population as a function of age, recruitment in the case of territorial species is also conditional on territory availability. Therefore, near carrying capacity there may be an accumulation of non-territorial individuals, which can rapidly fill territory vacancies, potentially compensating to an unknown extent the anthropogenic mortality of breeding adults (Krebs, 2002; Morales et al., 2010; Rohner, 1996). Hence, to fully understand the population-level consequences of varying anthropogenic mortality risk in territorial species, models should incorporate (1) the strict bounds to breeding population size resulting from territorial behaviour; the heterogeneity in exposure to mortality risks (2) across breeding territories and (3) between territorial and non-territorial individuals; (4) the limitations of recruitment to the breeding population resulting from territory availability; and (5) the potential role of non-territorial individuals in buffering fluctuations in the breeding population. These important processes tend to be overlooked in models assessing the effects of anthropogenic mortality on territorial animals, and only a few studies completely or partially account for them (Barbosa et al., 2020; Heurich et al., 2018). Nonetheless, those models are overly focused on the specificities of a single species within a particular study area, with limited extension to other contexts, making it difficult to generalize to other taxa and contexts.

Individual-Based Models (IBMs) provide a powerful and versatile tool to simulate the dynamics of complex populations and their responses to anthropogenic drivers (DeAngelis and Grimm, 2014), with potential applications to examine the population dynamics of long-lived territorial species. IBMs demonstrated their ability to represent complex territorial behaviours across a spectrum of species, ranging from shrews (Wang and Grimm, 2010) to tigers (Carter et al., 2015). Moreover, these models can effectively simulate the population-level effects of anthropogenic mortality, stemming from factors such as roadkills and illegal hunting, in species with both dispersant and territorial life cycles (Barbosa et al., 2020; Heurich et al., 2018). By modelling individuals and explicitly representing their behaviours and interactions, IBMs stand out as bottom-up models, in contrast to traditional model approaches (DeAngelis and Grimm, 2014). This bottom-up perspective allows for the emergence of population-level patterns through interactions among individuals and between individuals and their environment, having the potential to include spatial-explicit processes (Carter et al., 2015; DeAngelis and Grimm, 2014; Semeniuk et al., 2012). By allowing the modelling of both aged-structured and territoriality processes, IBMs have thus a high potential to improve our understanding of how anthropogenic mortality and its mitigation affect populations dynamics.

Here we provide a modelling framework based on IBMs to investigate the effects of anthropogenic mortality on territorial, long-lived predators, explicitly incorporating key processes that are specific to territorial species and that can be easily generalized to several species. The framework is then illustrated with a case study focusing on the Bonelli’s eagle *Aquila* *fasciata* and electrocution at power lines. This was considered an adequate model system, because even low levels of mortality by electrocution can drive local Bonelli's eagle population to extinction (Hernández-Matías et al., 2015; Rollan et al., 2010). Moreover, detailed ecological and demographic information on the Bonelli's eagle is available from studies carried out over the past decades on several populations. However, while previous population matrix models for the Bonelli's eagle have already shown that viability is strongly affected by anthropogenic mortality, none of these have explicitly considered individual-based population processes related to territoriality. We use our IBM framework to provide a more realistic estimation of the impacts of anthropogenic mortality on Bonelli's eagles, estimating changes in population growth rates resulting from variation in exposure to mortality risks on (i) different life stages (i.e., territorial versus non-territorial individuals, or both), and (ii) different sets of territories (i.e., few versus multiple territories). Finally, we discuss the application of our framework to comparable territorial species affected by anthropogenic mortality.

3.2 Methods

3.2.1 Model species

The Bonelli's eagle is a long-lived territorial raptor, usually recruiting between the ages of three and four (Hernández-Matías et al., 2010). Each pair typically produces up to two fledglings annually, with rare instances of three (Araújo et al., 1974; Gil-Sánchez et al., 2004; Hernández-Matías et al., 2013; L. Palma, *unpubl. data*). Breeding birds are sedentary and monogamous, showing a strong pair bonding and fidelity to the breeding territory, both within and between years (Bosch et al., 2010). Like other territorial eagles, there is a transient nomadic phase after the post-fledging dependence period and until the territorial recruitment, when birds disperse over hundreds or even thousands of kilometres (Balbontín and Ferrer, 2009; Real and Mañosa, 2001). Currently, the species is categorized as Least Concern in Europe and worldwide, although it is declining throughout most of its range due to human-related threats (BirdLife International, 2022). Anthropogenic mortality from electrocution in power lines and direct persecution are pointed out as relevant sources of mortality for this species (Hernández-Matías et al., 2015; Real et al., 2001).

Our study focused on the Bonelli's eagle population of southern Portugal (south of the Tagus River), which has been steadily increasing in numbers and expanding in range since the early 1990s, from 33 up to over a hundred breeding pairs at present (Dias et al., 2017; Palma et al., 2013). Breeding pairs typically establish home ranges with a mean of 141.6 ± 71.1 km^2 (Marques et al., 2022). Data collected from this population over a 20-year period allowed to estimate its demographic parameters and revealed that it acts as a source within the Western European metapopulation, comprising Portugal, Spain and France (Hernández-Matías et al., 2013).

3.2.2 Model description

We implemented an Individual-Based Modelling (IBM) framework using NetLogo (Tisue and Wilensky, 2004; Wilensky, 1999) to estimate the impacts of anthropogenic mortality on Bonelli's eagle populations. A complete, detailed model description, following the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2020, 2010, 2006) is presented in the Appendix C. The code is available here:

https://github.com/TCrispimMendes/IBM_Anthropogenic_Mortality_on_Territorial_Predators

Below, we present a brief overview of the model's structure and processes, as recommended by Grimm et al. (2020). All simulation runs for testing and analysing the model were performed using the "*NLRX*" package (Salecker et al., 2019) in R (R Core Team, 2020).

The overall purpose of our model was to understand how exposure to additional anthropogenic mortality impacts long-lived raptors species with territorial behaviour. Specifically, we wanted to estimate changes in population growth rates resulting from different probabilities of additional mortality affecting (i) territorial versus non-territorial individuals (or both), and (ii) few versus multiple territories. To ensure realism of our model to achieve this goal, we used a pattern-oriented modelling (POM) strategy (Grimm et al., 2005; Grimm and Railsback, 2012) to simulate individual-level patterns and behaviours in mortality, age structure, reproduction, dispersion, and territoriality.

The model included three entities, characterised by the state variables listed in Table 3.1: Patches (grid cells) representing spatial units used by Bonelli's eagles (i.e., territories for breeding birds), Birds (agents) representing individual Bonelli's eagles, and the Global Environment (i.e., Observer in NetLogo), the only entity at the system level, which controlled the submodels and the probabilities of additional mortality, while also keeping track of simulated time. The model spatial extent simulated the geographical context of the population, including 131 Patches potentially used by breeding pairs (type "A" Patches), and another 50 Patches that can only be used by non-territorial individuals (type "B" Patches). As we lack detailed empirical data about the range and settlement areas and the size of home ranges used by the non-territorial birds of the Bonelli's' eagle population in southern Portugal, we chose a number of patches of type "B" that was sufficient to accommodate the non-breeding birds predicted for a population with a stable age distribution of 131 pairs (the defined carrying capacity in the model). This calculation was conducted assuming a delay in recruitment as a density-dependent mechanism, which occurs when the carrying capacity of patches occupiable by territorial individuals (type "A") is reached. In this scenario, we assumed that recruitment only takes place in the 4th year of life, rather than being able to occur in the 2nd and 3rd years. In this case, considering the basal recruitment probability of 0.93 for individuals aged 4 years, for a population of 262 territorial individuals (131 pairs) with a stable age distribution, it is anticipated that there will be 236 non-territorial individuals. Given our model's carrying capacity of 5 non-territorial individuals per Patch, this suggests the need for at least 48 type "B" Patches to accommodate all non-territorial individuals. Additionally, considering the potential reduction in recruitment probability for individuals aged 4, we chose to conservatively include 50 "B" Patches in the model to ensure adequate space for the maximum expected population when the carrying capacity of "A" Patches is reached.

Each Patch was also characterised by the absence or presence of exposure to additional mortality, the latter involving different mortality probabilities. Birds were categorised according to their territoriality/ breeding status and by their sex and age class, which defines the corresponding values of the demographic parameters. The model ran at 1-year time-steps, representing the annual life cycle of the species. The temporal extent was 50 years, which was considered long enough to analyse the demographic consequences of additional mortality.

The model was structured in seven processes or submodels, two performed by the Global Environment: (i) *time update* and (ii) *outputs update and collection*; and five concerning Birds: (iii) *survival*, (iv) *ageing*, (v) *reproduction*, (vi) *territorial recruitment*, and (vii) *dispersal*. Individuals performed each process at each time-step, and the model was designed to collect outputs on the population, namely the annual population growth rate, the number of breeding pairs in year 50, the number of years of population persistence, and the mean annual survival. To better understand how the exposition to additional mortality affected these birds the model also collected the proportion of Birds dying in Patches with exposure to additional mortality, the proportion of Birds in those patches at the end of the simulation, as well as the probabilities of dispersion and recruitment to them. The model used asynchronous updating, in which the agents update the state variables one at a time as they execute a submodel that uses the variable. To avoid artefacts of execution order, there was no hierarchy among agents of the same type (i.e., age or sex), and so the order in which agents conduct each process is random and varies at each time-step.

Table 3.1 List of entities intervening in the model, with their state variables, corresponding units, and range of possible values.

Entity/State Variable	Description	Unit (Values)
Patches		
type	Patch type (suitable or not for breeding territories)	Categoric (“A”; “B”)
additional_mortality	Define the presence of additional mortality sources	Boolean (True; False)
occupied_M	Define if a breeding male occupies the Patch	Boolean (True; False)
occupied_F	Define if a breeding female occupies the Patch	Boolean (True; False)
non_territorial	Number of non-territorial birds in the Patch	Integer (0 - 5)
Birds		
ID	Unique identification code	Integer (-)
Sex	Individual’s sex	Categoric (“F”; “M”)
Age	Individual’s age	Integer (1 - 20)
age_class	Individual’s age class	Ordinal categoric (“Fledgling”; “Juvenile”; “Immature”; “Subadult”; “Adult”)
territorial	Define if the individual is territorial (breeder) or not	Boolean (True; False)
patch_type	Type of current Patch	Categoric (“A”; “B”)
Global Environment		
sim_year	Current year of simulation	Integer (1 - 50)
patches_AM	Percentage of Patches with additional mortality sources	Integer (0 - 100)
mortality_AM_NT	Yearly death probability from additional mortality sources to non-breeders	Integer (0 - 100)
mortality_AM_T	Yearly death probability from additional mortality sources to breeders	Integer (0 - 100)

3.2.3 Key assumptions and model parametrization

We specified an IBM framework considering a generalisation of the spatial and social structures of the Bonelli’s eagle, which is akin of that of many other territorial birds of prey. First, we considered a study area divided according to a regular grid of Patches, some of which can be occupied by a breeding pair or, transitorily, by a single breeding adult. This assumption implies that all territories are geometrically equivalent, though real home ranges vary widely in shape and size. This simplification is reasonable because our model does not require Birds to interact with environmental features within their home-ranges, e.g., to forage or nest. Second, although we assumed that all Patches have the same size and shape, we considered that habitat conditions of the Patches can be of either type “A” or “B”, according to whether they are suitable or not for setting breeding territories. Specifically, we assumed that only type “A” Patches can be used by breeding individuals, while both type “A” Patches unoccupied by breeders and type “B” Patches can be used by up to a maximum of five non-territorial individuals. This assumption was taken to mimic the spatial organisation of territorial versus non-territorial individuals in real populations, where the later tend to occupy areas less suitable to the former (Newton, 1992). It ignores however other sources of variation in habitat quality potentially affecting population viability, which were incorporated implicitly by specifying random variation in the values of demographic parameters across territories. Third, Patches occupied by territorial pairs can only house the members of the couple and their annual offspring, thus mirroring the behaviour of territorial birds. We assumed that territorial individuals reproduce and stay within the same Patch until dying. We believe this assumption is warranted, because there are few reported instances of breeders shifting across territories or losing their territorial status (Martínez-Miranzo et al., 2016).

Regarding dispersion, we assumed that juveniles produced each year can move freely throughout the study area after fledging and until recruiting into a vacant territory, because the scale of movements undertaken by non-territorial Bonelli’s eagles is much larger than the size of the study area (Hernández-Matías et al., 2010). Although juvenile Birds can reach all the Patches, they will only disperse into the available ones, i.e., Patches not occupied by any territorial Bird and occupied by up to other 4 non-territorial Birds. When multiple Patches are available, Birds choose type “A” Patches due to their higher quality. Additionally, Birds will also recruit into any available Patch of the study area. Given the predominant role of male raptors in establishing and maintaining territories (Newton 1979), effective recruitment occurs only under one of two conditions: (i) when an unpaired territorial bird of the opposite sex is available; or 2) for males, when a type 'A' patch is unoccupied by any territorial individual, enabling the establishment of a new territory. Movement trajectories and seasonal patterns were not explicitly incorporated to avoid overly complex models, and so we assumed that juveniles disperse and non-territorial individuals seek recruitment opportunities throughout the study area by visiting any empty or occupied Patch.

Finally, migration out of the study area occurs when all Patches are occupied at their carrying capacity. To maintain model simplicity, immigration was not included, a choice deemed reasonable given that the Bonelli’s eagle population in southern Portugal was previously identified as a source within the Western European metapopulation (Hernández-Matías et al., 2013).

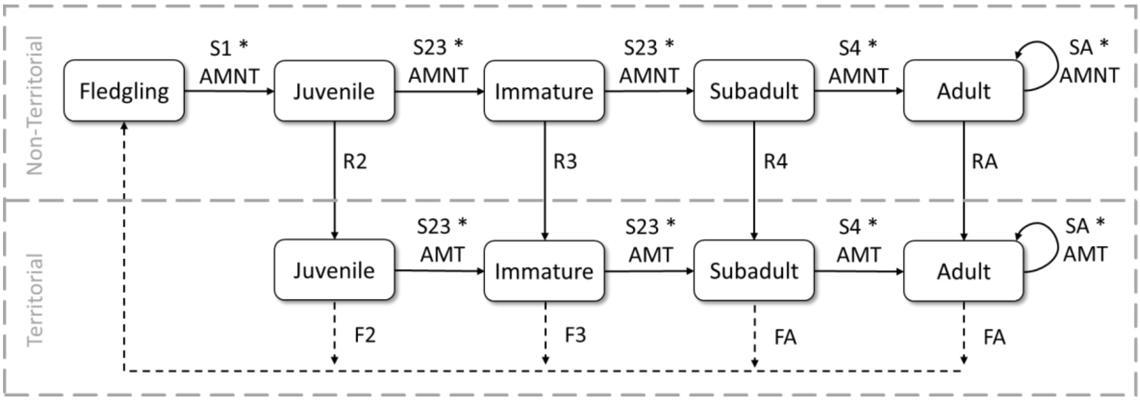

Figure 3.1 Structure of the Bonelli's eagle life cycle. The solid arrows represent the transitions between age classes and territorial state, while the dashed arrows represent productivity, based on fertility values. S represents the survival rates of individuals during their first (S1), second and third (S23), fourth (S4), and fifth and subsequent (adult) years of life (SA). AMNT and AMT represent the exposure to additional mortality for non-territorial and territorial individuals, respectively. R represents the propensity to become territorial in immature birds (R2), subadults (R3), first-year adults (R4), and adults (RA). F represents fertilities for any given age class (F2, F3, and FA being fertility of two- and three-year olds and adults, respectively).

Following Hernández-Matías et al. (2013), we specified a life-cycle structure with five age classes (Figure 3.1), with the demographic parameters of individuals determined by age class membership. Briefly, each year breeding females produce fledglings according to age-class specific fecundity rates, and each member of the breeding pair survives to the next year according to age-class specific survival rates. Fledglings are integrated into the non-territorial fraction of the population, staying there until dying or recruiting to the territorial breeding population according to age-class specific survival and recruitment rates. We limited the breeding population to a total of 131 pairs (i.e., carrying capacity), corresponding to 110% of the breeding population of southern Portugal in 2019, which was considered close to saturation (Dias et al., 2017). The model parameters were assigned based on empirical data from our focal population or, when not available, they were inferred from other Western Europe populations (Table 3.2).

To model the effects of electrocution on the population dynamics, we considered exposure to additional mortality by reducing the baseline survival rate by a given probability, which varied across simulated scenarios (see section 3.2.4 for details). The additional mortality affects the overall probability of mortality according to the formula:

$$Probability\ of\ mortality = 1 - (S \times (1 - AM))$$

Where *S* stands for survival of the individual's age class and *AM* stands for the annual additional mortality probability for the individual's breeding status.

Exposure to additional mortality was specified only for some Patches selected randomly and not for the entire population, as power lines typically cross some territories but not others. The proportion of Patches exposed to additional mortality varied across simulated scenarios. We also considered that exposure to mortality could affect breeders and non-breeders differently.

Table 3.2 Summary of parameter information used in the IBM of Bonelli’s eagles and population dynamics in the southern Portugal population. *parameter inferred from other populations from Western Europe.

Parameter	Values	Source
Age-classes		Hernández-Matías et al. (2013)
Fledgling	Age 1	
Juvenile	Age 2	
Immature	Age 3	
Subadult	Age 4	
Adult	Age >=5	
Survival		Hernández-Matías et al. (2013)
S1 (fledgling)	0.662946	
S23 (juvenile and immature)	0.719976	
S4 (subadult)	0.874833	
SA (adult)	0.937492	
Maximum age individuals can reach	20 years	delHoyo et al. (1992)
Recruitment		Hernández-Matías et al. (2013)
R1 (fledgling)	0	
R2 (juvenile)	0.160763*	
R3 (immature)	0.679674*	
R4 (subadult)	0.934197*	
RA (adult)	1*	
Fertility		Hernández-Matías et al. (2013)
F1 (fledgling)	0	
F2 (juvenile)	0.285714*	
F3 (immature)	0.5	
F4 (subadult)	0.830328	
FA (adult)	0.830328	

3.2.4 Model validation and simulation experiments

The sensitivity analysis was performed by estimating the impact on annual population growth rates of varying the input parameters (initial population size, number of patches of types “A” and “B”, recruitment, survival and fertility) between 10% above and below their default value following a randomised one-factor-at-a-time design (Campolongo et al., 2007; Morris, 1991). The analysis used the Morris screening method because of its low computational effort requirements (Morris, 1991). For each parameter, the method evaluates its relative importance, linear and additive or nonlinear effect, and interactions with other parameters (Campolongo et al., 2007; Morris, 1991; Thiele et al., 2014). Specifically, for each parameter we estimated: (i) μ - the overall influence; and (ii) σ - the standard deviation of the elementary effects, as an estimate of non-linear and/or interaction effects. The number of tested settings is determined by the formula $r \times (K + 1)$, where r represents the number of elementary effects or trajectories computed per parameter (K). With our selection of 1,000 trajectories, this resulted in 1,000 × (7 + 1) = 8,000 runs. These runs were conducted with four different random seeds, totalling 32,000 simulations.

A comparison of model outputs with empirical data from the southern Portugal population was used to evaluate the model performance. Hence, we checked if the model results reproduced the increase of the population in the period 1991-2019, from 33 to 119 breeding pairs (Palma et al., 2013). Although more empirical data would be needed to properly validate our model, this comparison should still provide relevant insights on model predictive accuracy. Given the absence of empirical evidence regarding the area available for non-territorial birds in southern Portugal, we also analysed how the number of breeding pairs fluctuates over the simulation period with 100 type “B” available patches (instead of 50).

We ran a set of experiments simulating the effects of exposure to additional mortality on: (i) only territorial birds; (ii) only non-territorial birds; or (iii) both classes. While scenarios where both territorial classes were affected are most likely in a wild population, analysing each class separately may provide deeper insights into the population impacts of additional mortality within each class. In each case, we simulated additional mortality affecting 0% (used as a reference value), 25%, 50% or 75% of the Patches. Also, we varied the probability of additional mortality within each Patch from 0 to 100%, with intervals of 10%. Models were run for 50 time-steps (50 years) and each experiment was completed with 1,000-replicates. We used declines in annual population growth rate, number of pairs and the number of years of population persistence (i.e., number of years that the population persisted until eventual its extinction) as a proxy for negative impacts resulting from exposure to additional mortality.

3.3 Results

3.3.1 Sensitivity analysis and model validation

According to the Morris screening method, the population is most sensitive to variation in adult survival (SA), which showed much higher μ and $\mu*$ values than the other parameters (Figure 3.2). However, the high value of σ suggests that some of the other demographic parameters also have a relevant role in the population dynamics. Survival rate from juveniles and immatures (S23) is the second most influential parameter, followed by fledgling survival (S1). The initial population size and the number of available Patches (both types) exhibit a limited but non-monotonic influence, indicating a degree of dependence on other model parameters.

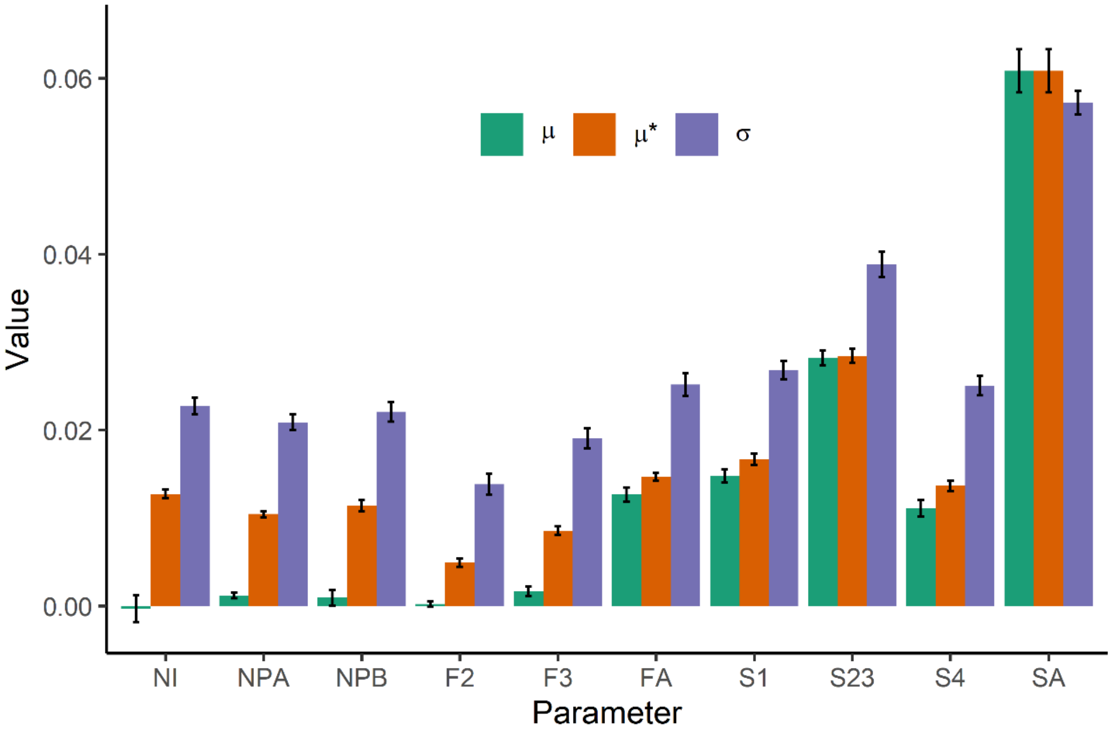

Figure 3.2 Results of the sensitivity analysis, using the Morris screening method. μ and $\mu*$ are indicators of the overall influence of the parameter on the annual population growth rate, but when $\mu*$ is high and μ is low, it indicates that there is a non-monotonic effect on the output; σ is an indicator of dependency of the other input factors (Thiele et al., 2014). NI represents the number of the breeding pairs of the initial population. NPA and NPB represent the number of available type "A" and type "B" Patches, respectively. S represents the survival rates of individuals during their first (S1), second and third (S23), fourth (S4), and fifth and subsequent (adult) years of life (SA). F represents fertilities for any given age class (F2, F3, and FA being fertility of two- and three-year olds and adults, respectively).

Regarding the model validation, the baseline scenario (comprising 131 type "A" and 50 type "B" Patches) provided a reasonable approximation to the number of Bonelli's eagle breeding pairs observed in southern Portugal between 1991 and 2019 (Figure 3.3). Regarding the scenarios with a 10% variation in the number of patches (Figure 3.3), we found that the population increase is consistent irrespective of the scenario simulated, with variations only occurring close to the carrying capacity. We also tested a fourth scenario, changing the number of type "B" Patches from 50 (baseline scenario) to 100 (Figure D.1 in Appendix D). The population growth curve was similar in both scenarios, suggesting that the sensitivity of the model to this parameter was low.

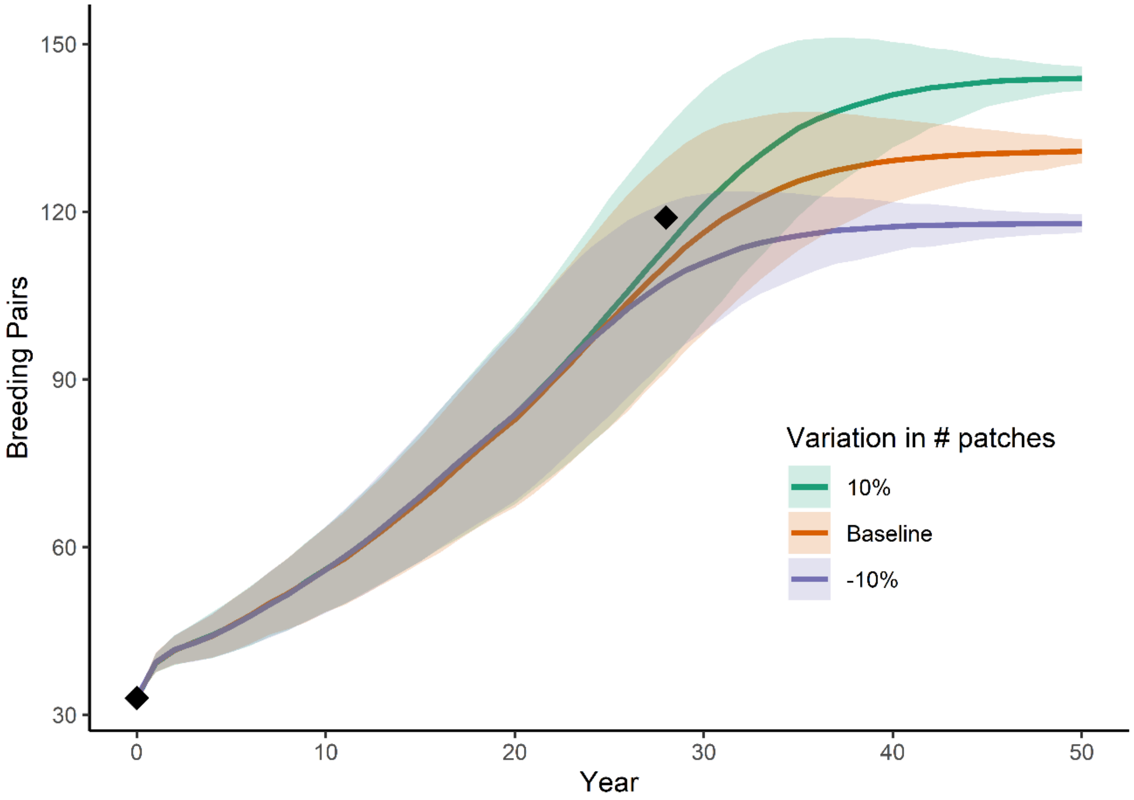

Figure 3.3 Estimated growth of the Bonelli's eagle population of southern Portugal during a 50-year period, considering three scenarios for the number of Patches (type "A" and "B") available in the study area: the baseline, used in further analyses, consists of 131 "A" Patches and 50 "B" Patches, while two other scenarios include a 10% variation in the number of available Patches. The lines and shadowed areas represent the mean number of breeding pairs and the standard deviation. The black diamonds represent the empirical value for the number of breeding pairs in 1991 and 2019 (28 years apart).

3.3.2 Impacts of exposure to additional mortality

The impacts of exposure to additional mortality on populational parameters varied widely depending on whether it affected territorial or non-territorial birds, or both (Figure 3.4).

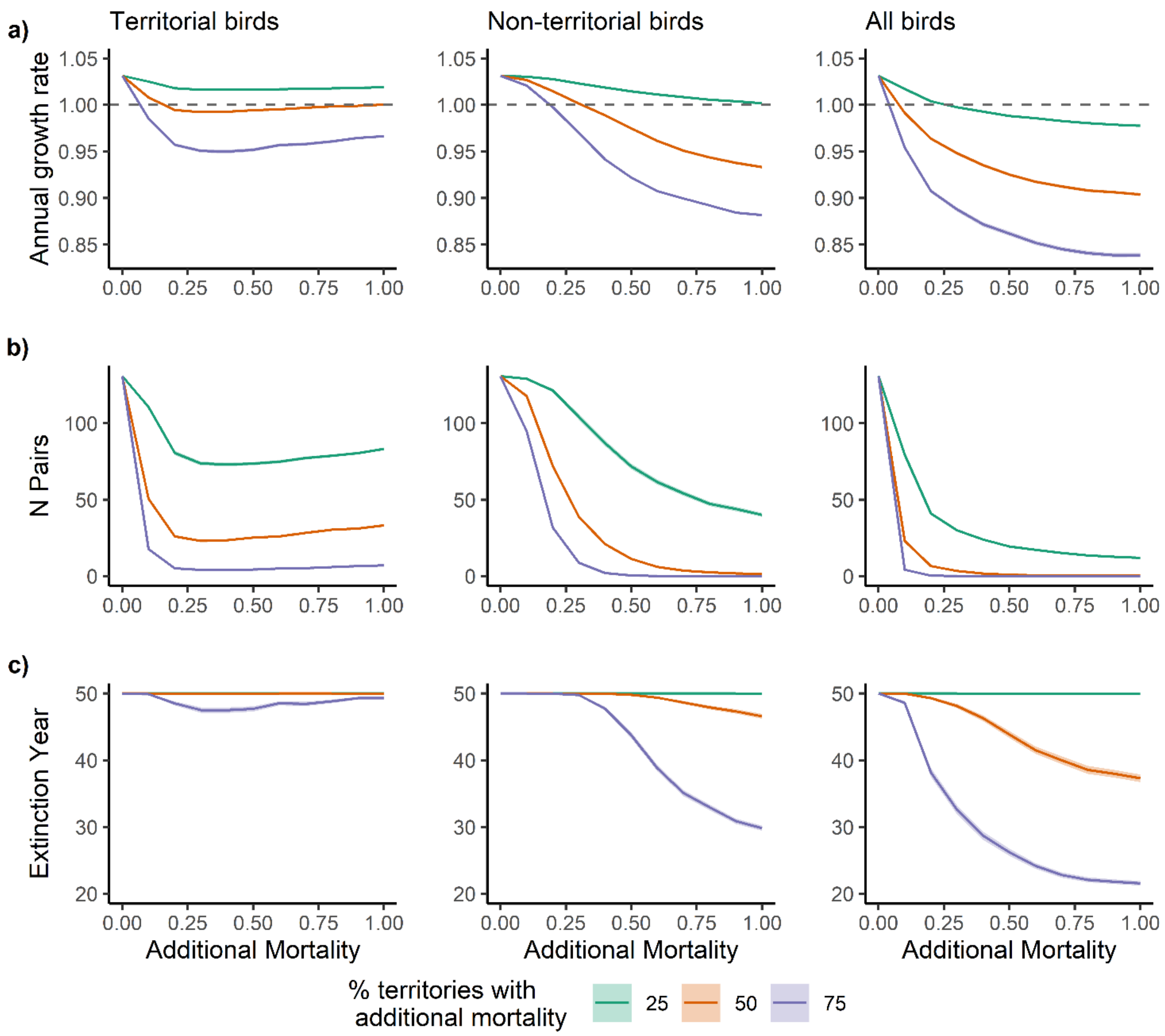

Figure 3.4 Impact of exposure to additional mortality in 25%, 50% and 75% of the Patches on the a) annual growth rate (λ = 1 represents the population trend threshold: if λ > 1 the population increases and if λ < 1 the population declines), b) number of breeding pairs in year 50 and c) number of years of population persistence (number of years that the population persisted until eventual its extinction), when affecting territorial, non-territorial and both territorial and non-territorial birds. Additional mortality values represent a percentage increase in the mortality probability. Lines are mean values and the shadowed areas represent the 95% confident-interval.

When additional mortality affects only territorial birds, the population growth rate decreases with an increasing proportion of Patches affected, with the population declining (λ) for >50% of Patches affected and the additional mortality probability >0.20 (Figure 3.4a). Surprisingly, while population growth rate decreased with increasing additional mortality probability up to about 0.20, it levelled off or very slightly increased thereafter (Figure 3.4a). Exposure to additional mortality impacted in the number of the breeding pairs, irrespective of the number of affected Patches, though the population size remained constant when the probability of additional mortality was > 0.20 (Figure 3.4b). During the 50-year simulation, population extinction occurred only when 75% of the territories were exposed to additional mortality (Figure 3.4c). Unexpectedly, the mean annual survival rate of the territorial birds remained constant with increasing probability of additional mortality (Figure D.2a in Appendix D), while the proportion of territorial birds dying in Patches exposed to additional mortality decreased (Figure D.2b in Appendix D). Such results reflect the fact that the Patches tend to become vacant with increasing both the exposure to and the probability of additional mortality (Figure D.2c in Appendix D).

When additional mortality affects only non-territorial birds, population growth rate also decreased strongly with both increasing proportion of Patches affected and increasing exposure to additional mortality, though remaining with λ>1 up to about 25% of Patches affected and additional mortality probability up to about 0.70 (Figure 3.4a). In comparison with territorial birds only, population impacts (growth rate; Figure 3.4a, population size; Figure 3.4b) of exposure to additional mortality of non-territorials were slightly lower for low probabilities of additional mortality (<0.20), but higher for higher mortality probabilities. Additionally, population extinction occurred across a broader range of mortality thresholds (Figure 3.4c). Also, as expected, the mean annual survival of non-territorial birds was lower than that of territorial birds (Figure D.2a in Appendix D), and the proportion of non-territorial birds dying in Patches exposed to additional mortality increased with increasing exposure and probability of additional mortality, being higher than the one resulting from the simulations that assumed effects on territorial birds only (Figure D.2b in Appendix D).

Overall, the strongest impacts of exposure to additional mortality were observed when both territorial and non-territorial birds were affected, with the population declining (λ<1) even for relatively small proportion of Patches affected and low probability of exposure to additional mortality (Figure 3.4a). Steep population declines (λ<0.9) and quick population extinction (Figure 3.4b and 3.4c) were predicted when the proportion of Patches affected was >75% and exposure to additional mortality probability >0.20, with the population declining (both in terms of number of territorial and non-territorial birds) mainly in the first 10-years of the simulation period in these scenarios (Figure D.3 in Appendix D). When additional mortality affects the entire population, the patterns of annual survival for both territorial and non-territorial birds, as well as the proportion of deaths occurring in patches exposed to additional mortality (Figure 3.5), are similar to those observed when each territorial class is affected individually (Figure D.2 in Appendix D).

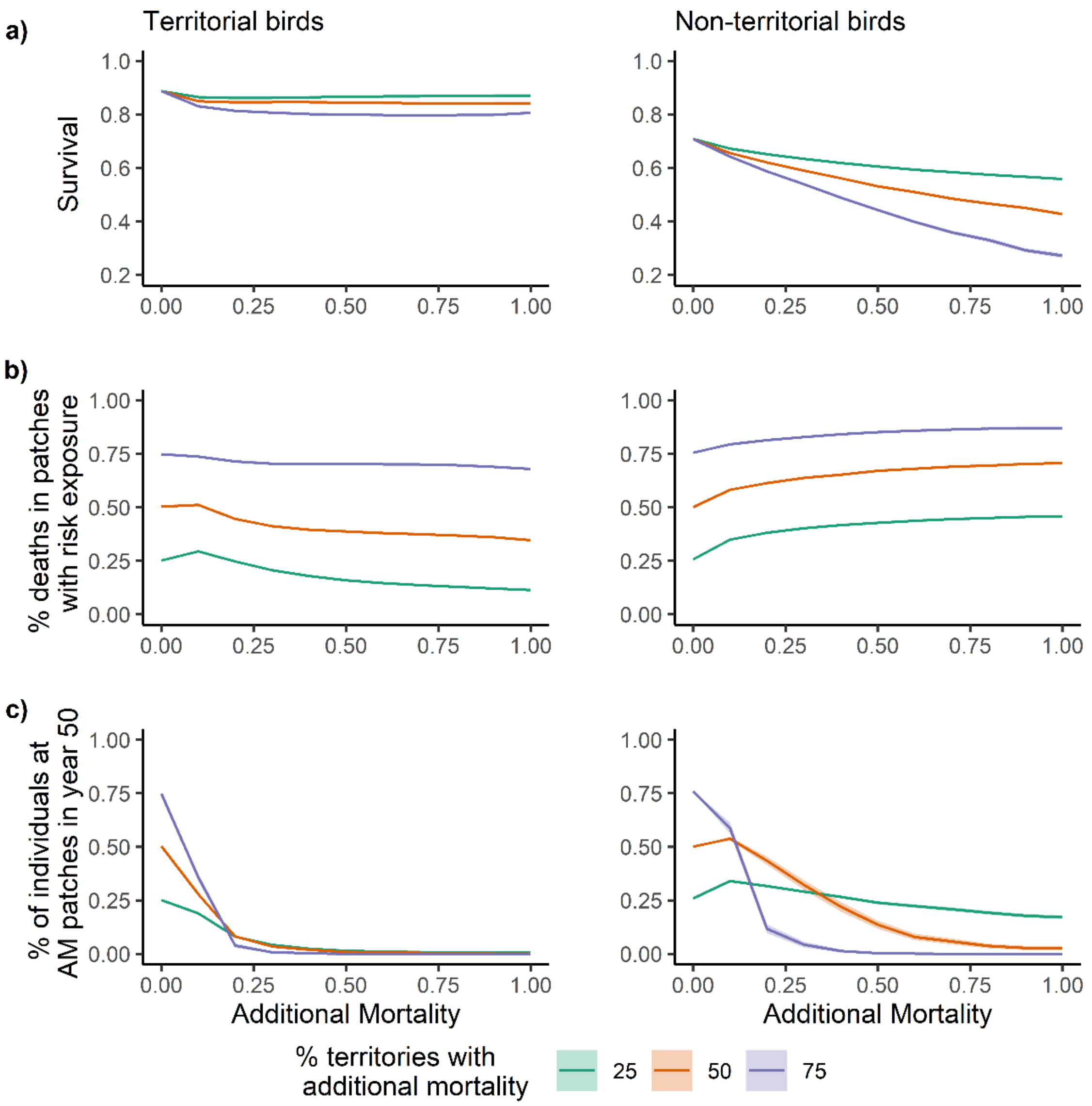

Figure 3.5 Impact of exposure to additional mortality in 25%, 50% and 75% of the Patches on the a) mean annual survival of territorial of territorial and non-territorial birds, b) proportion of deaths in Patches exposed to additional mortality during the 50-year simulation, and c) proportion of individuals in Patches exposed to additional mortality at the end of the 50-year simulation period, when affecting both territorial and non-territorial birds. Additional mortality values represent a percentage increase in the mortality probability. Lines are mean values, and the shadowed areas represent the 95% confident-interval.

When analysing the probability of dispersion and recruitment into patches exposed to additional mortality affecting the entire population, it is possible to observe that patches with additional mortality attract a higher number of dispersant birds, particularly when mortality affects 25% or 50% of the patches (Figure 3.6). Additionally, low levels of mortality (25% of patches exposed to a probability of 0.10 additional mortality) are also responsible for higher recruitment than expected into these patches (Figure 3.6).

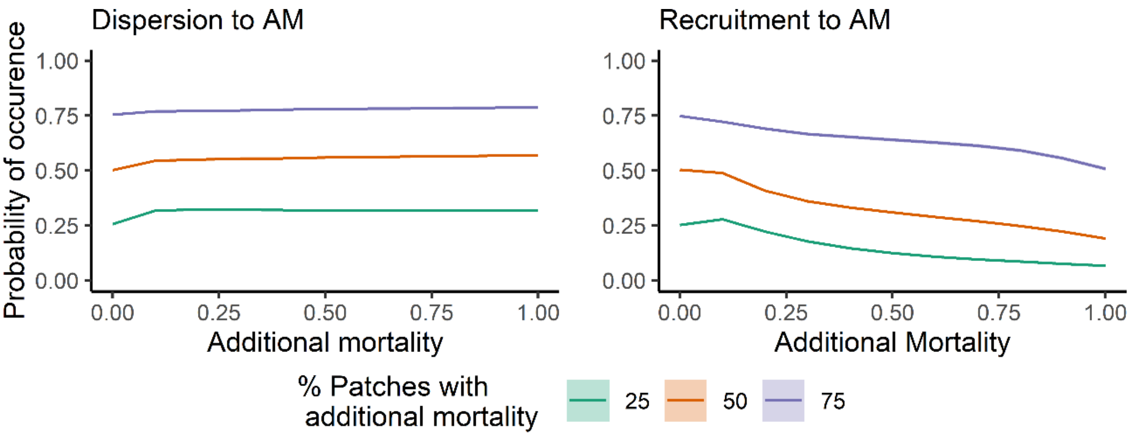

Figure 3.6 Impact of exposure to additional mortality in 25%, 50% and 75% of the Patches on the: (i) probability of dispersion (proportion of juvenile Birds dispersing) and (ii) probability of recruitment (proportion of non-territorial birds recruiting) into Patches exposed to additional mortality over the 50-year simulation period, when affecting both territorial and non-territorial birds. Additional mortality values represent a percentage increase in the mortality probability. Lines are mean values, and the shadowed areas represent the 95% confident-interval.

The patterns presented here are not dependent on the small size of the initial population. In fact, the results for our baseline model scenario, with an initial population of 33 pairs and a 50-year simulation, are quite similar to those obtained for a scenario with an initial stable population of 131 pairs (the carrying capacity of our model population), both for 50-year and 100-year simulation periods (Figure D.4 in Appendix D). The primary distinction lies in the annual population growth rate, with the stable population scenario showing a steeper decline with increasing additional mortality (Figure D.4a in Appendix D).

3.4 Discussion

Our study provides a framework based on an Individual-Based Model (IBM) specifically designed to evaluate the impacts of exposure to additional anthropogenic mortality on populations of territorial species. The application of the framework to a specific case study focusing on Bonelli's eagles in Southern Portugal, clearly illustrated the importance of accounting for such processes to gain a more complete understanding of the potential responses of territorial predators to infrastructures and other sources of anthropogenic mortality. For instance, heterogeneity in the spatial distribution of mortality risk appeared to be consequential, with population responses varying according to whether a few or multiple territories are affected by different mortality levels. Also, we found that impacts vary widely depending on whether mortality affects primarily territorial or non-territorial individuals (or both). Finally, results suggest that non-territorial individuals may have a critical role to sustain the population when mortality is concentrated on territorial adults, while the worst impacts occur when both territorial and non-territorial individuals are exposed to mortality risks. This information points out the importance of duly accounting for the non-territorial component of the population to design strategies to avoid and mitigate the impacts of anthropogenic mortality, as most efforts currently tend to concentrate on breeding territories (Penteriani et al., 2011). Although these results are specific for our case study involving Bonelli's eagles and electrocution in powerlines, we suggest that our IBM framework can be widely used to investigate population responses of other territorial species and other anthropogenic sources of mortality.

3.4.1 Consequences of anthropogenic mortality on a Bonelli's eagle population

The results suggest that our IBM provided a reasonable approximation to the dynamics of the focal Bonelli's eagle populations, thereby supporting the inferences drawn from the model. In particular, we found that the model was able to replicate the increase of the Bonelli's eagle population in southern Portugal over a 28-year period. This was accomplished even when considering different scenarios of available patches, a parameter for which less precise empirical data were available (Figure 3.3 and Figure D.1 in Appendix D). Such results suggest that our model achieved its intended purpose of simulating the population dynamics of this population.

In line with previous studies, the sensitivity analysis of our model clearly identified adult survival (broadly corresponding to territorial birds) as a key parameter for this population, as previously described for the Bonelli's eagle (Hernández-Matías et al., 2013). Overall, this result agrees with the widely accepted idea that population growth rate of long-lived vertebrate species with delayed maturity and reduced fertility, such as large raptors, is most sensitive to changes in breeding adult survival rate (Sæther and Bakke, 2000; Tack et al., 2017). Still, survival rates for other age classes were also relevant to the population trend, especially if compared with other demographic parameters as adult fertility. This confirms the high relevance of the non-breeding component of animal populations for their overall dynamics and persistence, as previously identified by other studies (reviewed by Penteriani et al., 2011).

Given the sensitivity of the population dynamics to adult survival, the strong impact of additional mortality on the non-territorial fraction of the population might seem surprising. While our simulations aligned with expectations by showing the greatest impacts when both territorial and non-territorial individuals faced additional mortality, it also produced a counterintuitive result showing that impacts were higher when only non-territorial individuals, as opposed to territorial individuals, were exposed to additional mortality risk. This is probably a consequence of territorial behaviour, because exposure to additional mortality risk within territories affects at most the annual survival probability of the two breeding adults. In contrast, the same level of exposure to additional mortality risk may affect multiple non-territorial individuals using each Patch. This idea aligns with empirical data indicating that mortality due to electrocution disproportionately affects juveniles and immatures rather than adults in the Bonelli's eagle (Hernández-Matías et al., 2015; Sousa, 2017) and other birds of prey (Hunt et al., 2017; Mojica et al., 2018). From a population demography perspective, this implies that for a given level of exposure to a mortality risk source, the effective decline in the population survival rate is greater when it affects non-territorial individuals compared to territorial individuals (as confirmed by our simulations; Figure 3.5a), because more non-territorial than territorial individuals tend to be exposed to the risk.

Different exposures to the same mortality risk likely influenced the key role revealed by our simulations on the importance of non-territorial birds (i.e., non-breeders) to sustain this population under anthropogenic mortality risks. First, the population starts to decline ($\lambda<1$) with intermediate or high levels of exposure of non-territorial individuals to additional mortality. This result suggests that such exposure compromises the pool of non-territorial individuals within the population, i.e., there is a shortage of non-territorial individuals to recruit into established territories whenever there is a vacancy, and thereby leading to population decline. Second, the availability of a large pool of non-territorial individuals is the responsible for the persistence of the population ($\lambda>1$) when intermediate or large levels of exposure to additional mortality affects a small fraction (25%) of the breeding territories, as the pool of non-territorial birds are rapidly recruited to the affected territories, buffering the impact of mortality. This is confirmed by the simulations of cumulatively impacting 25% of the area used by both territorial classes, showing that the population can only buffer ($\lambda > 1$) relatively small additional mortality probabilities (0.10). Conversely, when only 25% of the breeding territories were affected, the population still exhibited increasing trends, even with a 0.90 additional mortality probability, if the non-territorial class was not affected.

The mechanisms linked to territorial behaviour also explain the unforeseen similarity in populational outputs when the same fraction of territories is affected by intermediate and high mortality probabilities (>0.20), as evidenced by horizontal curves in both the annual growth rate (Figure 3.4a) and the number of breeding pairs (Figure 3.4b). In fact, in territories with higher mortality risk, there is an increased likelihood that both members of the breeding pair will die in the same year, leading to the vacancy of the territory. Conversely, in areas with low to intermediate exposure to mortality risk, it is more likely that only one member of the breeding pair will die in a given year, with the surviving member remaining in the territory and attracting a new member (Figure 3.6).

In the long run, a larger number of birds are likely to die at territories with low to intermediate mortality risk when compared to territories with higher mortality (Figure 3.5b, Figure 3.6). Such lower to intermediate mortality values thus appear to function as an ecological trap, constantly attracting non-territorial birds to recruit into these territories. However, over time, territories with intermediate and high mortality levels tend to become vacant of territorial birds, a phenomenon predicted by our simulations and supported by empirical data from populations of this species (Carrete et al., 2002). In this scenario, non-territorial birds are attracted to disperse into these patches exposed to additional mortality and vacated by territorial birds, which also appear to function as an ecological trap (Figure 3.6).

3.4.2 Importance of explicitly modelling territorial behaviour processes

In the scientific literature, numerous studies have demonstrated the integration of territoriality into population dynamic models, underscoring the significance of incorporating this behaviour (Carter et al., 2015; Wiegand et al., 2004). In the context of anthropogenic mortality, Heurich and colleagues (2018) provided a notable example when modelling lynx mortality resulting from road collisions, in a spatially explicit IBM framework. They achieved this by incorporating a spatial layer representing mortality risk across the study area, which affected all individuals in the population, and accounting for the location of the territories.

Despite these advancements, territoriality remains poorly addressed in models concerning the impacts of anthropogenic mortality. Many of such studies encompass pivotal processes in the population dynamics of wildlife populations. These include (i) age-structured processes, where crucial demographic parameters (e.g. fecundity, survival) are contingent upon individual attributes such as age and sex, (ii) stochasticity, which accommodates uncertainties in environmental and demographic parameters, and (iii) the management of density-dependent processes, manly through the introduction of a carrying capacity parameter (Borda-de-Água et al., 2014; Carrete et al., 2009; Cervantes et al., 2022; Chambert et al., 2023). The prevailing approach to address fatalities from anthropogenic sources commonly involves the inclusion of an annual count or rate of fatalities, which may impact individual classes (sex or age) differently. However, our results clearly show that an absolute mortality rate or value inadequately predicts the impact on population dynamics in territorial species. To have a more comprehensive knowledge on the population-level effects of anthropogenic mortality it is key to incorporate the mechanisms associated with territorial behaviour, including (i) making explicit the number of territories affected by additional mortality, as concentring or spreading mortality across territories have different impacts, (ii) the attraction of recruits into territories with mortality risk due to the mortality of a previous member, and (iii) the variable exposure to risks from territorial and non-territorial birds, meaning that the same hazard pylon can affect a different number of birds if placed in a breeding territory or in a settlement area.

3.4.3 Model generalization

Our IBM model was created to assess the effect of mortality by electrocution on a long-lived and territorial raptor, which life-cycle encompasses a nomadic and a transient stage, when individuals disperse to different locations, and a territorial stage, when birds became breeders and remain fixed to a specific home range. As the model is spatially implicit and is not tight to a particular study area, the model can be easily adapted to other populations of this or other species with similar life-cycles, by changing the demographic parameters according to the attributes of the population considered. Also, the model can be applied to study the long-term population impact of any factor affecting survival, either additional mortality or the effect of management actions.

The current IBM model has been simplified in its representation of some ecological processes, yet its level of complexity is contingent upon the extent of available ecological data for the studied system. Notably, the model presently encompasses only two categories of habitat quality, delineating Patches suitable for breeding territories and those exclusively applicable for non-breeding locations. Nevertheless, the heterogeneity of habitat quality, influenced by environmental factors, and the anticipated variation in the demographic parameters across breeding territories (Johnson, 2007), advocate for the inclusion of a habitat quality layer to bring it closer to reality. Moreover, the model could be advanced by adopting a spatially explicit framework through the integration of a cartographic layer depicting habitat quality or the boundaries of breeding territories (Carter et al., 2015; Kostova et al., 2004), along with associating diverse demographic parameters with each territory. The adoption of a spatially explicit framework facilitates the projection of the impact of distinct threats on a population, thereby enabling the prioritization of management or conservation strategies based on habitat quality.

Further enhancements to the IBM could encompass the integration of new submodels simulating ecological processes such as movement patterns, migration (both inbound and outbound), and interactions with other species. Currently, the IBM only considers birds to be exposed to additional mortality in their settlement areas (Patches to where Birds dispersed) and breeding territories (Patches to where Birds recruited), without accounting for risks during the movements between these areas. Exposure to risks may be particularly significant during the dispersal period, when individuals typically use multiple settlement areas and large movements across them are expected (Balbontín and Ferrer, 2009; Real and Mañosa, 2001). Therefore, a submodel addressing movements trajectories (both dispersant and migratory movements) across the study area could be developed within a spatially explicit framework, providing insights into individual movements and identifying locations with heightened threats and risks. This approach could be useful to, for instance, identify critical mortality hotspots for long-lived territorial species, and prioritize areas for mitigation (Barbosa et al., 2020). Another enhancement to the IBM model would involve further developing the migration process, specifically by incorporating the flow of individuals to and from the modelled population, as individual exchanges across populations are expected in many territorial species. The model developed in this study only accounts for emigration when all available patches are fully occupied, and immigration has not been implemented. Finally, potential future upgrades might involve considering interactions with other species to address intra-specific competition. This ecological dynamic could restrict the population growth of a territorial species, and was not implemented in the model.

Overall, our IBM model allows a flexible modelling framework to analyse the population dynamics of territorial species, including the effects of anthropogenic mortality.

3.4.4 Recommendations for minimizing bird electrocutions at power lines

As highlighted in our study (Figure 3.2; see section 3.4.1), electrocutions at power lines have a negative and direct impact on the studied population survival rate, which is the most important demographic parameter in raptors population dynamics (Tack et al., 2017). Electrocutions are a source of significant mortality in many raptor populations (González et al., 2007; Martínez et al., 2016; Mojica et al., 2018; Real et al., 2001), thus reducing such mortality may be the most far-reaching conservation measure (Hernández-Matías et al., 2015). This might be achieved by retrofitting distribution lines, through the insulation of conductors or burying the lines, measures that have been implemented worldwide, successfully reducing the electrocution risk for several raptor species (Chevallier et al., 2015; Dixon et al., 2018; López-López et al., 2011).

The fact that intermediate or high mortality rates within the same territories have the same impact on the population growth rate and population size (Figure 3.4a and 3.4b) and that territories with intermediate and high mortality risk tend to become vacant (Figure 3.5c), suggests that each breeding territory should be considered as a mitigation unit, where all pylons posing electrocution risk should be intervened whenever mitigation actions are put in place.

Our results highlight the importance of taking into consideration all individuals' life stages in a population, juveniles, floaters and breeding birds, i.e., both breeding and pre-adult settlement areas, when planning the mitigating of electrocutions. Conservation practices traditionally favour breeding home ranges, and management actions aiming at reducing mortality rates of the non-territorial component of populations are frequently relegated to a secondary role (Penteriani et al., 2011). Our IBM simulations show that this may be an ineffective strategy, as additional sources of mortality, either affecting the territorial or the non-territorial fractions of the population, always have important population impacts (Figure 3.4). In reality, our study highlights the key role of non-territorial individuals in sustaining populations of territorial species facing anthropogenic mortality sources, strongly suggesting that conservation and land planning strategies should account this fraction of the population.

Acknowledgements

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Author contributions

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3.5 References

Adams, E.S., 2001. Approaches to the Study of Territory Size and Shape. Annu. Rev. Ecol. Syst. 32, 277–303. https://doi.org/10.1146/annurev.ecolsys.32.081501.114034

Araújo, J., Arroyo, B., Bueno, J.M., 1974. Un nido de Águila Perdicera (*Hieraaetus fasciatus*) con tres pollos. Ardeola 20, 343–345.

Balbontín, J., Ferrer, M., 2009. Movements of juvenile Bonelli's Eagles *Aquila fasciata* during dispersal. Bird Study 56, 86–95. https://doi.org/10.1080/00063650802648374

Barbosa, P., Schumaker, N.H., Brandon, K.R., Bager, A., Grilo, C., 2020. Simulating the consequences of roads for wildlife population dynamics. Landsc. Urban Plan. 193, 103672. https://doi.org/10.1016/j.landurbplan.2019.103672

Bernardino, J., Bevanger, K., Barrientos, R., Dwyer, J.F., Marques, A.T., Martins, R.C., Shaw, J.M., Silva, J.P., Moreira, F., 2018. Bird collisions with power lines: State of the art and priority areas for research. Biol. Conserv. 222. https://doi.org/10.1016/j.biocon.2018.02.029

BirdLife International, 2022. Species factsheet: *Aquila fasciata*.

Borda-de-Água, L., Grilo, C., Pereira, H.M., 2014. Modeling the impact of road mortality on barn owl (*Tyto alba*) populations using age-structured models. Ecol. Modell. 276, 29–37. https://doi.org/10.1016/j.ecolmodel.2013.12.022

Bosch, R., Real, J., Tinto, A., Zozaya, E.L., Castell, C., 2010. Home-ranges and patterns of spatial use in territorial Bonelli's Eagles *Aquila fasciata*. Ibis (Lond. 1859). 152, 105–117. https://doi.org/10.1111/j.1474-919X.2009.00985.x

Campolongo, F., Cariboni, J., Saltelli, A., 2007. An effective screening design for sensitivity analysis of large models. Environ. Model. Softw. 22, 1509–1518. https://doi.org/10.1016/j.envsoft.2006.10.004

Carrete, M., Sánchez-Zapata, J.A., Benítez, J.R., Lobón, M., Donázar, J.A., 2009. Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. Biol. Conserv. 142, 2954–2961.

Carrete, M., Sánchez-Zapata, J.A., Martínez, J.E., Sánchez, M.A., Calvo, F., 2002. Factors influencing the decline of a Bonelli's eagle *Hieraaetus fasciatus* population in southeastern Spain: demography, habitat or competition? Biodivers. Conserv. 11, 975–985. https://doi.org/https://doi.org/10.1023/A:1015856924451

Carter, N., Levin, S., Barlow, A., Grimm, V., 2015. Modeling tiger population and territory dynamics using an agent-based approach. Ecol. Modell. 312, 347–362. https://doi.org/10.1016/j.ecolmodel.2015.06.008

Cervantes, F., Martins, M., Simmons, R.E., 2022. Population viability assessment of an endangered raptor using detection/non-detection data reveals susceptibility to anthropogenic impacts. R. Soc. Open Sci. 9. https://doi.org/10.1098/rsos.220043

Chambert, T., Duriez, O., Deleaux, M., Besnard, A., 2023. EolPop, a R-shiny tool for quantifying the demographic impact of species exposed to fatalities: Application to bird collisions with wind turbines. J. Environ. Manage. 345, 118923. https://doi.org/10.1016/j.jenvman.2023.118923

Chevallier, C., Hernández-Matías, A., Real, J., Vincent-Martin, N., Ravayrol, A., Besnard, A., 2015. Retrofitting of power lines effectively reduces mortality by electrocution in large birds: an example with the endangered Bonelli's eagle. J. Appl. Ecol. 52, 1465–1473. https://doi.org/10.1111/1365-2664.12476

DeAngelis, D.L., Grimm, V., 2014. Individual-based models in ecology after four decades. F1000Prime Rep. 6. https://doi.org/10.12703/P6-39

Dias, A., Palma, L., Carvalho, F., Neto, D., Real, J., Beja, P., 2017. The role of conservative versus innovative nesting behavior on the 25-year population expansion of an avian predator. Ecol. Evol. 7, 4241–4253. https://doi.org/10.1002/ece3.3007

Diffendorfer, J.E., Stanton, J.C., Beston, J.A., Thogmartin, W.E., Loss, S.R., Katzner, T.E., Johnson, D.H., Erickson, R.A., Merrill, M.D., Corum, M.D., 2021. Demographic and potential biological removal models identify raptor species sensitive to current and future wind energy. Ecosphere 12. https://doi.org/10.1002/ecs2.3531

Dillingham, P.W., Fletcher, D., 2008. Estimating the ability of birds to sustain additional human-caused mortalities using a simple decision rule and allometric relationships. Biol. Conserv. 141, 1783–1792. https://doi.org/10.1016/j.biocon.2008.04.022

Dixon, A., Bold, B., Tsolmonjav, P., Galtbalt, B., Batbayar, N., 2018. Efficacy of a mitigation method to reduce raptor electrocution at an electricity distribution line in Mongolia. Conserv. Evid. 15, 50–53.

Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. Annu. Rev. Ecol. Syst. 29, 207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Gil-Sánchez, J.M., Moleón, M., Otero, M., Bautista, J., 2004. A nine-year study of successful breeding in a Bonelli’s eagle population in southeast Spain: a basis for conservation. Biol. Conserv. 118, 685–694. https://doi.org/10.1016/j.biocon.2003.10.017

González, L.M., Margalida, A., Mañosa, S., Sánchez, R., Oria, J., Molina, J.I., Caldera, J., Aranda, A., Prada, L., 2007. Causes and spatio-temporal variations of non-natural mortality in the Vulnerable Spanish imperial eagle *Aquila adalberti* during a recovery period. Oryx 41, 495–502. https://doi.org/10.1017/S0030605307414119

Grilo, C., Borda-de-Água, L., Beja, P., Goolsby, E., Soanes, K., le Roux, A., Koroleva, E., Ferreira, F.Z., Gagné, S.A., Wang, Y., González-Suárez, M., 2021. Conservation threats from roadkill in the global road network. Glob. Ecol. Biogeogr. 30, 2200–2210. https://doi.org/10.1111/geb.13375

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe’er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, 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., 2012. Pattern-oriented modelling: a 'multi-scope' for predictive systems ecology. Philos. Trans. R. Soc. B Biol. Sci. 367, 298–310. https://doi.org/10.1098/rstb.2011.0180

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. Simul. 23. https://doi.org/10.18564/jasss.4259

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology. Science. 310, 987–991. https://doi.org/10.1126/science.1116681

Hall, M.A., Alverson, D.L., Metuzals, K.I., 2000. By-Catch: Problems and Solutions. Mar. Pollut. Bull. 41, 204–219. https://doi.org/10.1016/S0025-326X(00)00111-9

Hernández-Matías, A., Real, J., Moleón, M., Palma, L., Sánchez-Zapata, J.A., Pradel, R., Carrete, M., Gil-Sánchez, J.M., Beja, P., Balbontín, J., Vincent-Martin, N., Ravayrol, A., Benítez, J.R., Arroyo, B., Fernández, C., Ferreiro, E., García, J., 2013. From local monitoring to a broad-scale viability assessment: a case study for the Bonelli's Eagle in western Europe. Ecol. Monogr. 83, 239–261. https://doi.org/10.1890/12-1248.1

Hernández-Matías, A., Real, J., Parés, F., Pradel, R., 2015. Electrocution threatens the viability of populations of the endangered Bonelli's eagle (*Aquila fasciata*) in Southern Europe. Biol. Conserv. 191, 110–116. https://doi.org/10.1016/j.biocon.2015.06.028

Hernández-Matías, A., Real, J., Pradel, R., Ravayrol, A., Vincent-Martin, N., Bosca, F., Cheylan, G., 2010. Determinants of Territorial Recruitment in Bonelli's Eagle (*Aquila fasciata*) Populations. Auk 127, 173–184. https://doi.org/10.1525/auk.2009.09143

Heurich, M., Schultze-Naumburg, J., Piacenza, N., Magg, N., Červený, J., Engleder, T., Herdtfelder, M., Sladova, M., Kramer-Schadt, S., 2018. Illegal hunting as a major driver of the source-sink dynamics of a reintroduced lynx population in Central Europe. Biol. Conserv. 224, 355–365. https://doi.org/10.1016/j.biocon.2018.05.011

Hill, J.E., DeVault, T.L., Belant, J.L., 2019. Cause-specific mortality of the world's terrestrial vertebrates. Glob. Ecol. Biogeogr. 28, 680–689. https://doi.org/10.1111/geb.12881

Hill, J.E., DeVault, T.L., Wang, G., Belant, J.L., 2020. Anthropogenic mortality in mammals increases with the human footprint. Front. Ecol. Environ. 18, 13–18. https://doi.org/10.1002/fee.2127

Hunt, W.G., Wiens, J.D., Law, P.R., Fuller, M.R., Hunt, T.L., Driscoll, D.E., Jackman, R.E., 2017. Quantifying the demographic cost of human-related mortality to a raptor population. PLoS One 12, e0172232. https://doi.org/10.1371/journal.pone.0172232

Inskip, C., Zimmermann, A., 2009. Human-felid conflict: a review of patterns and priorities worldwide. Oryx 43, 18. https://doi.org/10.1017/S003060530899030X

Johnson, M.D., 2007. Measuring Habitat Quality: A Review. Condor 109, 489–504. https://doi.org/10.1093/condor/109.3.489

Kostova, T., Carlsen, T., Kercher, J., 2004. Individual-based spatially-explicit model of an herbivore and its resource: the effect of habitat reduction and fragmentation. C. R. Biol. 327, 261–276. https://doi.org/10.1016/j.crvi.2003.11.010

Krebs, C.J., 2002. Two complementary paradigms for analysing population dynamics. Philos. Trans. R. Soc. London. Ser. B Biol. Sci. 357, 1211–1219. https://doi.org/10.1098/rstb.2002.1122

López-López, P., Ferrer, M., Madero, A., Casado, E., McGrady, M., 2011. Solving Man-Induced Large-Scale Conservation Problems: The Spanish Imperial Eagle and Power Lines. PLoS One 6, e17196. https://doi.org/10.1371/journal.pone.0017196

Loss, S.R., Will, T., Marra, P.P., 2015. Direct Mortality of Birds from Anthropogenic Causes. Annu. Rev. Ecol. Evol. Syst. 46, 99–120. https://doi.org/10.1146/annurev-ecolsys-112414-054133

Loveridge, A.J., Valeix, M., Elliot, N.B., Macdonald, D.W., 2017. The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. J. Appl. Ecol. 54, 815–825. https://doi.org/10.1111/1365-2664.12794

Madden, K.K., Rozhon, G.C., Dwyer, J.F., 2019. Conservation Letter: Raptor Persecution. J. Raptor Res. 53, 230. https://doi.org/10.3356/JRR-18-37

Marques, A.T., Batalha, H., Rodrigues, S., Costa, H., Pereira, M.J.R., Fonseca, C., Mascarenhas, M., Bernardino, J., 2014. Understanding bird collisions at wind farms: An updated review on the causes and possible mitigation strategies. Biol. Conserv. 179, 40–52. https://doi.org/10.1016/j.biocon.2014.08.017

Marques, A.T., Palma, L., Lourenço, R., Cangarato, R., Leitão, A., Mascarenhas, M., Tavares, J.T., Tomé, R., Moreira, F., Beja, P., 2022. Individual variability in space use near power lines by a long-lived territorial raptor. Ecol. Evol. 12. https://doi.org/10.1002/ece3.8811

Martínez-Miranzo, B., Banda, E., Gardiazábal, A., Ferreiro, E., Aguirre, J.I., 2016. Differential spatial use and spatial fidelity by breeders in Bonelli’s Eagle (*Aquila fasciata*). J. Ornithol. 157, 971–979. https://doi.org/10.1007/s10336-016-1347-1

Martínez, J.E., Zuberogoitia, I., Jiménez-Franco, M. V., Mañosa, S., Calvo, J.F., 2016. Spatio-temporal variations in mortality causes of two migratory forest raptors in Spain. Eur. J. Wildl. Res. 62, 109–118. https://doi.org/10.1007/s10344-015-0981-x

Mojica, E.K., Dwyer, J.F., Harness, R.E., Williams, G.E., Woodbridge, B., 2018. Review and synthesis of research investigating golden eagle electrocutions. J. Wildl. Manage. 82, 495–506. https://doi.org/10.1002/jwmg.21412

Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A., Merrill, E.H., Haydon, D.T., 2010. Building the bridge between animal movement and population dynamics. Philos. Trans. R. Soc. B Biol. Sci. 365, 2289–2301. https://doi.org/10.1098/rstb.2010.0082

Morris, M.D., 1991. Factorial Sampling Plans for Preliminary Computational Experiments. Technometrics 33, 161–174. https://doi.org/10.1080/00401706.1991.10484804

Newton, I., 1992. Experiments on the limitation of bird numbers by territorial behaviour. Biol. Rev. 67, 129–173. https://doi.org/10.1111/j.1469-185X.1992.tb01017.x

Palma, L., Beja, P., Sánchez, R., 2013. Twenty Years of Research and Conservation of Endangered Eagles in Portugal. Raptors Conserv. 27, 73–91.

Penteriani, V., Ferrer, M., Delgado, M.M., 2011. Floater strategies and dynamics in birds, and their importance in conservation biology: towards an understanding of nonbreeders in avian populations. Anim. Conserv. 14, 233–241. https://doi.org/10.1111/j.1469-1795.2010.00433.x

R Core Team, 2020. R: A language and environment for statistical computing.

Real, Grande, J.M., Mañosa, S., Sánchez-Zapata, J.A., 2001. Causes of death in different areas for Bonelli's Eagle *Hieraaetus fasciatus* in Spain. Bird Study 48, 221–228. https://doi.org/10.1080/00063650109461221

Real, J., Mañosa, S.A., 2001. Dispersal of juvenile and immature Bonnelli's Eagles in northeastern Spain. J. Raptor Res. 35, 9–14.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and Ecological Effects of the World's Largest Carnivores. Science. 343. https://doi.org/10.1126/science.1241484

Rohner, C., 1996. The Numerical Response of Great Horned Owls to the Snowshoe Hare Cycle: Consequences of Non-Territorial `Floaters' on Demography. J. Anim. Ecol. 65, 359. https://doi.org/10.2307/5882

Rollan, À., Real, J., Bosch, R., Tintó, A., Hernández-Matías, A., 2010. Modelling the risk of collision with power lines in Bonelli's Eagle *Hieraaetus fasciatus* and its conservation implications. Bird Conserv. Int. 20, 279–294. https://doi.org/10.1017/S0959270910000250

Sæther, B.E., Bakke, Ø., 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81, 642–653. https://doi.org/10.1890/0012-9658

Salecker, J., Sciaini, M., Meyer, K.M., Wiegand, K., 2019. The NLRX R package: A next-generation framework for reproducible NetLogo model analyses. Methods Ecol. Evol. 10, 1854–1863. https://doi.org/10.1111/2041-210X.13286

Schippers, P., Buij, R., Schotman, A., Verboom, J., Jeugd, H., Jongejans, E., 2020. Mortality limits used in wind energy impact assessment underestimate impacts of wind farms on bird populations. Ecol. Evol. 10, 6274–6287. https://doi.org/10.1002/ece3.6360

Semeniuk, C.A.D., Musiani, M., Hebblewhite, M., Grindal, S., Marceau, D.J., 2012. Incorporating behavioral–ecological strategies in pattern-oriented modeling of caribou habitat use in a highly industrialized landscape. Ecol. Modell. 243, 18–32. https://doi.org/10.1016/j.ecolmodel.2012.06.004

Sousa, J., 2017. Eletrocussão de aves em apoios da rede elétrica e métodos de correção (Tese de Mestrado). Faculdade de Ciências da Universidade de Lisboa.

Tack, J.D., Noon, B.R., Bowen, Z.H., Strybos, L., Fedy, B.C., 2017. No Substitute for Survival: Perturbation Analyses Using a Golden Eagle Population Model Reveal Limits to Managing for Take. J. Raptor Res. 51, 258–272. https://doi.org/10.3356/JRR-16-32.1

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. Simul. 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.

Wang, M., Grimm, V., 2010. Population models in pesticide risk assessment: Lessons for assessing population-level effects, recovery, and alternative exposure scenarios from modeling a small mammal. Environ. Toxicol. Chem. 29, 1292–1300. https://doi.org/10.1002/etc.151

Wiegand, T., Knauer, F., Kaczensky, P., Naves, J., 2004. Expansion of Brown Bears (*Ursus arctos*) into the Eastern Alps: A Spatially Explicit Population Model. Biodivers. Conserv. 13, 79–114. https://doi.org/10.1023/B:BIOC.0000004314.38828.db

Wilensky, U., 1999. NetLogo. Evanston, IL: Center for connected learning and computer-based modeling, Northwestern University.

Chapter 4

High-resolution species distribution modelling reveals spatio-temporal variability of habitat suitability in a declining grassland bird

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Chapter 4 – High-resolution species distribution modelling reveals spatio-temporal variability of habitat suitability in a declining grassland bird

Abstract

Context: Species Distribution Models (SDMs) may provide accurate predictions of species occurrence across space and time, being critical for effective conservation planning.

Objectives: Focusing on the little bustard (*Tetrax tetrax*), an endangered grassland bird, we aimed to: (i) characterise the drivers of the species distribution along its key phenological phases (winter, breeding, and post-breeding); and (ii) quantify spatio-temporal variation in habitat suitability across phenological phases and over the years 2005-2021.

Methods: Combining remotely sensed metrics at high temporal resolution (MODIS) with long-term (> 12 years) GPS telemetry data collected for 91 individuals at one of the species' main strongholds within the Iberian Peninsula, we built SDMs (250m resolution) for the species key phenological phases.

Results: The use of both dynamic and static predictors unveiled previously unknown ecological responses by little bustards, revealing a marked change in the spatial distribution of suitable habitat among phenological phases. Long-term habitat suitability trends showed considerable fluctuations, mainly in the breeding and post-breeding phases. Overall, SDM projections into the past revealed that while the species' winter and post-breeding habitats apparently increased since 2005, suitable habitat during the species' most critical phenological phase, breeding, apparently reduced in area over time.

Conclusions: Our findings show that matching remotely sensed data with GPS tracking data results in accurate habitat suitability predictions throughout the yearly cycle. Additionally, our findings stress the importance of quantifying habitat loss and its potential impact on little bustard decline over nearly 20 years. Spatio-temporal variations in habitat suitability are also identified in this work, which can help prioritize conservation areas, particularly the breeding areas that have remained stable over time, as this is a key requirement for little bustard lek breeding system.

Keywords

GPS telemetry; little bustard; movement ecology; random forests; remote sensing; *Tetrax tetrax*

4.1 Introduction

Understanding the patterns and processes that govern species distribution is critical for mitigating the widespread decline of biodiversity. This knowledge is essential for accurate and successful conservation planning (Guisan et al., 2013). In this context, Species Distribution Models (SDMs, similar to Ecological Niche Models; Elith & Leathwick, 2009; Guisan et al. 2013) have gained considerable attention in recent decades, particularly given their utility for supporting biodiversity policy and decision processes (Araújo and Guisan, 2006; Guisan et al., 2013). SDMs are based on the concept of the ecological niche (Ponti and Sannolo, 2022), which describes the range of suitable biotic and abiotic conditions wherein a species is able to survive and reproduce (Colwell and Rangel, 2009) as determined from species occurrence data. By identifying the most important environmental predictors of species occurrence, SDMs allow for the prediction of the species' potential distribution across space and time (Elith and Leathwick, 2009), thereby serving as key tools to support conservation and management initiatives.

Despite the many developments in the field, SDMs may be subject to some caveats related, for instance, to phenological variation in species' ecological requirements, which may be blurred when using traditional approaches based on static correlative predictors, thus affecting the inferences that can be drawn from the data. Therefore, realistic and useful SDMs should reflect the seasonality related to species' life-history events that drive their responses to spatial and temporal environmental change (Smeraldo et al., 2018). Although phenology is one of the most important factors in determining an organism's ecological requirements, it has received little attention when modelling the potential distribution ranges of many species that exhibit spatial variation in habitat suitability across phenological phases (Milanesi et al., 2020; Ponti and Sannolo, 2022; Smeraldo et al., 2018). The ecological requirements of migratory species, for instance, can change throughout the year, and their key environmental predictors at one phase may not be applicable at another (Chuine, 2010). Additionally, to better understand the distribution patterns of such species over the long-term, the reconstruction of a species' historic distribution range can be used to understand the influence of interannual environmental and climatic fluctuations (Ponti and Sannolo, 2022). Yet, quantifying species distribution along phenological phases requires careful spatial and temporal matching of occurrence data with relevant environmental and climatic predictors (Elith and Leathwick, 2009; Milanesi et al., 2020).

Matching high-resolution GPS animal tracking technology and satellite remote sensing products presents promising opportunities for the development of accurate SDMs over large spatial and temporal scales. Currently, GPS tracking technologies can provide a large number of an animal's movement steps with a high spatial and temporal resolution for species of various sizes and ecologies (Kays et al., 2015; Nathan et al., 2008). Similarly, recent developments in satellite remote sensing provide the opportunity to affordably monitor environmental changes at fine spatial and temporal scales (Neumann et al., 2015). Remote sensing techniques currently provide access to topographic data, landscape biophysical and structural parameters, and climatic conditions (e.g., through general circulation models) with a resolution ranging from coarse to fine spatio-temporal scales (Kays et al., 2015). This makes remote-sensing products particularly good candidates for describing phenology-specific responses of species to environmental change (Cord et al., 2013).

For Steppe birds, which are among the most endangered terrestrial vertebrate species worldwide (BirdLife International, 2022), we lack a thorough understanding the drivers of their distribution across key phenological phases. Such information is now urgently required to correctly infer their long-term declining trends and identify critically important conservation areas throughout the phenological cycle. In a European context, the Iberian Peninsula is known to support large populations of several threatened steppe and farmland bird species (Traba et al., 2013). However, due to habitat loss caused mostly by agriculture intensification, farmland birds have markedly declined in recent decades (Silva et al., 2022; Traba and Morales, 2019). Among these, the little bustard (*Tetrax tetrax*) has shown particularly alarming declining trends, being globally classified as Near-Threatened (BirdLife International, 2018) and as Vulnerable in Europe (BirdLife International, 2021), including Spain (López-Jiménez et al., 2021). The Iberian Peninsula is a stronghold for the species, with the Extremadura region ranking among its most crucial conservation areas (Morales and Bretagnolle, 2022). Conservation planning and effective management of little bustard populations throughout the annual cycle could greatly benefit from a precise, temporally and spatially explicit SDM.

Here we used a 12-year GPS telemetry dataset from 91 tagged little bustards in southern Iberia and high resolution remotely sensed environmental metrics to generate seasonal SDMs (250m resolution) regarding the key phenological phases of the species (e.g. Smeraldo et al., 2018). Our main aims were to: i) identify the drivers of little bustard distribution and characterise the species' response (in terms of probability of occurrence) to these, across its key phenological phases (winter, breeding, and post-breeding); and ii) quantify the spatio-temporal variation (i.e., degree of stability) in habitat suitability across phenological phases and over the years (2005-

2021). Overall, by considering phenology-related variations in the little bustard's responses to environmental change across space and time, we expect our approach will provide novel insights on key ecological traits that are affecting long-term population trends.

4.2 Methods

4.2.1 Study area and study species

The Extremadura region, located in the southwest of Spain, is characterised by a meso-Mediterranean climate with warm, dry summers and cold, humid winters (Rivas-Martínez et al., 2002). Globally, the landscape of Extremadura is heterogeneous and fragmented, dominated by grazing and agriculture, with cereals and permanent crops grown on productive and irrigated plains. The region is subdivided into two provinces: Badajoz in the south and Cáceres in the north (Figure 4.1). While Cáceres is characterised by pastures and semi-natural meadows with native oak forests and permanent pastures, Badajoz presents vast open areas that are predominantly made up of arable land.

Several Special Protection Areas (SPAs) have been identified as priority sites for the preservation of the little bustard in Extremadura (Figure 4.1). These areas represent the breeding grounds for roughly 65% of the population in the region (García De La Morena et al., 2018; Traba et al., 2022). Still, the little bustard has experienced a continued population decline over the last decades (de Juana, 2009; López Ávila and Hidalgo de Trucios, 1998), with a decrease in the Extremadura region of 33.2% in the winter population and 53.3% in the breeding population between the 2005 and 2016 national surveys (García De La Morena et al., 2018).

The annual cycle of the little bustard is subdivided into three distinct phenological phases: breeding, post-breeding, and winter (Silva et al., 2015, 2014). The species exhibits gregarious behaviour for the majority of the annual cycle, except for the breeding phase, when males establish territories (Jiguet et al., 2000). The Iberian population can be classified as partially migratory, with a small portion of individuals exhibiting strictly sedentary behaviour and the remainder displaying a range of migratory patterns. Food availability and environmental factors, such as ambient temperature, soil productivity, and vegetation height, are thought to have an impact on seasonal movements (García de La Morena et al., 2015; Silva et al., 2015, 2007). These patterns are typically synchronised to the phenological phases of the species, including regular movements that vary in timing and spatial range (García de La Morena et al., 2015).

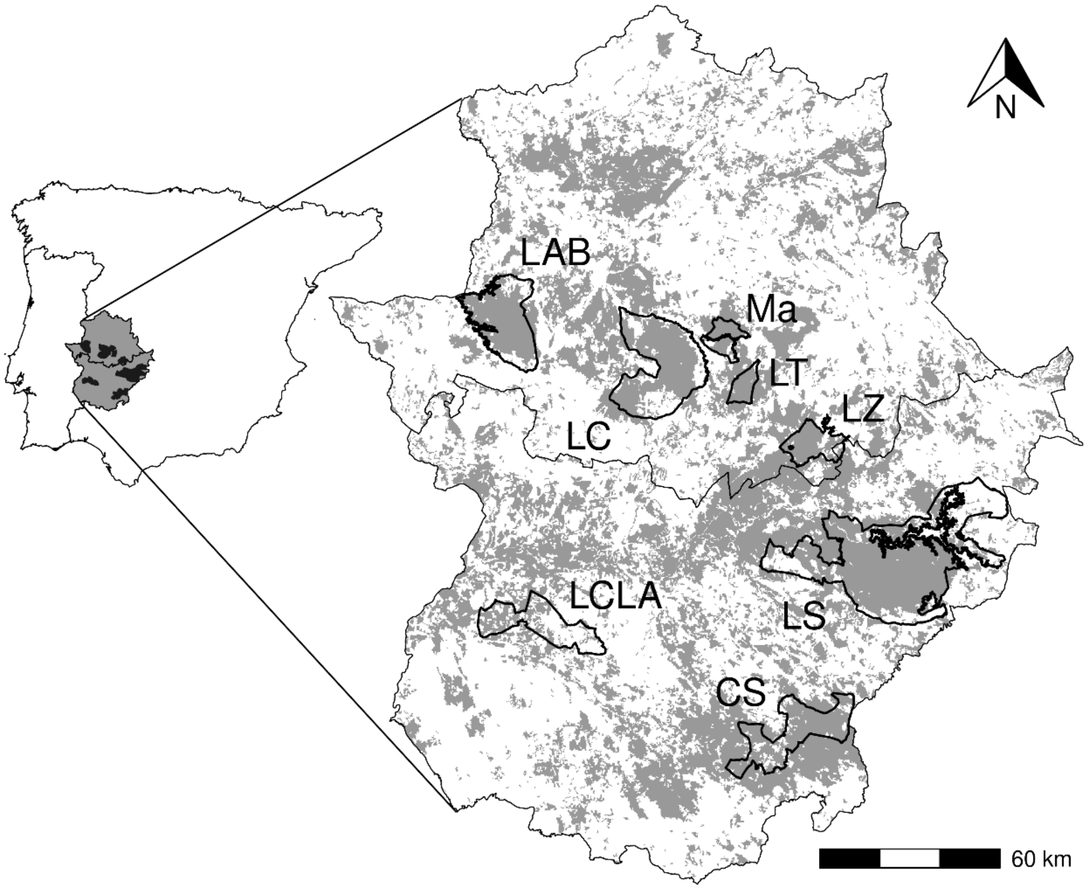

Figure 4.1 Location of the study area in the Iberian Peninsula. The provinces of Cáceres and Badajoz are located north and south, respectively. The areas in grey show the potential geographical range for the little bustard, based on land cover classes taken from the European CORINE Land Cover. Special Protection Areas (SPAs) are shown by the polygons with black outlines (LC - Llanos de Cáceres y Sierra de Fuentes; LT - Llanos de Trujillo; LZ - Llanos de Zorita y Embalse de Sierra Brava; LAB - Llanos de Alcantara y Brozas; Ma – Magasca; CS - Campiña sur - Embalse de Arroyo Conejos; LS - La Serena y Sierras Periféricas).

4.2.2 Little bustard data

Little bustard presences and pseudo-absences were used to inform the SDMs. Presences were obtained from a 12-year GPS telemetry data set of 91 little bustards (all males, due to the challenges and difficulties of capturing females). Individuals were captured in Extremadura and Alentejo (Portugal) between 2009 and 2020 and fitted with highly precise GPS solar ARGOS Platform Transmitter Terminals (https://www.microwavetelemetry.com/) and solar GPS/GSM tags from Movetech Telemetry (https://movetech-telemetry.com/), E-Obs (https://e-obs.de/)

and Ornitela OT (https://www.ornitela.com/) (e.g. Gudka et al., 2019). Data from Alentejo region were included in order to better inform SDMs (see Appendix F). The data set was temporally filtered in order to obtain locations for the core periods of the three distinct phases of the little bustard yearly cycle: breeding (April 1–May 15), post-breeding (July 15–September 15), and winter (December 15–February 15). Then, we standardised the contribution of all the available individuals to avoid overrepresentation of some locations, as little bustard is highly site faithful during the different stages of the year (Alonso et al. 2019). For each bird, we selected a single biological phase per year and, within this phase, only a single location per day. Overall, 2214 locations of 41 individuals were used for the winter phase, 2225 locations of 82 individuals were used for the breeding phase, and 2877 locations of 59 individuals were used for the post-breeding phase, with 45.9% of these locations being in southern Portugal.

Pseudo-absences were generated in the same number of presences for each phenological phase (as recommended by Barbet-Massin et al. (2012) for Random Forests), following the distribution of land cover, at a minimum distance of 250 m to soften false absence error rates (Iturbide et al., 2015), and a maximum distance of 50 km for the breeding phase or 80 km for the post-breeding and winter phases (average distance of movements by phenological phase; Silva et al. 2014), to deal with possible inflated results (e.g., over-predictions) (see Appendix F for further details).

4.2.3 Predictor variables

As predictor variables of habitat suitability for little bustard during the different phenological phases, we included remote sensing products from optical (i.e., MODIS; or Moderate Resolution Imaging Spectroradiometer) and synthetic aperture radar (SAR) sensors (PALSAR1/2; or Phased Array Type L-Band Synthetic Aperture Radar) to infer key biophysical characteristics and habitat metrics from the spectral information, jointly with textural and structural variables to describe the “horizontal” and “vertical” complexity of the landscape. More conventional variables were also used in describing soil and topography, as well as human pressure (Table 4.1). Given the plethora of predictors considered, these were divided into biophysical, anthropogenic, and topographic predictors, each with a different spatial resolution, therefore subdivided into “static” (landscape “snapshots”) and “dynamic” (time-series) (Table 4.1). The calculation of variables was originally derived from multispectral remote sensing time series, that in turn allowed high-quality data agreement with telemetry observations (Milanesi et al., 2020), utilizing the Google Earth Engine (GEE) cloud platform (Gorelick et al., 2017).

Table 4.1 Predictors included in the seasonal SDMs of the little bustard in Extremadura, Spain. The variables are catalogued as topographic, anthropogenic, and biophysical, while being subdivided based on their spatial and temporal resolution.

Type	Predictor name	Description	Spatial resolution	Temporal resolution
Topographic	Slope	Measure the terrain inclination in degrees	30 m	Static
	TRI	Terrain Ruggedness Index, calculate the amount of elevation difference between adjacent cells		
	TWI	Terrain Water Index, measure the areas of drainage, or where water can accumulate		
	Altitude	Altitude		
Anthropogenic	Dist_MR	Measure the distance to roadways/anthropogenic areas, tied to a maximum of 3km		
	Dist_PL	Measure the distance to power lines <60kV, tied to a maximum of 3km		
Biophysical	OCD	Organic Carbon density	250 m	
	pH	pH of the soil		
	SC	Sand content		
	BD	Bulk density		
	Bio1	Bioclimatic variable - Annual Mean Temperature	1000 m	
	Bio2	Bioclimatic variable - Mean Diurnal Range (Mean of monthly (max temp - min temp))		
	Bio12	Bioclimatic variable - Annual Precipitation		
	Bio14	Bioclimatic variable - Precipitation of Driest Month		
	RED	Red spectral band	250 m	Dynamic - Daily
	NIR	Near-infrared spectral band		
	NDVI	Normalized Difference Vegetation Index, measures the vegetation productivity		
	MSAVI2	Modified Soil Adjusted Vegetation Index 2, measures vegetation productivity with greater sensitivity in bare areas		
	GLCM_M	Measures the mean of the NDVI values of the pixel with adjacent pixels		
	GLCM_V	Measures the variation of the NDVI values of the pixel with the adjacent pixels		
	GLCM_H	Measures the homogeneity of the NDVI values of the pixel with the adjacent pixels		
	GLCM_C	Measures the contrast of the NDVI values of the pixel with the adjacent pixels		
	GPP	Gross Primary Production, measures the biomass	500 m	Dynamic - 8-day composite
	PDSI	Palmer Drought Severity Index, measure the level of aridity		
	LST	Land surface temperature, measures the temperature at ground level	1000 m	
	HH	PALSAR - Horizontal transmitting, horizontal receiving signal	25 m	Dynamic - Annual
	HV	PALSAR - Horizontal transmitting, vertical receiving signal		
	CLC	Corine Land Cover classes	100 m	
	IMD	Imperviousness, measure the level of urbanization	250 m	

In detail, satellite imageries were aggregated, corrected, and analysed, and the spatio-temporal concordance was addressed between calculated predictors and telemetry observations. These operations were carried out following the GEE_xtract framework presented in (Valerio et al., 2024), aiming to extract high-quality data, while providing an overview of the biophysical characteristics of agricultural and steppe habitats in the Mediterranean region. This involved landscape characteristics such as spectral data (red band - RED; near-infrared spectral band - NIR), vegetation conditions (Normalized Difference Vegetation Index - NDVI; Modified Soil Adjusted Vegetation Index 2 - MSAVI2), biomass (Gross Primary Production - GPP), drought assessment (Palmer Drought Severity Index - PDSI) and land surface temperatures (LST) (Cerasoli et al., 2018; Fernández et al., 2010; Valerio et al., 2023; von Keyserlingk et al., 2021) (Table E.1 from Appendix E). To infer vegetation's horizontal structure, Gray-level co-occurrence matrix (GLCM) indices (Haralick et al., 1973) were calculated through the NDVI, providing summary statistics of texture patterns, such as mean (GLCM_M) and variance (GLCM_V), as well as contrast metrics, including homogeneity (GLCM_H) and contrast (GLCM_C) (Fernández et al., 2010; Wood et al., 2012). Additionally, yearly mosaics of L-band SAR data with combined polarizations (horizontal transmitting/horizontal receiving - HH polarization; horizontal transmitting/vertical receiving - HV polarization) from ALOS PALSAR satellites were used to infer the vertical structure of vegetation (Lucas et al., 2010). To incorporate information regarding the spatial density distribution of artificially sealed areas, an indicator of human imperviousness (IMD) was obtained from the Copernicus programme (Copernicus Land Monitoring Service, 2021), in addition to the Corine land cover classes (CLC) which were used as categorical predictors. Moreover, the modelling process incorporated a collection of static predictors as well, which relate to relatively stable landscape characteristics. These predictors encompassed: i) soil properties (pH; sand content – SC; organic carbon density - OCD; bulk density - BD; Poggio et al., 2021); ii) bioclimatic conditions (annual mean temperature - BIO1; mean diurnal range - BIO2; annual precipitation - BIO12; precipitation of driest month - BIO14; Fick & Hijmans, 2017); iii) as well as topographic attributes (altitude, slope, terrain ruggedness index - TRI, and wetness index - TWI; Conrad et al., 2015; Crippen et al., 2016); and iv) anthropogenic information (distance from major roads - Dist_MR; distance from power lines - Dist_PL; GeoFabrik, 2021). All topographic variables were calculated using the equation provided in Table E.1 (Appendix E) through the software SAGA GIS (v.2.1.4; Conrad et al., 2015). Further descriptions of predictors' environmental meaning and biological rationale can be found in Table 4.1 and E.1, respectively.

4.2.4 Habitat Suitability Modelling

SDMs were employed to determine the variation in habitat suitability for the little bustard both spatially across phenological phases (seasonal SDMs) and temporally over the years. We used presences and pseudo-absences as response variables and both dynamic and static predictors as explanatory variables. Following the parametrisation in Valerio et al. (2020), models were run as probabilistic classifications by selecting Random Forests (Breiman, 2001), for which the variant algorithm "Boruta" (R package v.6.0.0; Kursa & Rudnicki, 2010) was used for a prior screening procedure to identify and filter out irrelevant predictors. The selection process relied on analyses that determined “confirmed” and “rejected” predictors by comparing the importance of predictors with that of their randomised copies, in which values were shuffled (Kursa and Rudnicki, 2010).

Each multivariate SDM with retained predictors was developed using tenfold cross-validations, and evaluated using a set of five accuracy metrics derived from the confusion matrix. These metrics included sensitivity, which measures the proportion of correctly classified occurrences, and specificity, which assesses the proportion of correctly classified absences (Fielding and Bell, 1997). Both metrics varies from 0 to 1, with values > 0.9 being indicative of good to excellent discriminant accuracy (Plante and Vance, 1994). Additionally, we included the area under the receiver operating characteristic (ROC) curve, often referred to as AUC (Swets, 1988). Here, values near 1 indicate a high level of predictability by the model (e.g. Araújo et al., 2005). To further enhance the evaluation process, the Boyce Index (Boyce et al., 2002) was integrated, with calculations carried out using the "modEvA" R package (v.3.9; Barbosa et al., 2013). This index varies from −1 to 1, with values close to 1 indicating that the model's predictions are consistent with the presences’ distribution (Jiménez and Soberón, 2020). To complement the evaluation, we also included the Matthews' correlation coefficient (Baldi et al., 2000; MCC; Matthews, 1975). The inclusion of MCC is particularly valuable due to its robustness, as it considers all categories of the confusion matrix, encompassing true positives, true negatives, false positives, and false negatives. This metric also varies from −1 to 1, with values of 1 indicating perfect classification (Chicco and Jurman, 2020).

Finally, to distinguish between suitable and unsuitable areas, the continuous probability maps were converted to binary using a cutoff. This cutoff was calculated independently for each phenological phase as the average of four different threshold selection methods. The methods we used include: i) minimizing the absolute difference between sensitivity and specificity (SeSpeql); ii) maximizing the sum of sensitivity and specificity (SeSpmax); iii) maintaining the original prevalence (PredPrev = Obs); and iv) taking the mean of the probabilities of occurrence of occupied locations for presence/absence data as the threshold (AvgProb) (see Liu et al. 2005, 2013; Nenzén and Araújo 2011, for detailed explanation). The models were subsequently projected for the Extremadura region between 2005 and 2021, covering the period between the first Spanish national census and the present. For detailed information on the modelling process, see Appendix F.

4.2.5 Spatio-temporal variation in habitat suitability

4.2.5.1 Spatial variation in habitat suitability across phenological phases

The median habitat suitability (HS), which reflects the species' expected probability of occurrence, was calculated for the last three years (2019–2021) in order to evaluate the current habitat suitability for the little bustard at each phenological phase. To visualise the spatial variation in habitat suitability between consecutive phenological phases, we calculated the difference between the HS values of a given phase minus those of the next phase. This allowed us to determine the variations in suitability at each location. Then, the percentage of suitable habitat (HS >cutoff; specific for each phenological phase) overlap between phases was calculated, as well as the pairwise niche overlap using Schoener’s D (Schoener, 1968) with the function “raster.overlap” from the R package “ENMTools” (Warren et al., 2010). This metric, which compares the corresponding values for each cell in two grids to determine how similar potential distributions are, ranges between 0 (no similarity) and 1 (identical potential distribution) (Broennimann et al., 2012).

4.2.5.2 Temporal variation in habitat suitability

To assess the stability in habitat suitability over time, we estimated, for each phenological phase, the coefficient of variation of the HS between 2005 and 2021, calculated for each pixel and expressed as a percentage, using the “CV” function from the R package “raster” (Hijmans, 2023). This enabled the most stable zones to be distinguished from those with greater variation in suitability over the period under consideration. Then, to visualise the temporal progression of sites with suitable habitat (HS >cutoff, specific for each phenological phase) between 2005 and 2021, we compared the baseline situation (HS median between 2005 and 2007) with the current situation (HS median between 2019 and 2021). The areas where suitable habitat decreased or increased, as well as the areas that remained stable above the suitability threshold, were then identified and measured for each phenological phase. Finally, to estimate the fluctuations in the availability of suitable habitat (HS >cutoff) in each phenological phase over the period

2005–2021, we calculated the area covered by all pixels classified as suitable for the species in each phase of each year.

4.3 Results

4.3.1 Seasonal little bustard SDMs

Explanatory predictors grouped as "dynamic" were among the most relevant variables in our seasonal SDM approach, in particular those referred to as landscape horizontal structure (textural) predictors (GLCM_C and GLCM_V, respectively NDVI-based texture contrast and variance metrics) jointly with those describing vertical structure (HV polarization) (Figure 4.2). Conversely, the most influential static predictors were those describing soil properties (sand content - SC), bioclimate (annual precipitation - Bio12; annual mean temperature - Bio1; and precipitation of driest month - Bio14), and topography (terrain ruggedness index - TRI; and terrain water index - TWI). Both the importance scores of the predictors in explaining the distribution of little bustards (Figure 4.2) and their ecological response curves (see Figure E.3 in Appendix E) vary between phenological phases. The NDVI-based texture contrast (GLCM_C) was the most important predictor during the winter phase and displayed a positive relationship with little bustard locations, where contrast in vegetation characteristics contributed to increase the probability of occurrence of the species, similar to the NDVI-based texture variance (GLCM_V). This effect was less significant during the post-breeding phase (Figure 4.2), and relationships become negative during the breeding phase (see Figure E.3 in Appendix E). The HV polarization (HV) was also an important predictor during the winter and breeding phases, where the lower the values of HV (relating to herbaceous vegetation), the higher the probability of little bustard occurrence. In relation to the soil sand content (SC) predictor, there was evidence for a relatively higher probability of species occurrence within areas of low sand content values, which is likely related to more productive soils. Conversely, when SC exceeds 35% (weight %), the little bustard appears to avoid these soils. The topographic predictors, namely terrain ruggedness index (TRI) and terrain water index (TWI), held higher importance scores during both the post-breeding and winter phases, maintaining a stable negative (low topographic heterogeneity) and positive (higher water potential accumulation) relationship with little bustard occurrence, respectively. The bioclimatic predictors were more significant during the post-breeding phase (Bio1 and Bio12) and breeding (Bio1 and Bio14), with Bio12 (Annual Precipitation) and Bio14 (Precipitation of Driest Month) exerting a positive effect, while Bio1 (Annual Mean Temperature) exerting a positive and a negative effect during the post-breeding and breeding phases, respectively (Figure 4.2 and E.3).

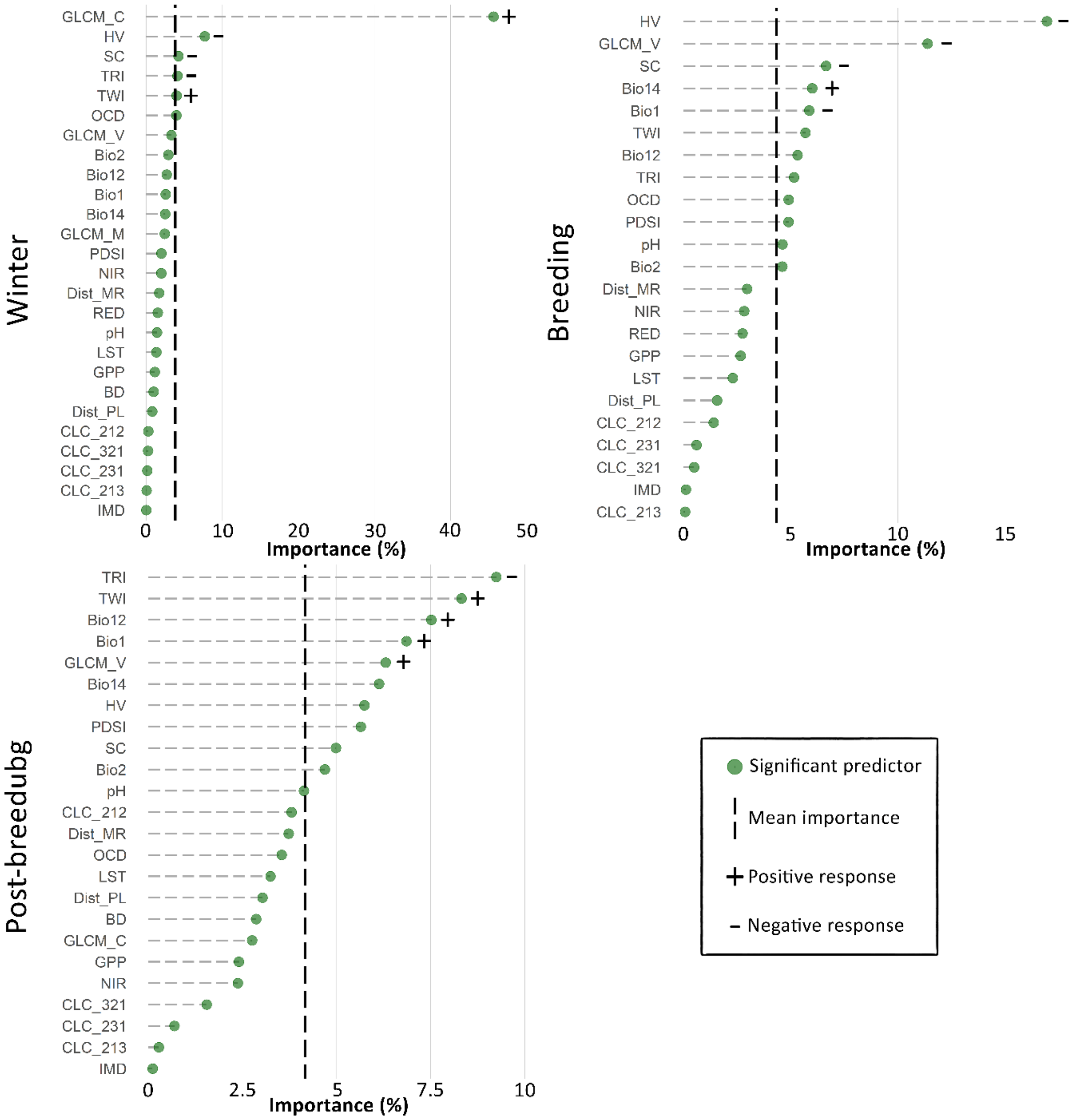

Figure 4.2 Importance scores, in explaining the little bustard distribution from Random Forests analysis for each phenological phase. The green dot indicates that the predictor was significant in the previous screening procedure (Boruta). The symbols "+" and "-" are attributed to the top five most relevant predictors and refer to whether the response curve was positive or negative. Response curves from partial dependence plots may be found for all predictors in Appendix E (Figure E.3).

All SDMs demonstrated high predictive power (Figure 4.3). In detail, the set of observations representing the most predictive phenological phase was breeding for all accuracy metrics, except for the Boyce index, where the most predictive phase was post-breeding. Excellent performances were observed, given the high AUC scores (>0.95), with no apparent differences between phases. High abilities were also found in predicting true presences (sensitivity>0.9) and false absences (specificity>0.9), though slightly better performances were detected in predicting true presences during breeding than in other phases. The MCC metric results indicated that most models performed with high accuracy scores (>0.85), as well as the Boyce index (>0.9) (Figure 4.3).

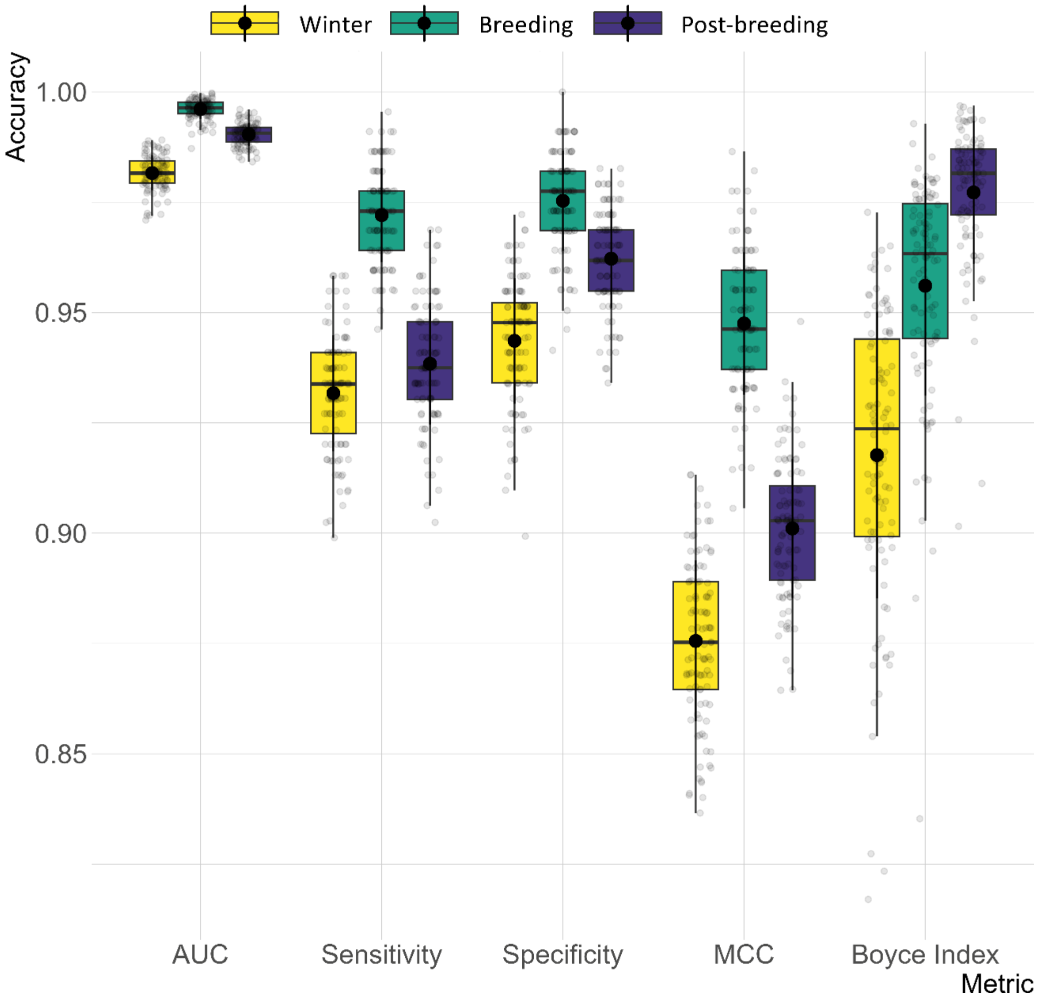

Figure 4.3 Differences in SDMs' performances across datasets representing distinct phenological phases. Model performance results are shown according to selected accuracy metrics: area under the receiver operating characteristic curve (AUC), sensitivity, specificity, and Matthews' correlation coefficient (MCC). Boxplots and grey dot points show the performance of cross-validation repetitions of Random Forests analyses, while black dots represent the mean performance.

4.3.2 Spatio-temporal variation in habitat suitability

4.3.2.1 Spatial variation in habitat suitability across phenological phases

Habitat suitability maps of the current situation (2019-2021; Figure 4.4a) suggest a clear change in the spatial distribution of suitable habitat among the three phenological phases. The distribution of the most suitable locations generally coincides with the interior of SPAs and their interface with the surrounding areas, during both the breeding and winter phases. Nonetheless, during the breeding phase, suitable areas are mostly concentrated in the eastern part of the province of Badajoz's, while during the winter phase, additional favourable habitats also can be found in the province of Cáceres' southern and central parts. The northwest of Cáceres and the southwest of Badajoz stand out as areas of lower suitability during both the breeding and winter phases. On the other hand, the post-breeding phase shows a more pronounced variation in the distribution of suitable areas. The areas of higher suitability during this phase are primarily located outside SPAs and are dispersed more widely across the study region (Figure 4.4a). The main suitable area during the post-breeding phase is located along the banks of the Guadiana River in the Extremadura region's central zone. The central and northwest zones of the province of Cáceres as well as the southeast region of the province of Badajoz also stand out for their high levels of suitability. In contrast, one of the least suitable areas during this phase is the Badajoz province's east central region.

Despite the minor seasonal variation of suitable habitat between the winter and breeding phases, differences were more noticeable inside SPAs, which have slightly decreased suitability indices, and in the north and south-central zones of the region, which have slight gains in habitat suitability (Figure 4.4b). Transitions involving the post-breeding phase are associated with stronger variation in suitability. As for the breeding phase transitions to the post-breeding phase, there is an increase in suitability in the areas surrounding the Guadiana River, in the central and northern areas of the province of Cáceres, as well as in the southeast area of the province of Badajoz. On the other hand, the central west and east zones of the provinces of Cáceres and Badajoz, respectively, exhibit a downward variation in suitability indices. As expected, given the similarity between the breeding and winter phases, the spatial variation of suitability in the breeding – post-breeding transition is opposite to that in the post-breeding – winter transition (Figure 4.4b).

The averaged suitability cutoff, used to identify suitable areas (HS value > cutoff), differs for each phenological phase (winter: 0,524; breeding: 0,500; post-breeding: 0,492; see Table E.3 from Appendix E). In the current situation (2019-2021), this translates to 1616.93 km^2 of available

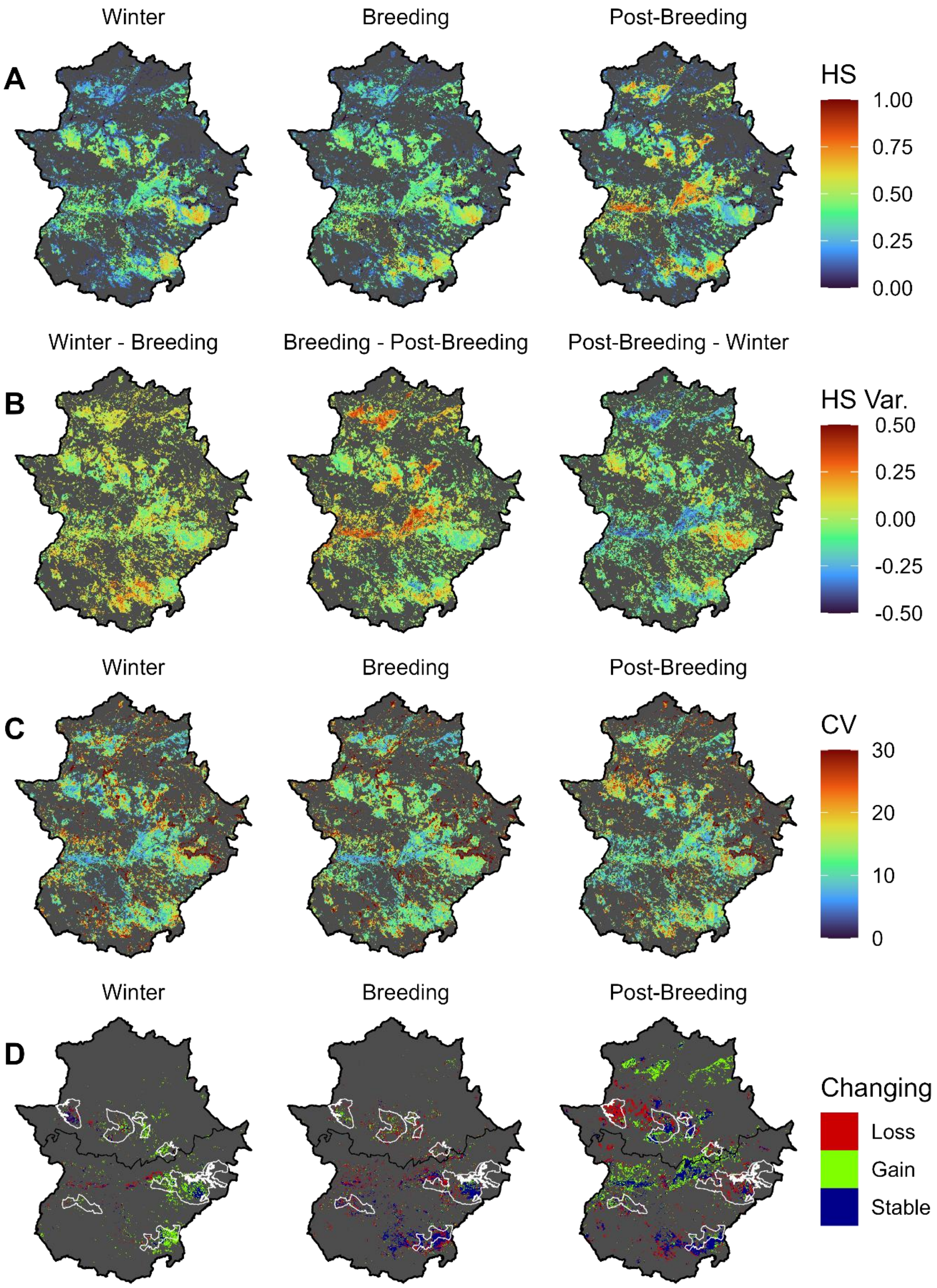

Figure 4.4 (a) – Current habitat suitability situation; (b) – Spatial variation in habitat suitability between consecutive phenological phases; (c) – Stability in habitat suitability over time (coefficient of variation of the HS between 2005 and 2021; truncated to 30 for visualisation purposes); (d) – Temporal progression of sites with suitable habitat (long-term changes from the baseline to the current period). The black-outlined polygons delineate the boundaries of the two provinces, while the white-outlined polygons delineate the Special Protection Areas (SPAs).

suitable habitat during the winter, 2100.51 km^2 during breeding, and 4500.98 km^2 during post-breeding. The seasonal overlap of suitable habitat is ultimately impacted by these differences in the availability of suitable areas. Despite the winter and breeding phases sharing only 681.99 km^2 of suitable areas, they show the highest similarity in the distribution of their HS values (D = 0.95), indicating a high spatial concordance in the suitability of habitats during the winter and breeding phases. Conversely, although the shared suitable area between breeding and post-breeding phases is substantially larger (1177.12 km^2), the distribution of their HS values is less similar (D = 0.85), indicating spatial discrepancy in the suitability of habitats between the breeding and post-breeding phases (Table 4.2). The post-breeding and winter phases, with an overlap of 885.3 km^2 of suitable areas, have the least similar distribution of HS values (D = 0.82). With regard to the location of suitable habitat in relation to SPAs, the winter phase has the highest percentage of suitable habitat within these areas (52.38%), followed by the breeding phase (38.36%), with the post-breeding phase presenting the lowest percentage (20.36%) (Table 4.3).

Table 4.2 Seasonal overlap of suitable habitat (HS >cutoff; winter cutoff: 0.524; breeding cutoff: 0.500; post-breeding cutoff: 0.492). Overlap percentage over the total available per phase, overlapping area, and Schoener's "D" metric.

Phenological Phases	Seasonal overlap of suitable habitat (2019 – 2021)		
	Percentage (%)	**Area (km^2)**	**D**
winter – breeding	42.18	681.99	0.95
breeding - winter	32.47		
breeding – post-breeding	56.04	1177.12	0.85
post-breeding – breeding	26.15		
post-breeding – winter	19.67	885.3	0.82
winter – post-breeding	54.75		

4.3.2.2 Temporal variation in habitat suitability

Over the study period (2005-2021), zones near water reservoirs and water lines, which are typically unsuitable for little bustards, were those showing the greatest instability (i.e., greatest coefficient of variation) in the indices of habitat suitability (Figure 4.4c). Low to moderate instability was observed during the winter and breeding phases across the study area, with these zones mainly being connected to SPAs and their surroundings, which are typically suitable for the species. In both phases, the areas closest to the Guadiana River and in the northwest of the province of Cáceres are the most stable over time, despite not being suitable for the species during these phases. In contrast, the post-breeding phase displayed lesser stability overall, with the zones of greatest instability typically being those that were unsuitable for the species. However, similarly to other phases, low to moderate instability was observed in areas suitable for little bustards during the post-breeding phase (Figure 4.4c).

Table 4.3 Temporal progression of sites with suitable habitat (HS > cutoff) as an overall for each season and only within SPAs.

Phenological Phase	**Baseline (2005-2007) (Km^2)**	**Current (2019-2021) (Km^2)**	**Stable**		**Gain**		**Loss**		**Net Gain/Loss**	
			(Km^2)	**(%)**	**(Km^2)**	**(%)**	**(Km^2)**	**(%)**	**(Km^2)**	**(%)**
Winter	788	1616.9	499.2	63.4	1117.7	141.8	288.8	36.65	828.9	105.2
Winter (SPAs)	405.7	846.9	313.7	77.3	533.17	131.4	91.96	22.7	441.2	108.8
Breeding	2738.9	2100.5	1545.8	56.4	554.7	20.25	1193.11	43.6	-638.4	-23.3
Breeding (SPAs)	916	805.9	586.7	64.1	219.1	23.9	329.2	35.9	-110.1	-12
Post-breeding	4104.8	4501	2442	59.5	2059	50.2	1662.8	40.5	396.2	9.7
Post-breeding (SPAs)	1197.8	916.3	623.2	52	293.1	24.5	574.6	48	-281.5	-23.5

Comparing the baseline situation (2005-2007) with the current winter phase situation (2019-2021) in terms of the availability of suitable habitat (HS >cutoff), a net gain of 828.91 Km^2 (corresponding to 105.19% of the suitable area in the baseline situation) was recorded (Table 4.3). However, about 36.65% of the area that was suitable in the baseline situation is no longer suitable. These losses in suitability occurred mainly in the vicinity of the Guadiana River, whereas suitability gains were mainly registered in the interior and interface areas of the SPAs, primarily in the province of Badajoz (Figure 4.4d). It is also worth noting that suitable habitat is more stable inside SPAs (77.33%) than it is outside (63.35%) (Table 4.3). In the breeding phase, there was a 23.31% decrease in the available suitable area (a net loss of 638.42 km^2), with only 56.44% of the suitable area in the baseline situation remaining suitable (Table 4.3). Still, inside SPAs, the decrease in the available suitable area was smaller (12.02%) and that stability was higher (64.06%). The areas that remained stable were found mainly in the south and east of the province of Badajoz. The losses occurred in the vicinity of the Guadiana River and the central south zone of the province of Cáceres, as well as in the interface areas of the SPAs of Badajoz (Figure 4.4d). In the post-breeding phase, there was a slight overall increase in the availability of suitable habitat between the baseline and current situations (9.65%; a net gain of 396.2 km^2), with 59.49% of the suitable habitat at the baseline remaining stable (Table 4.3). However, within SPAs the situation is quite different, registering a 23.50% decrease in the availability of suitable areas (a net loss of 281.5 km^2) and a stability of only 52.03% of the suitable areas. While gains were primarily recorded in the central zone of the study area and the northern zone of the province of Cáceres, the majority of suitability losses occurred in the south and east of the province of Badajoz and the southwest zone of the province of Cáceres (Figure 4.4d). The Guadiana River area and the southeast of Badajoz province are the main locations where the habitat remained suitable.

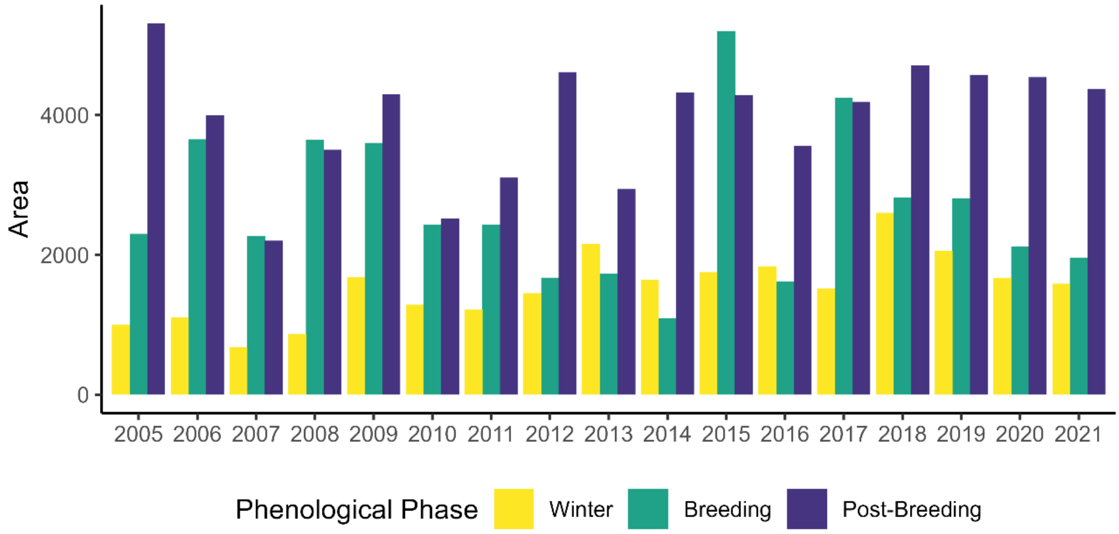

Figure 4.5 Area extent (km^2) of predicted suitable habitat for each phenological phase over the period 2005–2021. Calculated as the area covered by all pixels with HS values >cutoff.

Over time, the winter phase typically displayed the most spatially constrained area of suitable habitat, while the post-breeding phase consistently displayed the broader area of suitable habitat most of the time, according to the analysis of the predicted area of suitable habitat over the period 2005–2021 (Figure 4.5; E.5b and E.6). Large fluctuations in the availability of suitable habitats were observed over the period considered, mostly during the breeding and post-breeding phases. These fluctuations were not always synchronous between phenological phases, as was the case, for instance, between 2010 and 2013, when there was a tendency for habitat availability to decrease during the breeding phase and increase during the winter and post-breeding phases (Figure 4.5). Overall, a positive trend in the availability of suitable habitat is observed during the winter phase, whereas an apparent negative trend is observed during the breeding phase. The post-breeding phase does not show any apparent trend, despite the large fluctuations over time.

4.4 Discussion

Based on a detailed analysis of the spatial and temporal variation in habitat suitability of the little bustard, our study demonstrated clear seasonal variations in the spatial distribution of suitable habitat for the species along key phenological phases. Additionally, results also showed marked fluctuations in suitability over the past 17 years. When comparing the current situation to the baseline, we found an increase in suitability during the winter phase, a slight increase during the post-breeding phase, and a reduction in suitability during the breeding phase. Furthermore, our study also allowed the identification of locations where the habitat remains suitable over time, contributing to the definition of areas of high conservation value in future conservation planning (Silva et al., 2017).

Our study showed that the use of data with high temporal and spatial resolution from GPS telemetry and remote sensing, together with machine learning modelling procedures, allowed for a robust assessment of variation in species-specific habitat suitability along distinct phenological phases, as well as the prediction of the present and past potential distribution of migratory species. This methodology thus contributes to a thorough understanding of the dynamics in species potential distribution ranges over multiple phenological phases, as well as the identification of the most important habitat variables that predict species occurrence and on which conservation efforts should focus.

4.4.1 Potential distribution of the little bustard with seasonal SDMs

The accurate SDMs produced for each phenological phase showed that high-quality data used as input to Random Forest algorithms may present opportunities for providing information on the geographic distribution of species. Both static and dynamic predictors were found among the most explanatory variables in describing species occurrence, highlighting the relevance of including both types of predictors together with the modelling of each phenological phase separately (Frans et al., 2018). It should be noted that all of the CORINE Land Cover products fell below the mean importance threshold (Figure 4.2), highlighting the benefits of less conventional products with both SAR and optical information to highlight scarcely represented habitats (Valerio et al., 2020).

The winter model indicated that there is a greater probability for little bustards to occur within agricultural mosaics where herbaceous vegetation predominates, the soils are more productive, the topography is less rugged, and there is a tendency for very low or moderately high levels of water to accumulate. The representation of landscape mosaic in our analyses is supported by our textural predictors (i.e., NDVI-based texture contrast - GLCM_C) describing horizontal landscape complexity, since a positive response was found for contrasting NDVI values, given also the scale of the sensor grain (250m) and the window for the considered adjacent neighbour pixel. Concomitantly, the negative response for high backscattering values (i.e., HV polarization) supports the presence of a moderate vertical complexity of vegetation, since high backscatter values are associated with taller and more structured vegetation such as shrubs and trees (e.g. Valerio et al., 2023). These preferences are consistent with other studies showing that, during this phenological phase, little bustards select recent fallows and grassy vegetation, as well as hilltops, possibly as a predator avoidance strategy (Silva et al., 2004).

During breeding, little bustards showed a preference for areas dominated by herbaceous vegetation within more homogeneous landscapes, productive soils, intermediate levels of rainfall in the driest month, and moderate annual mean temperatures. These preferences are consistent with previous works showing a preference for vast expanses of grassland pastures or fallow lands with low land cover diversity, and a dominant grassland ecosystem (Morales et al., 2008; Moreira et al., 2012; Silva et al., 2010). Such choices are probably related to the species' lek mating system, in which breeding males seek conspicuousness for the sexual displays that take place in loose aggregations, whereas females seek a balance between visibility for anti-predator surveillance and cover provided by dense vegetation (Jiguet et al., 2000).

The most suitable areas for post-breeding, according to our model, coincide with depressions, where it is more likely to accumulate water and green vegetation that they feed on. Their occurrence also coincides with regions with higher average temperatures and higher annual precipitation, as well as some degree of heterogeneity in the landscape. Again, these preferences are in line with previous works that show a preference towards areas near water sources, on lower slopes, with more humidity, and with more green plants (Silva et al., 2007). Food availability is suggested to play a significant role in habitat selection and species distribution during post-breeding (Silva et al., 2007), with adults and chicks feeding mostly on green plants, in the period defined for post-breeding in our models (July 15 - September 15) (Jiguet et al., 2002).

4.4.2 Spatial variation in habitat suitability across phenological phases

According to our models, the extent and distribution of suitable habitat vary between phenological phases. During the winter phase, the area with suitable habitat is narrower and spatially more clustered, whereas it expands and spreads more widely during the breeding phase until it reaches its maximum extent in the post-breeding phase (Figures 4.4a and E.5b). These seasonal variations appear to reflect the behaviour of the little bustard, which exhibits territorial behaviour during breeding (Silva et al., 2017) and gregarious behaviour in the remaining phases (Silva et al., 2007, 2004). Outside the breeding season, little bustards congregate in flocks of varied sizes, but it is during the winter that they are more concentrated, creating the largest flocks.

The species' behavioural strategy appears to be influenced by food availability. During the winter, when there is plenty of food, the species shows greater habitat selectivity, which is possibly related to an anti-predatory strategy, increasing the level of aggregation in the most suitable habitats as the season progresses, providing food and protection (Morales et al., 2022; Silva et al., 2004). In the breeding phase, breeding males form dispersed leks at sites that were used in previous years (Silva et al., 2017), disperse over larger areas compared to the winter phase. Major shifts in the little bustard's distribution occur during post-breeding. This is probably because at the end of the breeding season, in late spring, vegetation dries out, restricting the little bustard's food resources and forcing individuals to migrate towards areas with more productive soils, which frequently coincide with irrigated fields with greater availability of green plants (García de La Morena et al., 2015; Silva et al., 2022, 2007). At this phase, flocks are usually small, ranging from a few birds to several tens, while occupying a wider range of habitats (Silva et al., 2007). There is a greater similarity in potential distribution of suitable habitat between the winter and breeding phases when compared to the post-breeding phase, suggesting that the scarcity of food during the summer leads to a change in occurrence patterns (Figure 4.4b and Table 4.2).

The distribution of suitable habitats during the winter and breeding phases greatly overlaps with the SPAs. Conversely, the most suitable areas for post-breeding are found outside SPAs, principally in the irrigation fields next to the Guadiana River, with only about 20% of these areas occurring within protected areas. On the other end of the spectrum is the winter phase, which has 52% of its total suitable area inside SPAs. In turn, the breeding phase presents about 38% of its suitable area inside SPAs, highlighting the importance of these areas for the conservation of the species, as demonstrated by the surveys done in Extremadura, which revealed that 65% of the breeding males are present inside SPAs (García De La Morena et al., 2018). When comparing the provinces of Badajoz and Cáceres in terms of the spatial distribution of suitable habitat, Badajoz has higher overall suitability, demonstrating greater availability of suitable habitat at all phenological phases. This results from the differences in landscape characteristics between the two provinces, with Badajoz having a higher availability of open habitats compared to Cáceres.

The fact that our study relied on GPS data provided solely by males may be considered a limitation. However, because females tend to occur in areas close to males (except for the chick-rearing period that was not included within the breeding phase considered in our analysis) (Morales et al., 2022; Silva et al., 2014), we did not expect that male and female preferences would differ at the level at which we analysed the data (Devoucoux et al., 2018).

4.4.3 Temporal variation in habitat suitability

Over the last two decades, the little bustard population from Extremadura has experienced a sharp decline, dropping as much as 53% between 2005 and 2016 (García De La Morena et al., 2018), a trend that is ongoing (SEO BirdLife, pers. comm.). This trend coincides with a gradual loss of suitability over time (Figures 4.4d, 4.5, and Table 4.3), particularly in the breeding phase, when the amount of suitable habitat for the species dropped by 23% over the period considered (2005–2021). Noticeably, only 56% of the breeding habitat remained stable during this period, which is a known requirement for viable breeding areas due to the species' high breeding site fidelity (Silva et al., 2017), highlighting the possible negative effects of the instability observed over time. However, despite the high level of instability, the availability of suitable habitat increased during the winter and, to a lesser extent, in the post-breeding phases too. These findings suggest that while the available winter and post-breeding habitats do not appear to pose a limitation for the species' conservation in Extremadura, the reduced availability of breeding sites may be acting as a bottleneck during a critical period in the population dynamics of this species. Even though there is considerable uncertainty with the demographic parameters of the breeding population of Extremadura, there is evidence suggesting that habitat loss and degradation, along with climate change, particularly during the breeding season, have adversely affected both the productivity and survival of females (Silva et al., 2022). Furthermore, there is a notable issue of high adult mortality associated with power lines (Marcelino et al., 2017).

While the long-term temporal variation in habitat suitability can be related mainly to land-use conversion (Silva et al., 2022), the large fluctuations in the availability of suitable habitat recorded between years (Figure 4.5) and the variations in average suitability (see Figure E.5 in Appendix E) may be related to the inter-annual variation in climatic and biotic conditions (i.e., vegetation condition) (Estrada et al., 2016; García de La Morena et al., 2015). This spatial variation in suitable areas may have serious impacts on the species since little bustards have marked philopatric habits, returning to the same places in consecutive years (Alonso et al., 2019; Silva et al., 2017). In this sense, it is also noteworthy that new potential habitats may not be immediately occupied, as this implies an additional energy expenditure when birds actively search for them (Holt, 2003).

The analysis of the temporal variation of habitat suitability highlighted the importance of SPAs for the little bustard, particularly during the breeding and winter phases. In addition to the higher average HS values over time within the SPAs, the stability of suitable habitat was also higher within these areas during these two phenological phases when compared to the non-SPA areas. Furthermore, in percentage terms, less habitat was lost inside the SPAs during these two phases, which may indicate that they are buffering against habitat loss and degradation up to a certain extent. However, although in post-breeding there was an overall gain in suitable habitat, within the SPAs the pattern was opposite, with important losses being recorded. These results may be, at least in part, explained by the fact that SPAs were designed with a focus on preserving breeding areas and by the land-use conversion restrictions existing in these protected areas.

It is worth mentioning, however, that results on how habitat suitability changes over space and time are intrinsically linked to the cutoff value used to generate the binary maps. This value changes with each phenological phase and affects the area that is considered to be suitable (>cutoff) or unsuitable (<cutoff), influencing the areas of overlap between phenological phases and the trends over time.

4.4.4 Conservation implications

The research presented here demonstrates fluctuations in the habitat suitability of the little bustard over time considering all phenological phases, and an apparent decline in the breeding phase. These results support the hypothesis that, at the population level, habitat instability and degradation are contributing towards the species decline, given the species' high fidelity to the same locations between years. Our modelling procedure identified most important dynamic predictors defining the species' phenological niches. These predictors were found to be mainly related to the structural characteristics of the habitat, rainfall rates, and average air temperatures, making the species vulnerable not only to habitat shifts but also to climate change.

In terms of conservation, priority should therefore be given to the promotion of high-quality habitat through the encouragement of traditional extensive agricultural practices, which primarily provide important habitat during the breeding and winter phases (Silva et al., 2010, 2004). Habitat stability over time is critically important to ensure high breeding densities and consequently breeding success by favouring its lekking breeding system (Silva et al., 2017, 2014). The results also highlight the importance of SPAs in the conservation of little bustards, especially during winter and breeding, given the apparent buffer effect they exert against habitat suitability loss and the greater proportion of habitat suitability stability found within these phenological phases. Taking into account the amount of suitable habitat found at the interface between the SPAs and the areas outside them, expanding these special protection areas could be beneficial for the species.

Our modelling procedure and the predictions regarding bird occurrence associated with the calculated cut-off value indicate that the changes in suitability vary across both time and space. These changes, however, significantly align with already identified breeding areas, including those deemed critically important as Special Protection Areas (SPAs), alongside post-breeding and wintering locations. The models developed here can therefore serve as a crucial decision-support tool for conservation efforts, by providing accurate, spatially explicit probability estimates of little bustards’ current and historical occurrence as well as details on the key environmental factors affecting the species at various phenological phases. Highly suitable areas that show stability over time should be considered of high conservation priority, particularly during the breeding phase. Overall, our approach offers relevant complementary information to existing research on the ecology and conservation of the little bustard. This information is particularly important for contextualizing the factors contributing to the species' decline over time in a spatially explicit manner, thereby facilitating integrated decision-making.

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Author contributions

All authors contributed critically to conceive the ideas and designed methodology; **TCM**, **FV** and **ATM** prepared the data; **FV** employed the modelling process; **TCM** analysed the data; **TCM** and **JPS** led the writing of the manuscript. **All authors** contributed critically to the drafts and gave final approval for publication.

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4.5 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

Araújo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. J Biogeogr 33, 1677–1688. https://doi.org/10.1111/j.1365-2699.2006.01584.x

Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. Glob Chang Biol 11, 1504–1513. https://doi.org/10.1111/j.1365-2486.2005.01000.x

Baldi, P., Brunak, S., Chauvin, Y., Andersen, C.A.F., Nielsen, H., 2000. Assessing the accuracy of prediction algorithms for classification: An overview. Bioinformatics 16, 412–424. https://doi.org/10.1093/bioinformatics/16.5.412

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: How, where and how many? Methods Ecol Evol 3, 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Barbosa, A.M., Real, R., Muñoz, A.R., Brown, J.A., 2013. New measures for assessing model equilibrium and prediction mismatch in species distribution models. Divers Distrib 19, 1333–1338. https://doi.org/10.1111/ddi.12100

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. Luxembourg: Publications Office of the European Union. https://doi.org/10.2779/959320

BirdLife International, 2018. *Tetrax tetrax*. The IUCN Red List of Threatened Species 2018: e.T22691896A129913710. https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22691896A129913710.en

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecol Modell 157, 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Breiman, L., 2001. Random Forests. Mach Learn 45, 5–32. https://doi.org/10.1023/A:1010933404324

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E., Graham, C.H., Guisan, A., 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography 21, 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x

Cerasoli, S., Campagnolo, M., Faria, J., Nogueira, C., da Conceição Caldeira, M., 2018. On estimating the gross primary productivity of Mediterranean grasslands under different fertilization regimes using vegetation indices and hyperspectral reflectance. Biogeosciences 15, 5455–5471. https://doi.org/10.5194/bg-15-5455-2018

Chicco, D., Jurman, G., 2020. The advantages of the Matthews correlation coefficient (MCC) over F1 score and accuracy in binary classification evaluation. BMC Genomics 21, 1–13. https://doi.org/10.1186/s12864-019-6413-7

Chuine, I., 2010. Why does phenology drive species distribution? Philosophical Transactions of the Royal Society B: Biological Sciences 365, 3149–3160. https://doi.org/10.1098/rstb.2010.0142

Colwell, R.K., Rangel, T.F., 2009. Hutchinson's duality: The once and future niche. Proc Natl Acad Sci U S A 106, 19651–19658. https://doi.org/10.1073/pnas.0901650106

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., Böhner, J., 2015. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. Geosci Model Dev 8, 1991–2007. https://doi.org/10.5194/gmd-8-1991-2015

Cord, A.F., Meentemeyer, R.K., Leitão, P.J., Václavík, T., 2013. Modelling species distributions with remote sensing data: Bridging disciplinary perspectives. J Biogeogr 40, 2226–2227. https://doi.org/10.1111/jbi.12199

Crippen, R., Buckley, S., Agram, P., Belz, E., Gurrola, E., Hensley, S., Kobrick, M., Lavalle, M., Martin, J., Neumann, M., Nguyen, Q., Rosen, P., Shimada, J., Simard, M., Tung, W., 2016. NASADEM global elevation model: Methods and progress. International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives 41, 125–128. https://doi.org/10.5194/isprsarchives-XLI-B4-125-2016

de Juana, E., 2009. The dramatic decline of the little bustard *Tetrax tetrax* in Extremadura (Spain). Ardeola 56, 119–125.

Devoucoux, P., Besnard, A., Bretagnolle, V., 2018. Sex-dependent habitat selection in a high-density Little Bustard *Tetrax tetrax* population in southern France, and the implications for conservation. Ibis 161, 310–324. https://doi.org/10.1111/ibi.12606

Elith, J., Leathwick, J.R., 2009. Species distribution models: Ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Estrada, A., Delgado, M.P., Arroyo, B., Traba, J., Morales, M.B., 2016. Forecasting large-scale habitat suitability of European bustards under climate change: The role of environmental and geographic variables. PLoS One 11, 1–17. https://doi.org/10.1371/journal.pone.0149810

European Union, Copernicus Land Monitoring Service (2021). Available online: https://land.copernicus.eu/ (accessed on 20 October 2021).

Fernández, N., Paruelo, J.M., Delibes, M., 2010. Ecosystem functioning of protected and altered Mediterranean environments: A remote sensing classification in Doñana, Spain. Remote Sens Environ 114, 211–220. https://doi.org/10.1016/j.rse.2009.09.001

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37, 4302–4315. https://doi.org/10.1002/joc.5086

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24, 38–49. https://doi.org/10.1017/S0376892997000088

Frans, V.F., Augé, A.A., Edelhoff, H., Erasmi, S., Balkenhol, N., Engler, J.O., 2018. Quantifying apart what belongs together: A multi-state species distribution modelling framework for species using distinct habitats. Methods Ecol Evol 9, 98–108. https://doi.org/10.1111/2041-210X.12847

García De La Morena, E.L., Bota, G., Mañosa, S., Morales, M., 2018. El Sisón Común en España. II Censo Nacional. SEO/Birdlife. Madrid, Madrid.

García de La Morena, E.L., Morales, M.B., Bota, G., Silva, João Paulo, Ponjoan, A., Suárez, F., Mañosa, S., Juana, E. de, García De La Morena, E.L., Morales, M.B., Bota, G., Silva, Joao Paulo, Ponjoan, A., Suárez, F., Mañosa, S., de Juana, E., 2015. Migration Patterns of Iberian Little Bustards *Tetrax tetrax*. Ardeola 62, 95–112. https://doi.org/10.13157/arla.62.1.2015.95

GeohjFabrik. GeoFabrik: Download Server for OpenStreetMap data. 2021. Web Based Download Application: Available online: http://download.geofabrik.de/ (accessed on 20 October 2021).

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sens Environ 202, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Gudka, M., Santos, C.D., Dolman, P.M., Abad-Gómez, J.M., Silva, J.P., 2019. Feeling the heat: Elevated temperature affects male display activity of a lekking grassland bird. PLoS One 14, e0221999. https://doi.org/10.1371/journal.pone.0221999

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

Haralick, R.M., Shanmugam, K., Dinstein, I., 1973. Textural Features for Image Classification. IEEE Trans Syst Man Cybern SMC-3, 610–621. https://doi.org/10.1109/TSMC.1973.4309314

Hijmans, R., 2023. raster: Geographic Data Analysis and Modeling. R package version 3.6-26, https://rspatial.org/raster.

Holt, R.D., 2003. On the evolutionary ecology of species' ranges. Evol Ecol Res 5, 159–178.

Iturbide, M., Bedia, J., Herrera, S., del Hierro, O., Pinto, M., Gutiérrez, J.M., 2015. A framework for species distribution modelling with improved pseudo-absence generation. Ecol Modell 312, 166–174. https://doi.org/10.1016/j.ecolmodel.2015.05.018

Jiguet, F., Arroyo, B., Bretagnolle, V., 2000. Lek mating systems: a case study in the Little Bustard *Tetrax tetrax*. Behavioural Processes 51, 63–82. https://doi.org/10.1016/S0376-6357(00)00119-4

Jiguet, F., Jaulin, S., Arroyo, B., 2002. Resource defence on exploded leks: Do male little bustards, *T. Tetrax*, control resources for females? Anim Behav 63, 899–905. https://doi.org/10.1006/anbe.2001.1970

Jiménez, L., Soberón, J., 2020. Leaving the area under the receiving operating characteristic curve behind: An evaluation method for species distribution modelling applications based on presence-only data. Methods Ecol Evol 11, 1571–1586. https://doi.org/10.1111/2041-210X.13479

Kays, R., Crofoot, M.C., Jetz, W., Wikelski, M., 2015. Terrestrial animal tracking as an eye on life and planet. Science (1979) 348, aaa2478. https://doi.org/10.1126/science.aaa2478

Kursa, M.B., Rudnicki, W.R., 2010. Feature selection with the boruta package. J Stat Softw 36, 1–13. https://doi.org/10.18637/jss.v036.i11

Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393. https://doi.org/10.1111/j.0906-7590.2005.03957.x

Liu, C., White, M., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. J Biogeogr 40, 778–789. https://doi.org/10.1111/jbi.12058

López Ávila, P., Hidalgo de Trucios, S., 1998. Revisión del status del Sisón: Evolución en Extremadura, in: Junta de Extremadura (Ed.), Conservación de La Naturaleza y Los Espacios Protegidos de Extremadura. Mérida, pp. 115–121.

López-Jiménez, Nicolás, García de la Morena, E., Bota, G., Mañosa, S., Morales, M.B., Traba, J., 2021. Sisón Comun, *Tetrax tetrax*, in: López-Jiménez, N. (Ed.), Libro Rojo de Las Aves de España. SEO/BirdLife, Madrid, pp. 521–527.

Lucas, R., Bunting, P., Clewley, D., Armston, J., Fairfax, R., Fensham, R., Accad, A., Kelley, J., Laidlaw, M., Eyre, T., Bowen, M., Carreiras, J., Bray, S., Metcalfe, D., Dwyer, J., Shimada, M., 2010. An Evaluation of the ALOS PALSAR L-Band Backscatter—Above Ground Biomass Relationship Queensland, Australia: Impacts of Surface Moisture Condition and Vegetation Structure. IEEE J Sel Top Appl Earth Obs Remote Sens 3, 576–593. https://doi.org/10.1109/JSTARS.2010.2086436

Marcelino, J., Moreira, F., Mañosa, S., Cuscó, F., Morales, M.B., García De La Morena, E.L., Bota, G., Palmeirim, J.M., Silva, J.P., 2017. 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

Matthews, B.W., 1975. Comparison of the predicted and observed secondary structure of T4 phage lysozyme. BBA - Protein Structure 405, 442–451. https://doi.org/10.1016/0005-2795(75)90109-9

Milanesi, P., Della Rocca, F., Robinson, R.A., 2020. Integrating dynamic environmental predictors and species occurrences: Toward true dynamic species distribution models. Ecol Evol 10, 1087–1092. https://doi.org/10.1002/ece3.5938

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., Mañosa, S., Villers, A., Morena, E.L.G. de la, 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., 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 Oecologica 34, 345–353. https://doi.org/10.1016/j.actao.2008.06.009

Moreira, F., Silva, J.P., Estanque, B., Palmeirim, J.M., Lecoq, M., Pinto, M., Leitão, D., Alonso, I., Pedroso, R., Santos, E., Catry, T., Silva, P., Henriques, I., Delgado, A., 2012. Mosaic-level inference of the impact of land cover changes in agricultural landscapes on biodiversity: A case-study with a threatened Grassland bird. PLoS One 7, 1–10. https://doi.org/10.1371/journal.pone.0038876

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences 105, 19052–19059. https://doi.org/10.1073/pnas.0800375105

Nenzén, H.K., Araújo, M.B., 2011. Choice of threshold alters projections of species range shifts under climate change. Ecol Modell 222, 3346–3354. https://doi.org/10.1016/j.ecolmodel.2011.07.011

Neumann, W., Martinuzzi, S., Estes, A.B., Pidgeon, A.M., Dettki, H., Ericsson, G., Radeloff, V.C., 2015. Opportunities for the application of advanced remotely-sensed data in ecological studies of terrestrial animal movement. Mov Ecol 3, 8. https://doi.org/10.1186/s40462-015-0036-7

Plante, E., Vance, R., 1994. Selection of Preschool Language Tests. Lang Speech Hear Serv Sch 25, 15–24. https://doi.org/10.1044/0161-1461.2501.15

Poggio, L., de Sousa, L.M., Batjes, N.H., Heuvelink, G.B.M., Kempen, B., Ribeiro, E., Rossiter, D., 2021. SoilGrids 2.0: Producing soil information for the globe with quantified spatial uncertainty. Soil 7, 217–240. https://doi.org/10.5194/soil-7-217-2021

Ponti, R., Sannolo, M., 2022. The importance of including phenology when modelling species ecological niche. Ecography 1–15. https://doi.org/10.1111/ecog.06143

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 Geobotanica 15, 5–432.

Schoener, T.W., 1968. The Anolis Lizards of Bimini: Resource Partitioning in a Complex Fauna. Ecology 49, 704–726. https://doi.org/10.2307/1935534

Silva, J.P., Arroyo, B., Marques, A.T., Morales, M.B., Devoucoux, P., Mougeot, F., 2022. Threats Affecting Little Bustards: Human Impacts, in: Bretagnolle, V., Traba, J., Morales, M.B. (Eds.), Little Bustard: Ecology and Conservation. Springer Nature, Switzerland, pp. 243–272. https://doi.org/10.1007/978-3-030-84902-3

Silva, J.P., Catry, I., Palmeirim, J.M., Moreira, F., 2015. Freezing heat: Thermally imposed constraints on the daily activity patterns of a free-ranging grassland bird. Ecosphere 6. https://doi.org/10.1890/ES14-00454.1

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., 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., Palmeirim, J.M., Moreira, F., 2010. Higher breeding densities of the threatened little bustard *Tetrax tetrax* occur in larger grassland fields: Implications for conservation. Biol Conserv 143, 2553–2558. https://doi.org/10.1016/j.biocon.2010.06.023

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

Smeraldo, S., Di Febbraro, M., Bosso, L., Flaquer, C., Guixé, D., Lisón, F., Meschede, A., Juste, J., Prüger, J., Puig-Montserrat, X., Russo, D., 2018. Ignoring seasonal changes in the ecological niche of non-migratory species may lead to biases in potential distribution models: lessons from bats. Biodivers Conserv 27, 2425–2441. https://doi.org/10.1007/s10531-018-1545-7

Swets, J.A., 1988. Measuring the Accuracy of Diagnostic Systems. Science (1979) 240, 1285–1293. https://doi.org/10.1126/science.3287615

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

Traba, J., Sastre, P., Morales, M.B., 2013. Factors determining species richness and composition of steppe bird communities in Peninsular Spain: grass-steppe vs. shrub-steppe bird species, in: Morales, M.B., Traba, J. (Eds.), Steppe Ecosystems. Biological Diversity, Management and Restoration. NOVA Publishers, pp. 47–72.

Valerio, F., Ferreira, E., Godinho, S., Pita, R., Mira, A., Fernandes, N., Santos, S.M., 2020. Predicting Microhabitat Suitability for an Endangered Small Mammal Using Sentinel-2 Data. Remote Sens (Basel) 12, 562. https://doi.org/10.3390/rs12030562

Valerio, F., Godinho, S., Marques, A.T., Crispim-Mendes, T., Pita, R., Silva, J.P., 2024. GEE_xtract: High-quality remote sensing data preparation and extraction for multiple spatio-temporal ecological scaling. Ecol Inform 80, 102502. https://doi.org/10.1016/j.ecoinf.2024.102502

Valerio, F., Godinho, S., Salgueiro, P., Medinas, D., Manghi, G., Mira, A., Pedroso, N.M., Ferreira, E.M., Craveiro, J., Costa, P., Santos, S.M., 2023. Integrating remote sensing data on habitat suitability and functional connectivity to inform multitaxa roadkill mitigation plans 38, 3335–3352. Landsc Ecol. https://doi.org/10.1007/s10980-022-01587-6

von Keyserlingk, J., de Hoop, M., Mayor, A.G., Dekker, S.C., Rietkerk, M., Foerster, S., 2021. Resilience of vegetation to drought: Studying the effect of grazing in a Mediterranean rangeland using satellite time series. Remote Sens Environ 255, 112270. https://doi.org/10.1016/j.rse.2020.112270

Warren, D.L., Glor, R.E., Turelli, M., 2010. ENMTools: A toolbox for comparative studies of environmental niche models. Ecography 33, 607–611. https://doi.org/10.1111/j.1600-0587.2009.06142.x

Wood, E.M., Pidgeon, A.M., Radeloff, V.C., Keuler, N.S., 2012. Image texture as a remotely sensed measure of vegetation structure. Remote Sens Environ 121, 516–526. https://doi.org/10.1016/j.rse.2012.01.003

Chapter 5

Spatially explicit individual-based models as tools to address pressing conservation decisions: A case study with the little bustard

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Chapter 5 – Spatially explicit individual-based models as tools to address pressing conservation decisions: A case study with the little bustard

Abstract

Biodiversity is experiencing significant declines globally, largely driven by anthropogenic environmental and climate changes that alter species distribution and abundance. Successful conservation strategies are crucial for sustaining species and ecosystems, yet limited resources require targeted and cost-effective approaches. Predictive models, particularly Individual-Based Models (IBMs), offer promising alternatives to traditional methods by leveraging existing knowledge to anticipate the impacts of conservation interventions on targeted endangered taxa.

In this study we developed a spatially explicit demographic IBM, that can be readily used to evaluate different conservation scenarios and priorities for the critically declining little bustard (*Tetrax tetrax*) in Extremadura, Spain. Our IBM uses high-resolution habitat suitability models to simulate individual behaviours and interactions with the environment, focusing on assessing the outcomes of different efforts for mitigating anthropogenic mortality and enhancing habitat suitability over a 50-year timeframe (2022–2072). The model incorporates survival, reproduction, spatial organization, and migration processes over the species' annual cycle, providing insights into habitat use and population dynamics.

The integration of habitat suitability and demographic behaviour within the IBM enabled a detailed understanding of the population's response to habitat changes over time. The model calibration procedure supported the hypothesis that the survival of nests, chicks, and adult little bustards is positively correlated with habitat suitability. The simulations results provided insights into the population's response to habitat changes, identifying critically important areas for conservation and the necessary habitat improvements to halt population decline. Our approach revealed that coordinated actions aimed at enhancing habitat suitability and reducing anthropogenic mortality are the most effective strategies for the long-term recovery of the little bustard population.

Overall, this study demonstrates the utility of IBMs for ecological risk assessment and management. In particular, our model provided a high-resolution decision-support tool that facilitates the identification of cost-effective strategies to enhance habitat suitability and reduce

anthropogenic mortality of the little bustard in Extremadura. This will critically contribute to improve conservation efforts for this and other similar endangered species amidst ongoing environmental challenges.

Keywords

Anthropogenic mortality; cost-effective; management; movement ecology; *Tetrax tetrax*

5.1 Introduction

Biodiversity is currently facing substantial declines worldwide, primarily due to human-induced environmental and climate change, altering the distribution and abundance patterns of numerous species (Díaz et al., 2019; Lees et al., 2022; Powers and Jetz, 2019). Effective conservation strategies are essential to sustain both species and ecosystems (Zurell et al., 2022). However, limited time and financial resources often hinder the implementation of such strategies (McCarthy et al., 2012), requiring the use of targeted, precise, and well-founded conservation methods that maximize positive outcomes (Wintle et al., 2011). This involves determining the appropriate locations for implementing conservation actions and assessing the required level of effort to revert the declining trends of the species, ensuring an efficient allocation of limited resources (Gann et al., 2019).

Identifying the most cost-effective conservation actions requires a comprehensive understanding of spatiotemporal wildlife population distribution and abundance patterns, in order to better anticipate the impacts of conservation interventions (Guisan et al., 2013; Zurell et al., 2022). While long-term field experiments are typically required for such insights, they are often not feasible for species experiencing rapid population declines and necessitating immediate conservation actions. In this context, predictive models leveraging the existing scientific knowledge about target species offer a timely and cost-effective alternative to traditional field-based approaches (Cook et al., 2010; Pollock et al., 2020). In particular, predictive modelling, especially Individual-Based Models (IBMs), can play an important role throughout all stages of conservation planning, from problem framing and intervention design to implementation and impact evaluation (Travers et al., 2019). However, in practice, such approaches remain mostly inaccessible to managers, highlighting the need for tools that can be readily used to evaluate and prioritize 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, enabling the integration of individual heterogeneity and environmental dynamics to forecast population responses with unprecedented precision (McLane et al., 2011; Railsback and Grimm, 2019). IBMs adopt a bottom-up approach, wherein the behaviour and interactions between individuals and their environment drive emergent patterns and dynamics (Grimm and Railsback, 2005; Stillman et al., 2015). Their process-based structure and capacity to simulate spatially explicit processes by incorporating real-world spatial data, such as habitat maps and landscape features, makes these models particularly useful to anticipate the impacts of interventions and prioritize actions in the context of conservation (Grimm, 2005; Grimm and Railsback, 2005; McLane et al., 2011). These characteristics 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). However, the effective use of spatially explicit individual-based modelling by conservation practitioners for prioritizing cost-effective actions remains limited.

Grassland birds are among the most endangered terrestrial vertebrates in Europe, primarily due to habitat transformation caused by agricultural and livestock intensification (BirdLife International, 2022; Lees et al., 2022). The Iberian Peninsula represents a crucial refuge for numerous grassland bird species in Europe, many of which exhibit unfavourable conservation status (Traba and Morales, 2019). Among such species, the little bustard (*Tetrax tetrax*) stands out due to its significant population declines in recent decades, primarily caused by habitat loss (Morales and Bretagnolle, 2022a). Historically widespread across the Palearctic region, the little bustard currently has a highly fragmented distribution, with Western European populations confined to France, Spain, Portugal, and Sardinia (Morales and Bretagnolle, 2022b). This decline has led to the species classification as Vulnerable at the European level (BirdLife International, 2021). Notably, the Iberian Peninsula holds a significant population of the species, with the Spanish Extremadura region historically serving as a crucial stronghold (De Juana and Martínez, 1996; Morales and Bretagnolle, 2022a). However, 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., 2018, 2006). This decline is coupled with low breeding success, male-biased sex ratios (Serrano-Davies et al., 2023), and high mortality rates of adult birds, including from anthropogenic sources such as illegal hunting, roadkill, and notably power line collisions, which are recognised as the leading cause of "non-natural" mortality (Marcelino et al., 2017). These challenges underscore the urgency of conservation efforts to safeguard the little bustard population and its critical habitats in the region.

Stochastic population models have previously been developed to test the population viability (Inchausti and Bretagnolle, 2005; Morales et al., 2005a) and to evaluate the effect of population reinforcement (Bretagnolle and Inchausti, 2005) in French little bustard populations, or, more recently, 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 have incorporated detailed individual behaviour throughout the annual cycle or utilized a spatially explicit landscape, thus failing to realistically account for spatial context.

In this study, our aim was to develop a management support tool to aid in the conservation of the little bustard in Extremadura. Using IBM, we simulated individual behaviours and their interactions with the environment to forecast habitat use and population dynamics, considering different management strategies and their potential impacts on the population. Specifically, our key objectives were: 1) to develop and evaluate a high-resolution spatial-explicit IBM customized for the little bustard population of the Extremadura region; and 2) to assess the potential and usefulness of the model and gain comprehensive understanding of how to implement 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).

5.2 Methods

5.2.1 Study area and study species

The Extremadura region (SW Spain) is as an autonomous administrative entity vested with the authority for 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 (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 in the region has experienced an alarming population decline over the last decades (Traba et al., 2022). Between 2016 and 2022, the density of breeding males decreased by approximately 65%, reaching an overall decline of about 80% compared to 2005 (Silva et al., 2024, 2023b). This represents an increase from an annual decline rate of male densities of 5% between 2005 and 2016 to 11% between 2016 and 2022.

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

The Iberian population showcases partial migration, with some individuals being strictly sedentary and others displaying various migratory patterns influenced by factors like food availability and environmental conditions (Traba and Morales, 2019). Migration movements are synchronized with the species' phenological phases, featuring 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 shift, males may slightly adjust their locations to find optimal habitats meeting their requirements (Delgado et al., 2010; Morales et al., 2005b). Male little bustards predominantly engage in migratory movements in June/July, immediately following the breeding season, during the Iberian summer, when temperatures and vegetation dryness peak (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 start flocking in post-breeding areas (Silva et al., 2014). Females and their chicks join these flocks once the chicks acquire the ability to fly. In wintering quarters, flocks increase 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 male-biased sex ratios (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).

5.2.2 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 G), we provide a TRACE document ("TRAnsparent and Comprehensive model Evaludation"; Augusiak et al., 2014; Grimm et al., 2014; Schmolke et al., 2010) containing evidence that our model was thoughtfully 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., 2020, 2010, 2006) is provided in Section 2 ("Model description") of the TRACE document (Appendix G). 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).

The overall purpose of the model is to provide a decision support tool for conservation management initiatives targeting the little bustard population in Extremadura, Spain. Specifically, we aim to identify cost-effective management strategies to revert the declining trends of the little bustard population in Extremadura within a 50-year timeframe (2022 – 2072). This involves simulating 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 assess the model´s performance based on its ability to replicate demographic patterns from 2005 to 2022.

The model incorporates different entities, including habitat cells, several entities related to little bustards, categorized as males and 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). Nests and flocks contribute to 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 5.1.

Table 5.1 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 (0 - 1)
occupants	Current number of occupants of the cell	Numeric (-)
intervened	Indicates whether a habitat cell had a habitat improvement intervention	Boolean (True; False)
Male little bustards		
ID	Unique identification code	Numeric (-)
location	Location in the local patch	Numeric (spatial coordinates)
age	Age	Numeric (weeks)
migration_pattern	Migration pattern	Categoric (See Section 3.1 in Appendix G 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 (-)
location	Location in the local patch	Numeric (spatial coordinates)
age	Age	Numeric (weeks)
migration_pattern	Migration pattern	Categoric (See Section 3.1 in Appendix G 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 (-)
Nests		
female	Female's ID	Numeric (-)
Flocks		
size	Number of individuals within the flock	Numeric (-)
Global environment		
date	Date in current time-step	Date (day/month/year)
phenological_phase	Current phenological phase	Categoric ("breeding"; "migration_post-breeding"; "post-breeding"; "migration_winter"; "winter"; "migration_breeding")
nesting_prob	Current nesting probability	Numeric (0 – 1)
migration_prob	Current migration probability	Numeric (0 – 1)

Spatially, the model represents the Extremadura region at a resolution of 250 m (1004 x 1128 square cells). Temporally, the model operates on a weekly time step, simulating the little bustard's yearly cycle with distinct phenological phases and associated behavioural traits. The choice of this spatio-temporal resolution is justified by the necessity to accurately capture the fine-scale habitat preferences and movement patterns of the little bustard, enabling the realistic representation of habitat utilization, as well as critical life events such as breeding and migration dynamics. The model's time horizon includes an implementation phase (calibration, sensitivity analysis, and validation) spanning 17 years (01-04-2005 to 01-04-2022) and a main experiment phase, covering 50 years (01-04-2022 to 01-04-2072).

The key processes of the model are associated with specific behaviours and life events of the species. These processes are executed according to the phenological phase of the simulation (Figure 5.1), which is updated at each simulation step, together with the corresponding changes in habitat suitability values. Migration and mating probabilities are adjusted during 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 new nest, which, if successful, leads to the hatching of chicks three weeks later. During the migration phase, occurring between phenological phases, individuals migrate to the same location where they spent the corresponding phase in the previous year, making slight adjustments to the final location according to changes in habitat suitability and spatial distribution of other individuals. The distances between the locations at different phenological phases vary based on the migration pattern of each individual, which is defined at the beginning of the simulation and remains unchanged throughout the simulation (see Table G.3.2 and Section 3.1 in Appendix G). Additionally, during the migration phase to the breeding grounds, individuals also have the opportunity to disperse to a new breeding location (see Table 5.2 and Section 3.1 in Appendix G). Survival probabilities at each time step differ among groups of individuals or agents, including nests, chicks, adults, and breeding females (Figure 5.2 and see Section 2.7.7 in Appendix G).

The model incorporates several design concepts essential for achieving the necessary realism and complexity for its intended purpose. The most important relate to the phenology representation, socio-spatial organization, and the relationship between key demographic parameters of individuals and habitat suitability. Regarding species phenology representation, the model recreates the little bustard annual cycle and population dynamics based on decision rules reflecting the complex behaviours throughout the species' phenological phases (breeding, post-breeding, and winter), including migration periods between them. The annual cycle is therefore temporally segmented according to the different phenological phases, each characterized by specific habitat suitability determined by phase-specific drivers. This is achieved through the inclusion of high-resolution suitability maps (250 m) for each phenological phase, based on predictions from species distribution models (SDMs) developed in Crispim-Mendes et al. (2024). Habitat cells are characterized by a suitability value, derived from the averaged suitability of surrounding cells within a variable buffer for each phenological phase. This approach considers the average home-range size of individuals in each phenological phase, and effectively eliminates the challenge of considering their small-scale movements, with cells representing the centroids of an individual's home range. This dynamic characterization of habitat suitability is fundamental for guiding socio-spatial organization and migration movements, as well as reproduction and survival.

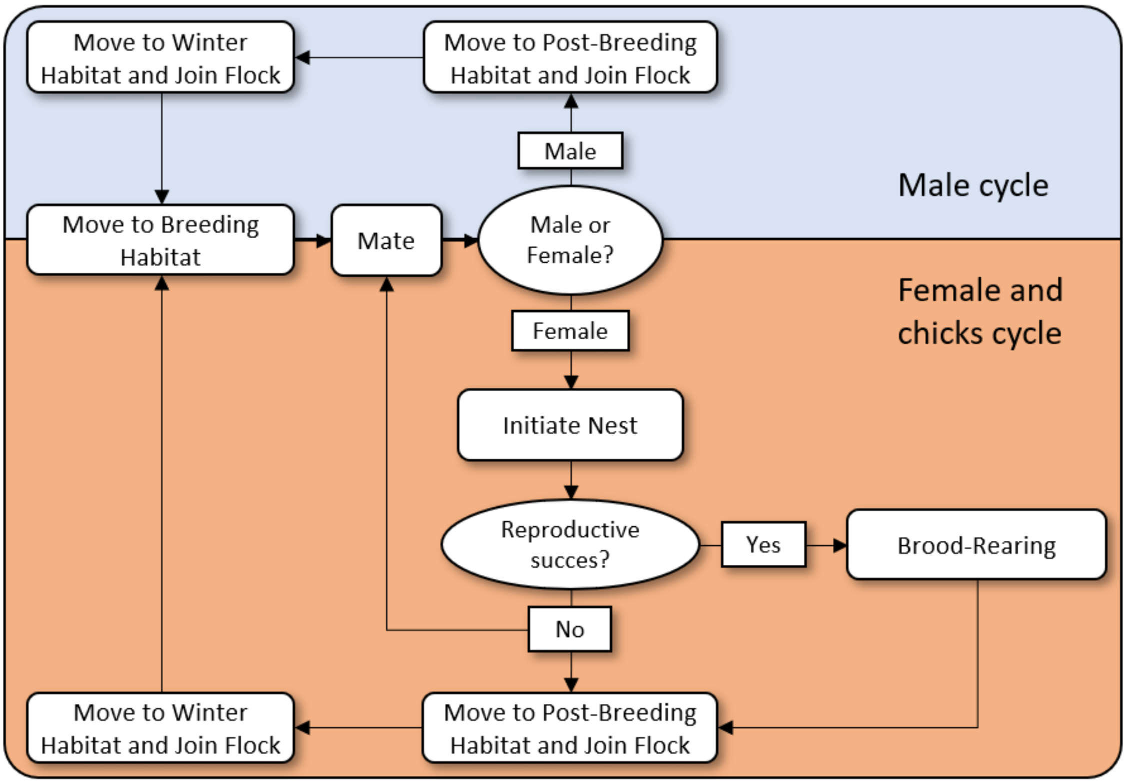

Figure 5.1 Flow diagram of the yearly-cycle processes included in the model.

Regarding socio-spatial organization, the model is grounded in the “exploded-lek” mating system principle described for the species (Jiguet and Bretagnolle, 2014; Morales et al., 2014). During the breeding phase, the model enforces territorial behaviour, allowing only one individual per habitat cell (250 m). In contrast, gregarious behaviour unfolds in the remaining phenological phases where the species forms flocks, grouping together based on flock-search radii (see Table 5.2 and Section 2.7.5 in Appendix G). The inclusion of different proportions of migration patterns identified in the Extremadura region (including movements within Extremadura and beyond, see

Table 5.2 and Section 3.1 in Appendix G), coupled with adaptive traits related to habitat selection and response to changes in suitability (e.g. Crispim-Mendes et al., 2024), adds realism to the model's representation of spatial utilization variability throughout the annual cycle.

Table 5.2 Summary of parameter information used in the IBM.

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

Habitat suitability directly impacts individual breeding success (females) and survival, as the model assumes that higher habitat suitability enhances nest success and individual survival. Different survival rates are applied to chicks and adults, as well as to breeding females and other adults during the breeding and chick-rearing phases, supported by empirical observations of sex ratio imbalances in populations within degraded locations (Serrano-Davies et al., 2023). The relationship between agents and habitat suitability is supported by the variables considered in the SDMs, which are anticipated to correlate with survival probability. These include topography and vegetation characteristics known to influence food availability and exposure to predation. This relationship enhances the model's realism, providing a direct and emergent response of the population to changes in habitat quality, whether due to natural factors like intra- and inter-annual variability, or anthropogenic factors, such as habitat destruction or improvement. Together, these design concepts provide a robust scientific foundation for modelling little bustards' behaviour and population dynamics in the Extremadura region, in line with the model's objectives.

5.2.3 Model development

5.2.3.1 Calibration

During model development, parameters with limited empirical data were calibrated, including the percentage of non-breeding females and the conspecific attraction radius during post-breeding and winter phases. Furthermore, the relationship between survival across various life stages of little bustards and the habitat suitability of their location was inferred through Logarithmic Regression. This involved calibrating parameters A and B of the Logarithmic Regression formula, survival ~ A + B ln (habitat suitability), where A represents the survival probability under optimal habitat suitability conditions (habitat suitability = 1), and B controls the slope of the curve, determining the strength of the correlation between survival and suitability within our model.

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

5.2.3.2 Sensitivity-analyses

A local sensitivity analysis was conducted using the Morris screening method (Morris, 1991), which employs an individually randomized one-factor-at-a-time design to estimate the impacts of changes in parameter values on model outputs. Input parameters were varied by 10% above and below their default value. This method assesses the relative importance of each parameter (μ^*), as well as their linear, additive, or nonlinear effects, and interactions with other parameters (σ) (Campolongo et al., 2007; Morris, 1991; Thiele et al., 2014). For more details, see Section 7 in Appendix G.

5.2.3.3 Validation

The model was validated against demographic data from the Extremadura region and other Iberian and French populations. Specifically, we considered parameters related to the estimates of the number of males in the provinces of Cáceres and Badajoz, based on the results of the national census conducted in 2016 (García de la Morena et al., 2018), and the regional census of 2022 (SEO, in prep), as well as various reproductive, survival, and socio-spatial organization parameters. For detailed information, see Section 8 in Appendix G.

5.2.4 Simulation experiments

For the main experiment, we explored various management strategies with the goal of identifying the most cost-effective ones. The primary focus was on enhancing productivity and increasing the effective population size in the Extremadura region over the medium to long term (up to 50 years), aiming to revert the current declining trend. This involved testing different criteria for selecting locations to implement conservation interventions aimed at increasing habitat suitability, along with exploring different mitigation levels of overall anthropogenic mortality.

For this purpose, we used our calibrated model to conduct simulations spanning from 2022 to 2072, covering a 50-year period. Population data was collected at years 5 and 10, and then subsequently every 10 years. We initiated the simulations using a database generated during the model validation process, containing the locations and state variable information of individuals in 2022 for each of the 100 simulations conducted. Habitat suitability maps were calculated as the median suitability over the last 10 years (between 2012 and 2022) for each phenological phase, remaining constant throughout the simulation period.

5.2.4.1 Conservation interventions

While conservation interventions to increase habitat suitability should primarily focus on enhancing female survival and productivity rates (Mañosa and Bota, 2023; Serrano-Davies et al., 2023; Silva et al., 2022), we opted to use male locations to identify intervention sites, due to the challenge of detecting females during the breeding phase and their tendency to nest near males (leks). We then assessed several sets of hierarchical rules to define conservation interventions related to both habitat suitability (in terms of location, number, extent, and magnitude) and mitigation of anthropogenic mortality, in order to determine the most cost-efficient management strategies. We start by defining the potential locations for intervention, testing one scenario without restrictions across the entire study area and another restricted to the interior of SPAs. Subsequently, we examined the selection of different fractions of male locations (0.25, 0.5, 0.75, and 1) present in those areas. Following the selection of intervention sites based on the centroid of males' home range, we evaluated different intervention radii (250m, 750m, and 1250m, corresponding to 1, 3, and 5 habitat cells in the model, respectively). Lastly, we tested different increments of the habitat suitability value (0.1, 0.2, and 0.3) representing different levels of investment in habitat restoration and practices to reduce human disturbance within the intervention locations.

In parallel, we tested the reduction of overall anthropogenic mortality within the population through a tiered approach. Each tier corresponds to a different annual probability of an individual dying due to anthropogenic causes (4 tiers in total). These tiers included one with the current mortality probability (0.06), another where mortality probability is completely eliminated (0), and two with intermediate reductions (0.04 and 0.02). It can be assumed that the scenario with 0.06 annual mortality represents a strategy without any mortality reduction measures, serving as the control scenario. Additionally, it can be roughly inferred that the scenario with 0.04 mortality represents a strategy where power line marking would be implemented, while complete elimination of anthropogenic mortality represents a conservation intervention entailing burying or rerouting power lines as well as more restrictive hunting activities and the implementation of effective roadkill mitigation measures across the whole road network. Conversely, the intermediate reduction scenario (0.02 annual mortality) would represent a mixed management strategy, involving burial of some lines and marking of the remaining ones. The exclusion of scenarios involving increased anthropogenic mortality assumes that future powerlines will be planned to avoid collisions with bustards.

We conducted tests on the different conservation management strategies resulting from the multiple combinations of interventions under consideration (288 combinations), with 10 replicates executed for each combination. Effective strategies were identified based on combinations yielding an annual population growth > 1. These strategies were then ranked based on their cost-effectiveness, given as the ratio between the observed annual population growth rate and the intervention area defined for habitat suitability enhancement. The ranking process was carried out for each year of data collection and for each tier of anthropogenic mortality, considering the combinations including the maximum increase in habitat suitability (set at 0.3).

5.3 Results

5.3.1 Model development

5.3.1.1 Calibration

The calibration process enabled the establishment of a correlation between habitat suitability and individual survival across various life stages of the little bustard. Notably, during the incubation period, nest failure showed 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) (Figure 5.2a). Similarly, during the chick development stage, spanning from birth to 8 weeks of age, a significant correlation was identified with habitat suitability (B = 0.076) alongside the second-lowest weekly survival probability under optimal habitat suitability conditions (A = 0.974) (Figure 5.2b).

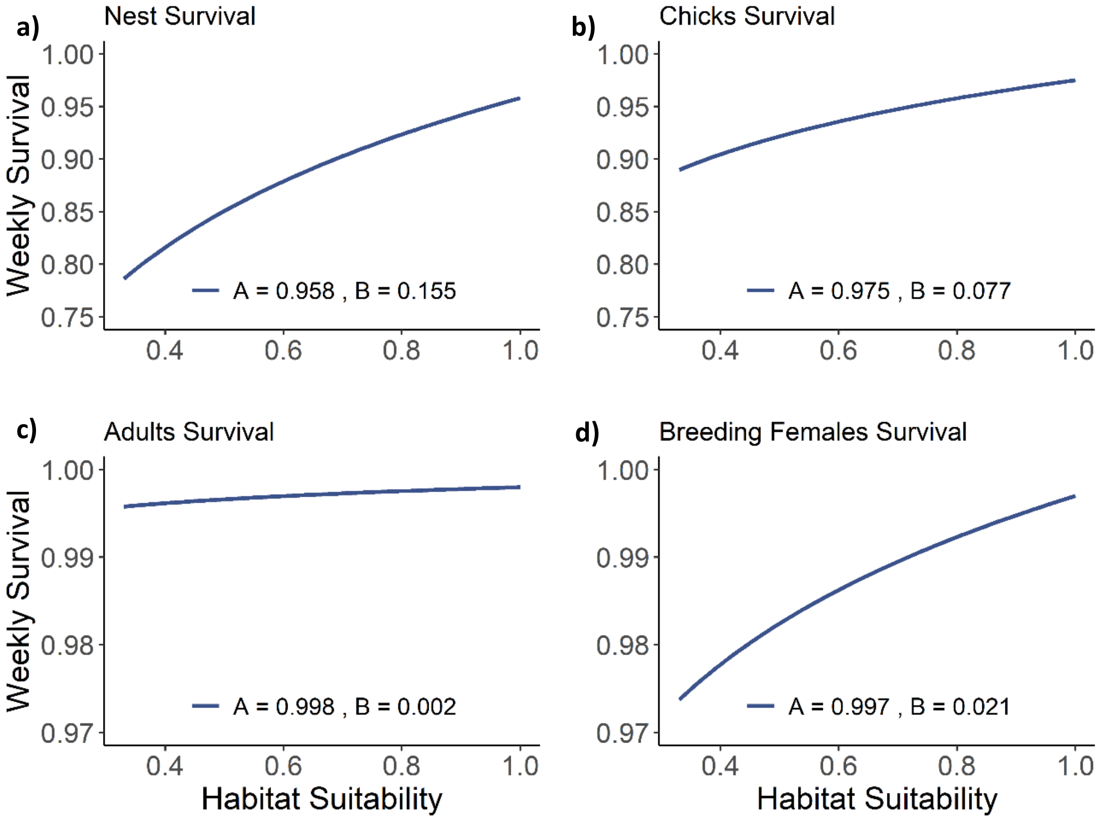

Figure 5.2 Calibrated survival curves of the various life stages of the little bustard relative to habitat suitability, obtained from logarithmic regression. The A and B values of each curve represent the mean of the posterior distributions after the rejection-ABC calibration process.

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 much stronger for breeding females (B = 0.021) compared to other adults (B = 0.002) (Figures 5.2c and d).

Regarding the percentage of non-breeding females, the calibration process indicated a value of 18.5%, although accepted values in the posterior distribution showed significant fluctuation between 15% and 23%, suggesting a low model sensitivity to this factor (see Table G.6.2 in Appendix G). 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 G.6.2 in Appendix G).

5.3.1.2 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 G.7.1 in Appendix G). Also influential in the annual growth rate were the survival rates of chicks and nests. However, these parameters were strongly influenced by the values in other parameters (high σ values). Except for adult survival, all remaining parameters exhibited non-monotonic effects on the growth rate, characterized by a high value of μ* and a low value of μ.

Regarding the influence on population sex ratio, sensitivity analyses emphasized the significance 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 G.7.2 in Appendix G). All these parameters were significantly influenced by the choice of other parameter values. Concerning the influence of parameters on the time until the extinction, adult survival and anthropogenic mortality emerged as the most important factors (see Figure G.7.3 in Appendix G).

5.3.1.3 Validation

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

The values of nest failure (41%; see Figure G.8.2 in Appendix G) fell within the ranges reported in other studies (Berthet et al., 2012; Bretagnolle et al., 2011; Cuscó et al., 2021; Lapiedra et al., 2011), as did the average number of juveniles per breeding female (0.76 juveniles; see Figure G.8.4 in Appendix G; e.g. Bretagnolle et al., 2018, 2011; Bretagnolle and Inchausti, 2005; Cuscó et al., 2021; Lapiedra et al., 2011; Tarjuelo et al., 2013), although the number of juveniles per female (0.65; see Figure G.8.3 in Appendix G) was slightly higher than in other studies (Bretagnolle et al., 2011; Cuscó et al., 2021; Inchausti and Bretagnolle, 2005; Lapiedra et al., 2011). Similarly, the median chick survival (0.5; see Figure G.8.5 in Appendix G) and breeding success (0.56; see Figure G.8.6 in Appendix G) aligned with values from previous research (e.g. Bretagnolle et al., 2018; Cuscó et al., 2021; Lapiedra et al., 2011).

The model also replicated the empirical average sex ratios (female sex ratio = 0.54; see Figure G.8.7 in Appendix G) and median annual male survival (75%; see Figure G.8.8 in Appendix G) rates, with the latter being slightly higher than the average calculated for the Extremadura region (Silva et al., 2024) but falling within expected ranges (Inchausti and Bretagnolle, 2005; Marcelino et al., 2017). Regarding habitat fidelity, the model produced similar values to the ones recorded in Extremadura, both at the home range (83%) and core area (46%) levels (see Figure G.8.9 in Appendix G).

5.3.2 Optimal management strategy

When examining the different simulated management strategies (Table 5.3), a significant disparity in the intervention areas resulting from these strategies is evident, ranging from 3.302 to 332.013 ha. As expected, strategies with similar selected male fractions and intervention radii but differing in location restrictions exhibit notably diverse intervention areas. Specifically, intervention areas were approximately three times larger when selection was performed without spatial constraints compared to those resulting from interventions restricted to SPAs. This discrepancy reflects the spatial distribution of individuals in the study area, suggesting that, based on our projections, only about one-third of individuals were within SPAs at the time management strategies were defined (2022). However, the percentage of SPA area covered by habitat suitability improvements in strategies with and without spatial restrictions remained similar in equivalent scenarios, ranging from 1% to 27%.

Regarding the percentage of females with home range centroids included in the intervention areas, there was also considerable variation, ranging from 7% to 100%, depending on the strategy. However, it is worth noting that the percentage increase observed when transitioning from a radius of 1 to 3 habitat cells was generally much higher than when transitioning from a radius of 3 to 5 habitat cells.

Table 5.3 Comparison of different management strategies simulated and associated intervention metrics to habitat suitability increase, including the total intervention area in the study area (Intervened Area), the intervention area within SPAs (Area SPAs), and the percentage of total SPA area intervened (% Area of SPAs). Also presented is the percentage of females whose home-range centroids are encompassed by the intervention area in the first year of intervention (2023; % Females inside), as well as the average percentage increase in habitat suitability at intervened locations with an increase of 0.3 (% HSI increase).

Location	Fraction of males	Radius	Intervened Area (ha)	Area SPAs	% area of SPAs	% Females inside	% HS increase
SPAs	0,25	1	3.302	-	1	7	56
		3	16.484	-	4	18	58
		5	40.982	-	11	23	61
	0,5	1	6.219	-	2	13	56
		3	28.769	-	7	27	59
		5	67.645	-	17	31	62
	0,75	1	8.788	-	2	18	57
		3	38.452	-	10	32	59
		5	86.786	-	22	34	63
	1	1	11.157	-	3	23	57
		3	46.750	-	12	34	60
		5	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

The percentage increase in habitat suitability (data referring to an increase of 0.3 in suitability) varied between 56% and 70%, depending on the strategy. Higher values mainly occurred with an increase in the intervention radius, as males tend to concentrate and establish their home range centroid in areas of higher suitability. Therefore, the farther away from male locations, the lower the expected suitability of habitat cells, resulting in a higher percentage of increase in habitat suitability in those cells. When comparing strategies with and without spatial restrictions, it was observed that the percentage of increase in habitat suitability was higher when there were no restrictions, demonstrating that the average suitability of locations where males are found outside SPAs is typically lower.

When assessing the performance of different management strategies, it becomes evident that the majority of the 288 tested strategies failed to yield annual population growth rates >1 over the simulated 50-year period (Figure 5.3). Narrowing our focus to scenarios where intervention area selection was confined to SPAs, out of the 36 strategies considering different interventions in habitat suitability, only 14 resulted in population growth rates >1 in at least one of the anthropogenic mortality reduction scenarios. Among these strategies, only 3 achieved annual population growth rates >1 when no mitigation of anthropogenic mortality is considered (anthropogenic mortality = 0.06). These successful management strategies involved selecting intervention areas encompassing at least 5 habitat cells around home-range centroid at least 50% of the breeding males, with a suitability increase of at least 0.3, resulting in intervention areas covering a minimum of 67,645 ha. However, even in the most ambitious strategy, where all male locations within SPAs were targeted and resulting intervention area is 101,638 ha, the annual population growth rate remained <1 during the initial 10 years when no mitigation measures are implemented to reduce anthropogenic mortality. In this scenario, the annual population growth rate by year 50 remained below 1.02. This strategy is also the only approach capable of fostering population growth five years after intervention begins, a pattern observed exclusively in scenarios under complete mitigation of anthropogenic mortality. In these scenarios, the annual population growth rates after 20- and 30-years surpass 1.05.

In management strategies including mitigation of anthropogenic mortality (anthropogenic mortality = 0.04 and 0.02), together with intervention areas encompassing at least 5 habitat cells around at least 50% of the breeding males within SPAs, and considering an increase in habitat suitability of at least 0.3, annual population growth rates >1 were observed 20 and 10 years after intervention initiation. However, in scenarios where intervention area was confined to SPAs, population growth rates were always <1 when interventions were limited to 1 habitat cell radius around selected males. The same lack of population growth was observed in scenarios where only a 0.1 increase in habitat suitability was applied, regardless of the intervention radius and the percentage of selected individuals.

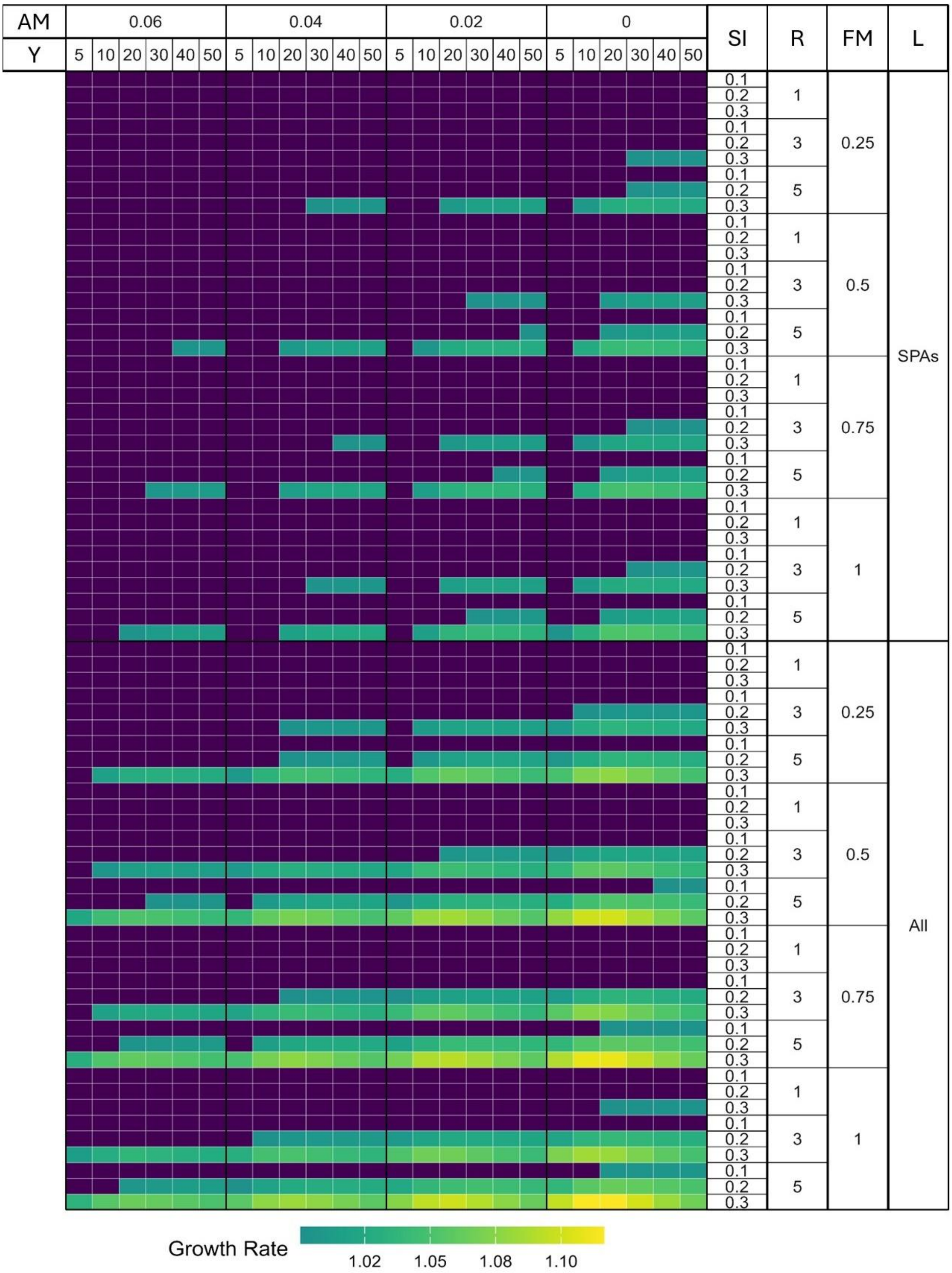

Figure 5.3 Annual growth rate over a 50-year period of the different management strategies simulated. AM – Annual anthropogenic mortality probability; Y - Years post-intervention; L – Location; FM – Fraction of males; R – Radius of intervention (in habitat cells); SI – Increase in habitat suitability. Strategies indicated in purple had population growth rates < 1.

When considering strategies where intervention area selection for suitability enhancement was conducted without spatial restrictions, most of them (20 out of 36) resulted in population growth in at least one of the anthropogenic mortality reduction scenarios. However, only 10 of these strategies yielded population growth rates >1 over the 50 simulated years in a scenario without mitigation of anthropogenic mortality. These successful strategies consistently implied an intervention radius of at least 3 habitat cells and an increase of habitat suitability > 0.2, resulting in an intervention area covering a minimum of 87,249 ha.

The only scenario capable of producing population growth rates >1 when intervention area selection was limited to 1 habitat cell radius around selected males was the scenario of total mitigation of anthropogenic mortality, with 100% of males selected, and an increase in habitat suitability of 0.3. Similarly, the only scenario capable of generating population growth rates >1 when the increase in habitat is limited to 0.1 was the one including total mitigation of anthropogenic mortality and considering a 5 habitat cell buffer (1250m radius) around all breeding males present in the study area.

Regarding the time required to achieve a population growth rate >1 without mitigating anthropogenic mortality and considering the smallest intervention area (215,813 ha), positive outcomes emerge after five years of initial intervention whenever 50% of the males are selected and a 5 habitat cell buffer is intervened for increasing habitat suitability by 0.3. Among the strategies including intermediate efforts for mitigating anthropogenic mortality, the one with the smallest intervention area (87,249 ha) resulting in population growth rates > 1 after five years of initial intervention requires considering 50% of the males and a 3 habitat cell buffer (750m radius) is intervened with a maximum increase in habitat suitability (0.3).

The highest annual growth values (> 1.1) were observed in strategies characterized by a total mitigation of anthropogenic mortality, where a minimum of 50% of the breeding males were selected, along with a 5 habitat cells intervention radius and an increase in habitat suitability of 0.3. However, it is important to note that even with habitat improvement interventions and, in some cases, mitigation of anthropogenic mortality, most of the scenarios tested (67%) still resulted in continued declining trends (annual growth < 1) even after 50 years of intervention (see Figure G.9.1 in Appendix G). Moreover, some of the scenarios (2%) may reach near-extinction levels (fewer than 50 individuals) within 30 years after the beginning of interventions (i.e., by 2053; see Figure G.9.2 in Appendix G). This percentage rises to 26% after 40 years and to 73% after 50 years post-interventions, with 5% of the scenarios leading to effective extinction after 50 years (i.e., by 2073). These strategies are generally characterized by reduced intervention radii, generally ranging from 1 to 3 habitat cells, increases in habitat suitability limited to 0.1 (or, in some cases 0.2), and scenarios where mitigation efforts for anthropogenic mortality are absent or reduced (i.e. anthropogenic mortalities of 0.06 and 0.04, respectively).

The results indicate that the most efficient strategies (in scenarios without reduction of mortality or minimal reduction) involve intervening in approximately 25% of the total breeding male locations, with a buffer of 5 habitat cells, resulting in an intervention area of about 127 thousand hectares. Alternatively, intervening in about 50% of breeding male locations, with a buffer of 3 habitat cells for the first 20 years (resulting intervention area of about 87 thousand hectares), and then increasing the buffer to 5 habitat cells (intervention area of 216 thousand hectares), also proves effective.

In scenarios with a higher mitigation of anthropogenic mortality (i.e., anthropogenic mortality = 0.02), the strategy of intervening with a 3 habitat cell buffer in 25% of breeding male locations for the first 20 years and subsequently expanding the area to 5 habitat cells appears to provide positive outcomes. However, the most efficient strategy would require intervening in 50% of breeding male locations. In a scenario of total reduction in anthropogenic mortality, the most efficient strategy to achieve population growth rates >1 appears to be intervening in 25% of breeding male locations present within the SPAs, with a 5 habitat cell buffer, representing an intervention area of about 41 thousand hectares.

However, despite being classified among the most efficient, most strategies highlighted in Figure 5.4 were unable to recover the population to the estimated numbers for 2005, even after 50 years. This is particularly evident in scenarios where improvements in habitat suitability are restricted to leks within the SPAs. In these cases, the only strategy achieving the number of little bustards recorded in 2005 was the scenario where anthropogenic mortality was completely eliminated, combined with the highest level of improvement in habitat suitability (i.e. 0.3) at 100% of the breeding male locations. However, with interventions targeting 75% of the breeding male locations across the entire region, the population could reach a population size close to that recorded in 2005 within 40 years, even without mitigating anthropogenic mortality. Similarly, with interventions at 50% of breeding male locations, this goal can be achieved within 50 years. If anthropogenic mortality reduction was considered, the 2005 population size could have been reached about 10 to 20 years earlier, depending on the percentage of mortality reduction.

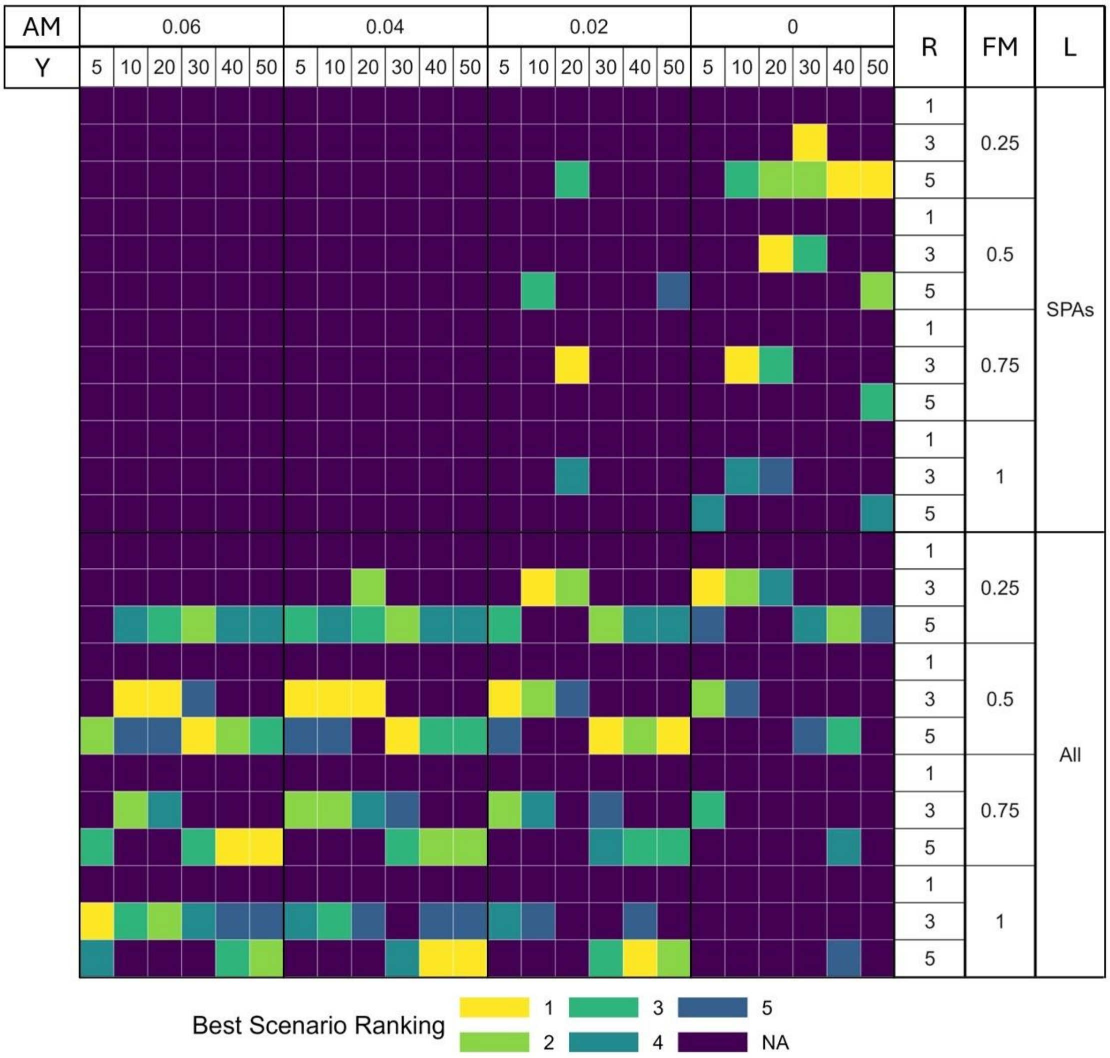

Figure 5.4 Ranking of the best management strategies simulated for each of the years with collected data and for the different anthropogenic mortality scenarios. This ranking was given by the ratio between the observed annual population growth and the intervention area allocated for enhancing habitat suitability. AM – Annual anthropogenic mortality probability; Y - Years post-intervention; L – Location; FM – Fraction of males; R – Radius of intervention (in habitat cells).

5.4 Discussion

Using an IBM for the little bustard population in the Extremadura region has proven effective in identifying the most cost-effective management strategies. This method provided deep insights into biological aspects needing intervention and optimized management strategies. The IBM approach allows for the assessment of how different strategies impact the overall population and evaluates its implementation costs (in terms of conservation efforts) through a cost-effectiveness analysis, facilitating the selection of the most appropriate strategy based on conservation objectives.

For the little bustard in Extremadura, our approach revealed that the most effective management strategies (i.e. those that minimize conservation efforts and maximize long-term species recovery), from those tested, involve coordinated actions aimed at enhancing habitat suitability and reducing anthropogenic mortality.

5.4.1 Model development

During model development, the calibration process confirmed our expectation of a positive correlation between habitat suitability and the survival of nests, chicks and adult little bustards. These findings align with prior studies documenting high nest failure rates due to nest destruction, predation, and abandonment in areas with low habitat suitability (Bravo et al., 2017; Bretagnolle et al., 2018; Cuscó et al., 2021). Additionally, the low productivity in these areas may be attributed to limited food availability and increased predation rates due to inadequate herbaceous cover, resulting in higher chick mortality (Lapiedra et al., 2011). The scarcity of resources in these areas appears to also impact adult females during the nesting and chick-rearing phases (Serrano-Davies et al., 2023), as evidenced by the reduced survival of breeding females compared to the rest of the adult population during the breeding phase (Figure 5.2). These differences in survival are in line with expectations considering the "exploded-lek" mating system of the species, where males do not contribute to offspring care (Serrano-Davies et al., 2023). Furthermore, during breeding, females concentrate their movements around the nest (Morales et al., 2014; Silva et al., 2014; Tarjuelo et al., 2013), which in cases of low habitat suitability, may further compromise their fitness, due to the scarcity of resources, during this already physiologically demanding period. The physiological condition of breeding females may be further compromised by increases in energy expenditure in cases of nest replacement, which is expected to occur due to the high rate of nest failure in low-quality habitats (Cuscó et al., 2021).

These results support the idea that lower survival of breeding females in areas of reduced habitat suitability is one of the main reasons for the observed skewed sex ratio in little bustard populations, as evidenced here by the sensitivity analysis. This highlights the breeding phase as the most critical period in the species' annual cycle, when individuals exhibit a greater dependence on habitat suitability. Increases in habitat suitability in this phenological phase are therefore expected to enhance both reproductive success and female survival by reducing energy expenditure and the risk of carry-over effects resulting from multiple breeding attempts, which are also likely to increase exposure to predation (Mañosa et al., 2022).

Sensitivity analyses also revealed that anthropogenic mortality is a key factor for the conservation of the little bustard, strongly influencing breeding success and overall sex ratio, and consequently affecting the population's annual growth rate and probability of extinction. These results are consistent with those published by Marcelino et al. (2017), which demonstrate that anthropogenic mortality may have a critical impact on the species, with values nearly as high as mortality attributed to predation.

Overall, our model successfully reproduced expected patterns in both socio-spatial organization and reproductive parameters, as well as the general population trend of the little bustard in Extremadura. The model validation process suggested that our model provides a reasonable approximation of the dynamics of the little bustard population in Extremadura, thereby supporting the inferences drawn from it.

5.4.2 Optimal management strategy

Although the analyses conducted in this study regarding the selection of the best management strategy for the little bustard in Extremadura constitute a preliminary theoretical exercise, there are significant insights that can be gleaned to assist in the development of an effective management conservation plan for the species. Most tested strategies were unable to produce population growth rates >1, even over a 50-year horizon, highlighting the inadequacy of isolated measures in achieving sustainable population growth rates (>1) over a 50-year horizon, and the challenges underpinning the conservation of the little bustard in Extremadura and across its distribution range. Furthermore, the possible near-extinction scenarios within a 30-year horizon and actual extinction within a 40–50-year horizon, as indicated by our simulations, emphasizes the urgent need for implementing targeted conservation measures for the species (see Figure G.9.2 in Appendix G). This highlights the critical importance of formulating conservation management strategies with a comprehensive, long-term scope, considering key ecological factors to the species. These strategies should prioritize actions aimed at halting the significant population decline observed in recent decades (García de la Morena et al., 2018, 2006), followed by concerted efforts to facilitate its recovery to viable population levels.

5.4.2.1 Manage just SPAs, or the species’ entire range?

Despite being one of the Spanish regions with the highest percentage of breeding males within SPAs, approximately 65% (Traba et al., 2022), our analysis reveals that a strategy focusing solely on implementing habitat suitability improvements within SPAs, without reducing anthropogenic mortality, may not be an effective conservation approach in Extremadura. Our findings suggest that, in these situations, reducing anthropogenic mortality is essential for a strategy to be efficient. Even with the implementation of both types of management measures, achieving population growth rates >1 over the 50 simulated years depends on the intensity of the implemented measures, with annual growth rates always relatively low when compared to strategies without spatial restrictions for increasing habitat suitability. On the other hand, efficient strategies without spatial restrictions are less dependent on the implementation of mitigation measures for anthropogenic mortality and require a lower effort to improve habitat suitability. However, it is noteworthy that the average suitability of male locations outside SPAs is generally lower compared to that within SPAs (Crispim-Mendes et al., 2024), which may indicate that the average intervention costs are likely to be higher outside SPAs compared to interventions carried out within them.

Our results also suggest that the selection of intervention sites for improving habitat suitability should also consider interventions for mitigating anthropogenic mortality, particularly within SPAs, where a large portion of the population congregates during the breeding season, and where intervention costs are expected to be lower. However, better outcomes are anticipated when interventions also extend to areas outside SPAs, prioritizing locations where the species persists at higher densities.

5.4.2.2 How much habitat should be managed?

Regarding the selection of intervention sites for improving habitat suitability, the method applied in our simulations utilizes the locations of breeding male individuals during the breeding season, namely the leks, assuming these areas should hold higher numbers of breeding females (Morales et al., 2014; Silva et al., 2014; Tarjuelo et al., 2013). Therefore, ensuring habitat quality and stability in these locations across years should significantly increase local densities (Silva et al., 2017) and the breeding success of little bustards (Morales et al., 2013). However, the skewed sex ratio favouring males and the lower survival rate of breeding females during the breeding phase emphasizes the importance of including females' settlement areas in the intervention sites for a successful management strategy. To achieve this, it is crucial to accurately define the most efficient intervention radius around male locations.

Our results demonstrate that the intervention radius should be relatively large. Strategies involving intervention in only a single habitat cell buffer (250m radius) around male locations yield much less favourable outcomes compared to strategies where buffers of 3 or 5 habitat cells (750m and 1250m radii respectively) are intervened. In fact, the only strategy with a single habitat cell intervention buffer resulting in population growth rates >1 implies intervention in all leks and complete elimination of anthropogenic mortality. Our cost-effective analysis of different management strategies in terms of population growth rate per intervention area, revealed that while strategies with a 3 habitat cells intervention buffer are sometimes selected in the top 5, these are usually associated with short to medium-term scenarios of intervention ranging from 5 to 30 years. Conversely, strategies considering 5 habitat cells intervention buffers tend to be more efficient in the medium to long term, in intervention scenarios spanning 30 to 50 years.

Although not considered in our cost-effective analysis, the percentage increase in habitat suitability tends to rise as the intervention buffer size increases. This indicates that as the distance from the centroid of male home ranges increases, the average habitat suitability decreases, leading to higher expected costs of habitat improvement interventions. Altogether, these results suggest that a more cost-effective strategy may involve a progressive implementation of habitat suitability improvements. This approach could start with a smaller intervention radius of approximately 750 m, which would be progressively expanded to about 1250 m, in accordance with local population growth. Such adaptive approach would have the advantage of reducing initial intervention costs and adjusting the conservation plan based on the species' population response. However, it is essential to consider that a realistic implementation of habitat suitability improvements should be carried out at the level of management units (land parcels). This approach allows for more precise and manageable interventions, fostering collaboration and agreements with landowners who play a crucial role in habitat conservation. Additionally, this method promotes long-term habitat stability by securing agreements that ensure consistent and sustainable habitat management practices.

Regarding the fraction of leks that should be intervened, our results indicate that the most efficient strategies involve intervening in approximately 50% of the leks within the study area. An exception occurs when anthropogenic mortality is completely eliminated. Under this scenario intervening in approximately 25% of the leks within the SPAs appears to be the most cost-effective solution. However, this decision should be made in consideration of the overall management approach, including factors such as the intervention buffer and spatial restrictions (SPAs vs. all areas), as well as the reduction of anthropogenic mortality and the intervention timeline.

5.4.2.3 How does the suitability need to be improved?

In our methodology, we considered three levels of suitability increase (0.1, 0.2, and 0.3) in the suitability index. This increment was applied uniformly to all selected intervention sites, regardless of their previous suitability. However, in a realistic scenario, most interventions would aim to improve medium to low suitability habitats, with the goal of implementing the most effective practices to maximize suitability increase. Although our approach is primarily conceptual, it enables us to assess the impact of various intervention levels on the population.

Our results reveal that marginal and intermediate gains in suitability (0.1 and 0.2) are insufficient to reverse the species' negative population trend without intervening in the majority of lek sites and significantly reducing anthropogenic mortality. Even in these scenarios, the annual growth rate values are much lower compared to scenarios with a suitability increase of 0.3. These findings reinforce the idea that when outlining agri-environmental measures, the focus must be on achieving optimal breeding habitat rather than partial improvements (Morales et al., 2013; Traba et al., 2022).

While habitat preferences at the model scale for males and females are considered similar (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 regarding habitat preferences by females. Therefore, when designing habitat management strategies aimed at improving suitability, it's essential to account for both male and female habitat preferences.

5.4.2.4 Anthropogenic mortality

One of the main insights derived from our results is that a management strategy solely aimed at enhancing breeding habitat suitability, without addressing anthropogenic mortality, is unlikely to achieve satisfactory outcomes. This pattern was also observed 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 an acceptable level of conservation effort from stakeholders, it is crucial to reduce both natural and anthropogenic mortality.

In our analysis, we addressed the reduction of anthropogenic mortality by applying scenarios with a uniform probability across the study area, ranging from no reduction to complete elimination. While this method 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 step for improving our model involves explicitly integrating the electrical grid of the study area, along with the probability of collision associated with each type of powerline. This adjustment would facilitate the testing of various mitigation strategies, such as line marking or burial, which have been implemented in different regions with varying efficiencies and potential cost disparities (Silva et al., 2023a).

5.4.2.5 Best strategy

One of the most critical aspects and an initial constraint in devising a management strategy is reconciling conservation objectives with the implementation costs in terms of conservation efforts, which are reflected in monetary expenses (Zurell et al., 2022). It's important to prioritize interventions that maximize conservation impact within financial constraints, with effective cost management ensuring that conservation efforts are both impactful and sustainable in the long term (Tallis et al., 2021).

Given the conceptual nature of our exercise, we also explored unrealistic management strategies that involve substantial monetary investment and impractical implementation, such as habitat improvement interventions at 100% of breeding male locations or the complete elimination of anthropogenic mortality. However, examining these alternatives provides valuable insights into the population's potential recovery under optimal conditions, serving as a benchmark for evaluating more feasible management strategies.

The analysis of the top-rated simulated strategies allows us to establish some guidelines for developing a management strategy for the little bustard in Extremadura. In scenarios without significant reduction in anthropogenic mortality, or with minimal reduction, our findings suggest that the most effective approaches entail targeting approximately 25% of male locations for habitat improvement within a buffer of 5 habitat cells, resulting in an intervention area of approximately 127 thousand hectares. Alternatively, intervention efforts could focus on around 50% of male locations, with a buffer of 3 habitat cells over the initial 20 years, covering an intervention area of about 87 thousand hectares. Subsequently, expanding the buffer to 5 habitat cells would increase the total area to 216 thousand hectares. Given the extensive coverage of 5 habitat cells buffers, a strategic approach may involve selectively expanding intervention areas based on the species' population response.

In scenarios with higher reduction of anthropogenic mortality, the strategy of intervening within a 3 habitat cells buffer in 25% of male locations during the initial 20 years, and expanding the area to 5 habitat cells subsequently, appears a promising alternative. However, the most efficient approach seems to be the same intervention buffer size, but applied to 50% of the males' locations. When anthropogenic mortality is mitigated, the most effective strategy for achieving population growth appears to be the intervention of 25% of the males' locations within the SPAs, with a 5 habitat cells buffer, representing an intervention area of approximately 41 thousand hectares.

Our results reveal, however, that the evaluation of management strategies should primarily focus on the expected outcomes rather than just their efficiency. As demonstrated in Figure G.9.2 of Appendix G, if the objective is to restore the population to the estimated numbers in 2005, several management strategies deemed efficient (i.e. yielding an annual population growth rate exceeding 1) would fail to produce the desired results, even over the long term.

When evaluating the costs of implementing a management strategy, it is also important to consider that intervention costs for anthropogenic mortality reduction may be high, even though they are incurred only once, while interventions for habitat improvement tend to be continuous over time. Therefore, finding the optimal balance between both is essential. In this regard, an improvement that can be made in our model is the use of realistic estimates of intervention costs for different measures. In designing a management strategy, it is also important to consider not only its cost-effectiveness but also the conservation objectives, such as the target population size to be achieved over time. Consequently, it's important to note that several strategies, especially the less ambitious ones, could entail a delay between the start of interventions and the reversal of the population trend. Finally, while a model like the one presented here can be extremely valuable in designing a management strategy for a threatened species, its implementation will always require an adaptative strategy, with regular population monitoring to track population response and allow adjustments to the applied methodology (Zurell et al., 2022).

5.4.3 Final Considerations and Future Prospects

The model developed in this study significantly enhanced our understanding of key aspects of the little bustard's biology that impact its survival, allowing the identification of most critical areas for targeting conservation actions in Extremadura. Additionally, it enabled the testing of various management strategies, helping to determine the most effective interventions for implementing a cost-effective conservation plan for the species. While some calibrated values and emerging model results still require confirmation, this model undoubtedly represents the best and most comprehensive tool currently available to assist in the species' conservation efforts. This approach highlights the huge potential of individual-based models (IBMs) as a support tool for understanding and managing complex ecological and demographic processes (Stillman et al., 2015).

The findings presented in this study serve as a cornerstone for future research, highlighting areas where our model can be enhanced to better reflect reality and improve its utility as a management tool. Enhancing the model's realism and predictive accuracy is paramount to its effectiveness in guiding conservation efforts. To achieve this, several key improvements have been identified. Firstly, incorporating data on migration and dispersal patterns, as well as habitat suitability maps specifically tailored for females would ensure that management strategies adequately consider the needs of both sexes. Furthermore, predictive habitat suitability maps for future scenarios should include alternative climate change projections, and account for inter-annual variation, in order to provide a more comprehensive assessment of habitat suitability under changing environmental conditions.

Regarding the simulation of management strategies, it would be important to include spatially explicit representations of anthropogenic mortality sources, such as power lines, to accurately assess their impact on population dynamics. Incorporating information on management units would also enhance realism, enabling the evaluation of conservation efforts at a finer spatial scale. Other conservation strategies could also be added, as captive breeding and release, as is being done in France (Attié et al., 2022). Moreover, including the average financial costs associated with each intervention type would facilitate a more thorough cost-benefit analysis, aiding decision-makers in selecting the most efficient and economically viable strategies. Finally, introducing the capability to test dynamic management strategies over time would allow for adaptive approaches, enabling adjustments based on observed population responses and ensuring the long-term effectiveness of conservation efforts.

One mortality factor not considered in the model, which is believed to have a significant impact on the population, is the scarcity of arthropods due to widespread herbicide and pesticide application (Bretagnolle et al., 2011). Arthropods are the primary component of chick diet during their first weeks of life (Jiguet, 2002), and their absence or scarcity greatly compromises chick survival (Inchausti and Bretagnolle, 2005; Morales et al., 2005a). While increasing habitat suitability may result in greater arthropod availability, research suggests that this relationship is more strongly influenced by the use of herbicides and pesticides rather than vegetation structure alone (Tarjuelo et al., 2019). Considering the species' strong philopatry, especially regarding breeding sites, this factor could lead to local extinction of the species in a relatively short period due to the lack of population renewal and potential increase in female mortality due to increased energy expenditure during reproduction (Bretagnolle et al., 2011).

Another noteworthy aspect is that interventions aimed at mitigating anthropogenic mortality and improving breeding habitat suitability for the little bustard are expected to have significant positive impacts on other steppe species sharing similar ecological requirements, such as the great bustard (*Otis tarda*) and the pin-tailed sandgrouse (*Pterocles alchata*). As described by Morales et al. (2023), this underscores the potential of the little bustard as an umbrella species, which can aid in better targeting conservation efforts, particularly for species linked to cereal and grassland-dominated landscapes.

In summary, this model represents a pivotal step in the development of a tool that adds value to supporting the formulation of management strategies for the little bustard (and potentially to other grassland birds) in Extremadura. Furthermore, it serves as an important tool for assessing the impact of anthropogenic mortality factors such as power lines or habitat loss due to solar farms. We therefore recommend that, whenever sufficient knowledge on the biology and ecology of a species is available, IBMs may provide an important tool to evaluate how populations will respond to different management strategies.

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Author contributions

All authors contributed critically to conceiving the ideas and designing the methodology. TCM prepared the data, developed the model and model documentation, analysed the results, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval.

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5.5 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

Attié, C., Munoz, A., Chevasson, O., Bretagnolle, V., 2022. Captive Breeding, Handling and Care, and the Impact of Releases on Wild Populations, in: Bretagnolle, V., Traba, J., Morales, M.B. (Eds.), Little Bustard: Ecology and Conservation. Springer Nature, Switzerland, pp. 193–223. https://doi.org/10.1007/978-3-030-84902-3

Augusiak, J., Van den Brink, P.J., Grimm, V., 2014. Merging validation and evaluation of ecological models to “evaludation”: 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. Journal of Sustainable Agriculture 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 Internationa, Cambridge, UK. BirdLife International.

BirdLife International, 2021. European Red List of Birds. Luxembourg: Publications Office of the European Union. https://doi.org/10.2779/959320

Boult, V.L., Quaife, 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 Conservation and Ecology 12. 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. Environmental Modelling & 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

De Juana, E., Martínez, C., 1996. Distribution and conservation status of the little bustard *Tetrax tetrax* in the Iberian Peninsula. Ardeola 43, 157–167.

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., Arneth, 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., Razzaque, 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 (1979) 366. https://doi.org/10.1126/science.aax3100

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., Bartell, 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., Decleer, K., Dixon, K.W., 2019. International principles and standards for the practice of ecological restoration. Second edition. Restor Ecol 27, 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

Grimm, V., 2005. Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology. Science (1979) 310, 987–991. https://doi.org/10.1126/science.1116681

Grimm, V., Augusiak, 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., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, 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. Journal of Artificial Societies and Social Simulation 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. Journal of Applied Ecology 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., 2002. Arthropods in diet of little bustards *Tetrax tetrax* during the breeding season in western France. Bird Study 49, 105–109. https://doi.org/10.1080/00063650209461253

Jiguet, F., Arroyo, B., Bretagnolle, V., 2000. Lek mating systems: a case study in the Little Bustard *Tetrax tetrax*. Behavioural Processes 51, 63–82. 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. Behavioural Processes 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., 2017. 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 (1979) 338, 946–949. https://doi.org/10.1126/science.1229803

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., 2022a. 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., 2022b. An update on the conservation status of the Little Bustard *Tetrax tetrax*: global and local population estimates, trends, and threats. Bird Conserv Int 32, 337–359. https://doi.org/10.1017/S0959270921000423

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., Morena, E.L.G. de la, 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, Á., 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 Oecologica 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

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 edi. ed. Princeton University Press, New Jersey, United States of America.

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 Geobotanica 15, 5–432.

Salecker, J., Sciaini, M., Meyer, K.M., Wiegand, K., 2019. The NLRX R 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., Arroyo, B., Marques, A.T., Morales, M.B., Devoucoux, P., Mougeot, F., 2022. Threats Affecting Little Bustards: Human Impacts, in: Bretagnolle, V., Traba, J., Morales, M.B. (Eds.), Little Bustard: Ecology and Conservation. Springer Nature, Switzerland, pp. 243–272. https://doi.org/10.1007/978-3-030-84902-3

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., 2023a. 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., Marques, A.T., Carrapato, C., Machado, R., Alcazar, R., Delgado, A., Godinho, C., Elias, G., Gameiro, J., 2023b. A nationwide collapse of a priority grassland bird related to livestock conversion and intensification. Sci Rep 1–10. https://doi.org/10.1038/s41598-023-36751-8

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

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

Tarjuelo, R., Morales, M.B., Arribas, L., Traba, J., 2019. Abundance of weeds and seeds but not of arthropods differs between arable habitats in an extensive Mediterranean farming system. Ecol Res 34, 624–636. https://doi.org/10.1111/1440-1703.12029

Thiele, J.C., Kurth, W., Grimm, V., 2014. Facilitating Parameter Estimation and Sensitivity Analysis of Agent-Based Models: A Cookbook Using NetLogo and "R." Journal of Artificial Societies and Social Simulation 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., Rasolofoson, 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

van der Vaart, E., Beaumont, M.A., Johnston, A.S.A., Sibly, 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

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., Kapitza, S., Bocedi, G., Travis, J., Fandos, G., 2022. Spatially explicit models for decision-making in animal conservation and restoration. Ecography 2022, 1–16. https://doi.org/10.1111/ecog.05787

Chapter 6

General discussion

Chapter 6 – General discussion

6.1 Overview - Agriculture development, energy transmission and biodiversity conservation

Human activities have historically influenced wildlife in multifaceted and complex ways (Powers and Jetz, 2019; Tilman et al., 2017). However, the significant growth and expansion of human populations and change in consumption patterns have led to the unprecedented conversion and degradation of natural habitats, alongside the proliferation of anthropogenic infrastructures (IPBES, 2019). These changes result in spatio-temporal alterations in landscapes, exposing wildlife to additional mortality factors, which may significantly impact ecosystems and biodiversity, posing serious threats to the survival of numerous species (Acevedo-Whitehouse and Duffus, 2009; Haddad et al., 2015).

To safeguard ecosystem functioning and ensure the survival of species impacted by human activities, ecologists need to respond with robust conservation strategies and tools to guide land-use policies and propose cost-effective management alternatives aimed at achieving sustainable development goals (Schwartz et al., 2018). Specifically, in urgent conservation scenarios, swift and well-informed actions are imperative, supported by a comprehensive understanding of how wildlife will respond to anthropogenic threats and conservation efforts (Heinrichs et al., 2018).

This issue is particularly pressing in the Mediterranean region, which has faced significant challenges over the last decades, partly due to the implementation of the Common Agricultural Policy (CAP), aimed at enhancing food self-sufficiency (Reif and Vermouzek, 2019; van Vliet et al., 2015). Substantial habitat fragmentation, degradation and simplification have occurred due to the conversion of natural landscapes into agricultural land, coupled with the intensification of crop and livestock production in already agriculturally used areas (Benton et al., 2003). These trends are particularly concerning for endangered species, requiring the identification of effective conservation strategies, optimal implementation sites, and the necessary level of intervention to stabilize populations (Zurell et al., 2022). Besides habitat and land use changes linked to agricultural intensification, other human activities also resulting in increased mortality risk for many farmland species, include direct percussion, pollution, climate change, and the development of transport and distribution infrastructures, such as roads, wind turbines, and power lines (Loss et al., 2015). For birds, one of the most significant sources of anthropogenic mortality is interaction with power line infrastructures, which tend to proliferate due to increasing demand for electricity (Bernardino et al., 2018; Loss et al., 2015). Depending on species-specific features such as morphology, sensory perception, flocking and flight behaviour, and individual conditions, different bird species may face varying levels of mortality risk from these infrastructures (Bernardino et al., 2018; Marques et al., 2014). For instance, raptors are particularly vulnerable to being struck by rotating wind turbines (Beston et al., 2016) or electrocuted on power lines (Janss, 2000). Conversely, poor fliers like bustards (Otididae) are at a higher risk of colliding with power lines (Janss, 2000). Overall, it is therefore crucial to understand how habitat and land use changes may affect biodiversity in Mediterranean farmland, and how infrastructure development impacts avian populations with different biological and ecological traits.

These imperatives highlight the growing importance of predictive ecology in contemporary wildlife management, aimed at optimizing biodiversity conservation outcomes (Mouquet et al., 2015; Pennekamp et al., 2017). This thesis explored a diverse array of technological, methodological, and scientific advancements to assess the response of endangered vertebrate species to various anthropogenic impacts, with the overarching goal of informing management actions and supporting conservation planning efforts. By investigating the conservation challenges faced by three distinct threatened species native to the Mediterranean region and occurring in the Iberian Peninsula, this thesis examined some of the most pressing anthropogenic impacts of our time, such as human-induced spatio-temporal habitat changes and anthropogenic mortality.

This chapter aims to summarize the key results and conclusions derived from the case studies discussed in the preceding chapters, emphasizing their significance in terms of conservation implications. It also discusses the potential usefulness and effectiveness of Individual-Based Models (IBMs) for conservation planning and offers suggestions for future research.

6.1.1 Research questions

Species distributions are profoundly shaped by historical environmental changes, as well as by their inherent ability to adapt to these changes, making them highly susceptible to both direct and indirect human-induced spatio-temporal habitat alterations (Boivin et al., 2016). Understanding the impacts of these anthropogenic changes on species persistence is pivotal for informed and effective wildlife conservation and restoration planning (Quintero et al., 2023).

This thesis comprehensively explored various dimensions of this issue, exemplified through the case studies focusing on threatened vertebrate species in Mediterranean farmland, including the

Cabrera vole (Chapter 2), the Bonelli´s eagle (Chapter 3) and the little bustard (Chapters 4, and 5). In particular, the thesis aimed to assess and compare the population performance of different taxa in different scenarios of habitat and landscape change related to human activities, infrastructure development, and conservation efforts to mitigate putative threats.

Throughout this thesis, we investigated the demographic impacts of spatio-temporal habitat changes, with particular emphasis on how patch spatial attributes and time to disturbance influence the emergence of source local populations within ephemeral habitats in highly dynamic landscapes (Chapters 2). Additionally, we explored how environmental changes across space and time impact the long-term population trends of natal philopatric farmland species (Chapters 4 and 5). The synthesis of findings from these studies provided critical insights for developing species conservation and management strategies amidst ongoing environmental change and anthropogenic pressures in the systems they occur.

Furthermore, this thesis explored the impacts of anthropogenic mortality on bird populations, specifically focusing on the effects of power lines. We investigated the demographic impacts of electrocution on territorial raptors (Chapter 3) and collisions with these structures by poor fliers like bustards (Chapter 5). These studies offer essential insights into how infrastructure development impacts avian species, highlighting the importance of incorporating species-specific behaviours and vulnerabilities into conservation strategies.

6.2 Synthesis of main findings

6.2.1 Effects of land-use change on threatened species in Mediterranean farmland

Chapter 2 delved into the demographic effects of dynamic landscapes on local populations. Many species presenting metapopulation-like spatial structure and dynamics have adapted to thrive in naturally dynamic ecosystems with frequent habitat turnover (e.g. in fire-prone areas and regions subject to severe water imbalances, droughts, or floods). However, the escalating frequency and intensity of human-induced disturbances (e.g. as agricultural intensification, shifts in land use, and climate change) pose significant challenges to their survival. Species inhabiting networks of ephemeral patches often exhibit source-sink dynamics, where some populations act as temporary sources between initial colonization and the disappearance of the patch due to disturbance (e.g. Frouz and Kindlmann, 2015; Reigada et al., 2015). Identifying specific habitat patch characteristics that enhance their potential to function as temporary sources is crucial for optimizing conservation strategies in these dynamic environments.

Our research on Cabrera voles in highly dynamic Mediterranean farmland revealed that variations in patch size, internal quality, connectivity, and lifespan can lead to significant temporal and spatial changes in the source-sink status of local populations. Patch size emerged as the most crucial attribute for population self-sustainability and potential contribution to other patches, especially in the first year after colonization. Larger patches initially behave as sinks but transition into sources over time, depending on habitat quality and connectivity. Patch internal quality showed a positive correlation with local population self-sustainability and their potential contribution to other patches, particularly after about three vole generation times (approximately one year) since initial colonization, when combined with the positive effects of patch size and connectivity. This highlights the critical role of habitat longevity in enabling local populations to establish and maintain themselves as temporary sources within metapopulations. Conversely, short patch lifespans (less than about three vole generation times) significantly limit local population self-sustainability and their potential to contribute to other patches. Our findings further support that the source-sink potential of individual patches cannot be accurately inferred from local habitat quality alone (Pulliam, 1988). Complex interactions with other spatial attributes, such as patch size and connectivity, play a significant role in the emergence of source populations. Populations in small, poorly connected patches were generally more vulnerable to stochastic extinction, even within high-quality habitats, highlighting the importance of considering multiple spatial factors in conservation planning.

In summary, our study emphasizes the necessity of considering patch spatial and temporal attributes when assessing the source-sink dynamics of local populations in heterogeneous environments. This comprehensive approach is essential for understanding and conserving species in landscapes undergoing rapid environmental changes and disturbances.

Chapters 4 and 5 focussed on long-term population trends of partially migratory farmland species with natal philopatric behaviour, using the little bustard in Extremadura, Spain, as a case study. Chapter 4 employed Species Distribution Models (SDMs) to elucidate on the drivers of little bustard distribution across key phenological phases (winter, breeding, and post-breeding) and to quantify spatio-temporal variations in habitat suitability. Building upon these findings, Chapter 5 employed a spatially explicit Individual-Based Model (IBM) based on the SDMs from Chapter 4. This IBM realistically integrated diverse behaviours of the little bustard in Extremadura, offering valuable insights into the species' response to environmental changes and the impacts on its population dynamics.

The results of Chapter 4 highlighted significant fluctuations in habitat suitability over time, particularly during the breeding and post-breeding phases, with an overall long-term decline in suitable habitat availability for little bustards in the Extremadura region. These findings strongly suggest that fluctuations in habitat suitability during critical phases are primary drivers of the observed negative population trend in the region.

Chapter 5 further corroborated these conclusions by using an IBM developed to accurately replicate the population trajectory of the little bustard in Extremadura. The IBM results confirmed that habitat changes, particularly reductions in suitable habitat during critical phases, are indeed a major cause of the population decline observed over the study period (2005 – 2022). Alarmingly, the model projections indicate that if current population trends persist, the little bustard could face extinction in the Extremadura region within the next 30 to 40 years.

However, the IBM simulations also provided solutions, suggesting that targeted conservation actions aimed at increasing habitat suitability and ensuring its long-term stability could reverse population decline. Simulations conducted with the IBM to identify the most effective conservation strategies demonstrated that increasing habitat suitability in lekking areas during the breeding phase could be sufficient to halt and reverse the population decline. Furthermore, the most effective strategies typically involve larger intervention buffers around leks, allowing females to nest in more suitable areas, which results in better reproductive outcomes. It also became evident that focusing interventions solely on leks within Special Protection Areas (SPAs) is insufficient to reverse the population trend. Habitat quality improvements must extend beyond these protected areas to be effective.

The IBM calibration process provided insights into the correlation between survival rates in various life cycle phases and the suitability of the habitats they occupy, highlighting the paramount importance of habitat quality for the species' survival. Notably, there is a strong correlation between habitat suitability and the survival of nests and chicks during their first seven weeks of life, as well as the survival of breeding females during the reproductive phase. These findings emphasize the importance of conservation strategies focused on maintaining and enhancing habitat quality, particularly during critical periods like breeding seasons, to support the persistence and recovery of vulnerable species like the little bustard in dynamic agricultural landscapes.

6.2.1.1 Conservation implications

Our IBM, developed through the Cabrera vole case study (Chapter 2), highlights that the emergence of source populations within ephemeral habitat patches depends on several key spatial attributes: patch size, internal quality, connectivity to other patches, and patch lifespan. Although the IBM did not account for specific sources of disturbance leading to patch destruction, it is crucial to consider whether such disturbances cause mortality among patch occupants or allow individuals to disperse to other patches. If patch destruction results in occupant mortality, larger, high-quality patches could function as ecological traps, attracting and housing a significant number of individuals who might perish before the patch can act as a source if destroyed shortly after colonization. Conversely, if patch destruction does not directly lead to occupant mortality, connectivity with other patches becomes crucial. Reduced connectivity could result in high mortality during dispersal, as individuals may struggle to find new suitable habitats, thereby increasing the risks associated with patch destruction. Therefore, ensuring the persistence of large, high-quality patches with adequate connectivity is essential, not only for supporting temporary source populations and facilitating dispersal and colonization but also for enhancing overall metapopulation resilience in fragmented landscapes. Therefore, effective conservation management strategies should specifically focus on minimizing disturbances such as agricultural activities and severe droughts in large, well-connected, high-quality patches.

In the case of the little bustard, insights from SDMs in Chapter 4 underscored the species' distinct ecological requirements across different phenological phases and the varying distribution of suitable habitats. This emphasizes the necessity of holistic conservation planning that takes into account the species' annual cycle. Particularly concerning is the decline in habitat suitability during the breeding phase over time, highlighting the critical need to concentrate conservation efforts during this pivotal period.

Chapter 5 further elucidated optimal conservation strategies using our IBM, demonstrating that enhancing habitat suitability within lekking areas during the breeding phase effectively mitigates population decline. However, the model indicates that the existing network of Special SPAs in Extremadura is insufficient to sustain the breeding population. Therefore, conservation efforts to enhance suitability must extend beyond SPAs to encompass leks throughout the entire study area. The results also suggest that to restore the population to the numbers recorded in 2005 (the year of the first national census) it will also be necessary to reduce anthropogenic sources of mortality.

6.2.2 Impacts of electricity power line transmission on threatened birds

Besides the impacts of rapid environmental changes related to agricultural activities, many species, particularly birds, are also impacted by anthropogenic mortality due to electrocution in power lines. This source of mortality may be particularly significant in many raptor populations

(González et al., 2007; Martínez et al., 2016; Mojica et al., 2018). Mortality occurs when their bodies simultaneously contact exposed energized wires or components with different electrical potentials (Bevanger, 1998, 1994). In Chapter 3, we used the case study of the Bonelli's eagle (*Aquila fasciata*) to explore the demographic effects of electrocution with power lines. For this purpose, we developed an IBM, which, although inspired by this case study, can be applied and generalized to different species and sources of additional mortality.

Our model results revealed that, in territorial species, the population impacts of electrocution are influenced by the spatial distribution of mortality risk across territories, the level of mortality risk, and the life stages affected (territorial vs. non-territorial individuals). In particular, our findings indicated that population-level impacts increase substantially under higher mortality risks. Interestingly, impacts are lower when these risks are concentrated in specific territories rather than spread across all territories. The highest population impacts occur when both territorial and non-territorial individuals are exposed to anthropogenic mortality risks, with a higher impact observed when only non-territorial individuals are affected compared to territorial individuals. This suggests that non-territorial individuals may play a crucial role in sustaining the population when mortality is concentrated on territorial adults. This is likely due to territorial behaviour, where increased mortality risk within territories affects only the survival of the two breeding adults, while the same level of exposure to additional mortality risk can affect multiple non-territorial individuals using the same patch.

Our results also indicated that, over time, territories with low to intermediate mortality risk are associated to a greater number of bird deaths compared to those with higher mortality rates. These areas act as ecological traps, continuously attracting non-territorial birds to settle and replace the territorial birds that die. Conversely, territories with higher mortality levels tend to become vacant of territorial birds as time progresses, a trend supported by empirical evidence from populations of this species (Carrete et al., 2002). This phenomenon leads non-territorial birds to be attracted to disperse into these patches, which also appear to function as ecological traps.

In the case of bustards, their medium- to large-sized bodies, combined with relatively short wings and tails, result in low flight manoeuvrability (Janss, 2000; Rayner, 1988), making them especially prone to collisions with power lines. For the little bustard, various anthropogenic mortality factors have been identified, such as illegal hunting and vehicle collisions. However, the most significant factor is collision with power lines, which accounts for the death of 3.4 - 3.8% of adult birds per year, one of the highest rates ever recorded for a particular species (Marcelino et al., 2017).

In Chapter 5, one feature included in our spatially-explicit IBM for the little bustard in the Extremadura region, Spain, was the probability of mortality due to anthropogenic causes. Although the model does not explicitly include the spatial source of anthropogenic mortality or differentiate its causes, the experiment conducted to identify optimal conservation strategies predominantly considered mortality due to collisions with power lines. The results of this experiment indicated that the complete recovery of the species is only feasible by reducing anthropogenic mortality. This conclusion aligns with a study conducted in Catalonia, Spain, which emphasized the importance of reducing both natural and anthropogenic mortality to ensure the long-term viability of the little bustard (Mañosa and Bota, 2023).

It is noteworthy that, although previous studies found that little bustards avoid the proximity of power lines during the breeding season (Silva et al., 2010) and summer (Lourie, 2016), the distance to power lines was not a relevant factor in the SDMs we developed for the three phenological phases of the species (Chapter 4). Therefore, it is expected that there is limited effect of these infrastructures, depending on the type of structure (transmission or distribution) and environmental context. A similar result was found in the selection of stopover sites by Alonso et al. (2019), who hypothesized that the species may not be able to see power lines in poor lighting conditions, as they arrive mostly late at night to the stopover locations.

6.2.2.1 Conservation implications

Overall, the results presented in Chapters 3 and 5 illustrate the significant impact that anthropogenic mortality due to power lines can have on wildlife populations, potentially leading to their extinction. In the case of the little bustard (Chapter 5), our findings suggest that implementing measures to partially mitigate anthropogenic mortality, alongside efforts to enhance habitat suitability, could potentially reverse the species' negative population trend in Extremadura and stabilize it. Conversely, for the Bonelli’s eagle (Chapter 3), the results indicate that each breeding territory should be treated as a unit where all existing pylons must be addressed when implementing mitigation actions to avoid creating ecological traps. Furthermore, the results emphasize the importance of considering both breeding and pre-adult settlement areas when planning measures to mitigate electrocutions.

While underground cabling and rerouting are the only methods that entirely eliminate the risk of bird electrocution and collision, there are currently cost-effective alternatives to mitigate these problems (Bernardino et al., 2018). For mitigating electrocutions, retrofitting distribution lines with insulated conductors and implementing safer designs that prevent the electrocution of large raptors has been successfully carried out worldwide, significantly reducing the risk for various raptor species (Chevallier et al., 2015; López-López et al., 2011). To address bird collisions, wire-marking is currently the most widely used mitigation measure due to its effectiveness and relatively low implementation costs (Bernardino et al., 2018; Lobermeier et al., 2015), reducing bird collisions with power lines by an average of 50%. However, this tends not to be the case for bustards, with conventional power markers having residual effect on reducing collision mortality (Silva et al., 2023).

In conclusion, the evidence presented in this thesis highlights the critical importance of addressing anthropogenic mortality through practical and scalable mitigation measures. By adopting a holistic approach that includes both habitat management and direct interventions to reduce mortality risks, we can significantly improve the conservation outcomes for species affected by power lines. This integrated strategy is vital for ensuring the long-term persistence of vulnerable wildlife populations in increasingly human-dominated landscapes.

6.2.3 Use of technological developments in conservation planning

Throughout this thesis, various technological resources have been used, whose advancements over the past few decades have elevated ecology and conservation planning to a new level. These advancements have enabled the collection of data with unprecedented resolution and the implementation of more complex analytical methodologies. One resource that has significantly evolved and revolutionized the study of movement ecology is the development in animal tracking technology. The data obtained through GPS trackers, which provide high temporal and spatial resolution data throughout the birds' different phenological stages, have been fundamental. This data allows for the inclusion of realistic movement rules and spatio-temporal organization in our models. This type of data was particularly important in Chapter 2 for defining complex socio-spatial organization rules within the patch for the Cabrera vole, and in Chapters 4 and 5 for developing the SDMs of the little bustard, defining migration and dispersal movements, and classifying the various migratory strategies in the IBM.

Another technological resource that has seen significant advancements is remote sensing. The use of information provided by this resource was crucial in the works presented in Chapters 4 and 5, especially in the development of the SDMs and in projecting habitat suitability maps for the little bustard across different phenological phases. The high spatial and temporal resolution currently offered allowed us to create maps with the necessary detail for our studies. The results presented in Chapter 4 highlight the benefits of using this type of product compared to more common ones like CORINE Land Cover. Remote sensing data are also relevant for capturing the structural complexity of habitats through landscape complexity metrics and for capturing the dynamism of the annual cycle and inter-annual variability through dynamic variables.

Critical to integrating animal tracking and remote sensing information are the algorithms used for creating SDMs. In our case, in Chapter 4, we opted to use machine learning algorithms, specifically the Random Forest algorithm. This methodology proved to be highly efficient, allowing the production of high-performance SDMs, as demonstrated through various accuracy metrics. This is just a small example of the potential that machine learning methods currently play in ecology and conservation planning, with significant advancements expected in this area in the coming decades with the emergence of new algorithms and applications. To take advantage of such techniques and others of high computational complexity, advancements in computational resources have been essential. The increasing availability of computational power and democratization of access to high-performance computing have revolutionized the way science is conducted today, enabling the analysis of big data and the implementation of extremely complex models.

A type of model that has gained prominence over the past few decades and has greatly benefited from advancements in computational resources is the Individual-Based Modelling. This model type, focusing on simulating the behaviour of individuals/agents and the interaction and diversity of these behaviours to make population behaviour emerge, offers an innovative approach with significant application potential in ecology and conservation planning. This feature allows the inclusion and exploration of the natural stochasticity present in natural systems, often ignored in population models, and enables the integration of different information sources such as SDMs and census and telemetry data, as demonstrated in Chapter 5.

As evidenced throughout this thesis, these models provide ecologists, conservationists and stakeholders with a highly versatile tool that can include various levels of complexity and realism according to the intended purpose. In Chapters 2 and 3, IBMs were used to conceptually explore different conservation-related issues. Although inspired by specific case studies, the results and insights from these two models are generalizable to various species with similar physical or behavioural characteristics. Conversely, the IBM presented in Chapter 5 is highly specific to a particular species, including habitat suitability maps developed specifically for the species (Chapter 4), used as a basis for defining the location and seasonal movements of each individual, as well as their survival. This type of application of IBMs, where complex behavioural rules are implemented considering the spatio-temporal dynamics of the landscape, provides these models significant potential to be used as management support tools, allowing for realistic testing of the expected population trajectories under different management scenarios. This approach can be particularly valuable for critically endangered species, especially when there are too few individuals or insufficient time to conduct field experiments (Heinrichs et al., 2018).

6.3 Final remarks for future research

Throughout this thesis, we used IBMs to elucidate critical aspects of how species, driven by their biology and ecology, respond to anthropogenic pressures. These pressures encompassed diverse impacts such as land use changes, habitat destruction, and the proliferation of power lines driven by escalating energy demand. Our investigations demonstrated how IBMs can significantly enhance conservation planning by improving effectiveness and optimizing cost-benefit outcomes. However, numerous avenues for future research remain unexplored, many of which were extensively discussed across the thesis and are summarized below.

In the study of human-induced spatio-temporal habitat changes in highly dynamic landscapes (Chapter 2), our IBM focused on testing the influence of patch characteristics and lifespan on the emergence of source local populations within ephemeral habitat patches. Future enhancements could include adapting the model to explicitly represent metapopulations, enabling exploration of landscape configuration effects and anthropogenic barriers on metapopulation persistence. Additionally, the model could incorporate varying probabilities of mortality associated with patch destruction, linked to disturbance type and intensity. Exploring mortality during dispersal movements, influenced by patch isolation and matrix hostility, represents another crucial avenue for further investigation.

The IBM presented in Chapter 3 examined the impact of anthropogenic mortality on a long-lived territorial raptor in a spatially implicit manner. Upgrading this model to a spatially explicit framework would enable more realistic representations of landscapes, additional mortality sources, and detailed individual movements throughout the annual cycle. Such improvements would facilitate detailed exploration of how mortality factors influence survival during dispersal, a critical phase marked by increased mobility and long-distance movements. Spatially explicit models could pinpoint mortality hotspots, providing essential data for conservation planning and prioritizing management strategies.

Both IBMs could benefit significantly from transitioning to a spatially explicit representation of the landscape using remote sensing variables, as exemplified in Chapters 4 and 5. This enhancement would add realism to the models and improve their predictive capabilities.

In Chapter 5, while our high-resolution spatially explicit IBM serves as a robust management tool, spatially explicit representation of anthropogenic mortality factors remains absent. Integrating these factors would facilitate the identification of mortality hotspots and enable testing of targeted conservation strategies to mitigate them. Furthermore, incorporating future suitability maps based on climate change models would enhance predictions of population trajectories under different conservation scenarios.

In conclusion, the findings of this thesis underscore the invaluable role of IBMs in evaluating how wildlife responds to anthropogenic pressures and different conservation strategies. Moving forward, these models represent indispensable tools for ecologists and conservation managers, offering critical insights that are essential for effective wildlife conservation and management in a rapidly changing world.

6.4 References

Acevedo-Whitehouse, K., Duffus, A.L.J., 2009. Effects of environmental change on wildlife health. Philosophical Transactions of the Royal Society B: Biological Sciences 364, 3429–3438. https://doi.org/10.1098/rstb.2009.0128

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

Benton, T., Vickery, J., Wilson, J., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol Evol 18, 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9

Bernardino, J., Bevanger, K., Barrientos, R., Dwyer, J.F., Marques, A.T., Martins, R.C., Shaw, J.M., Silva, J.P., Moreira, F., 2018. Bird collisions with power lines: State of the art and priority areas for research. Biol Conserv 222, 1–13. https://doi.org/10.1016/j.biocon.2018.02.029

Beston, J.A., Diffendorfer, J.E., Loss, S.R., Johnson, D.H., 2016. Prioritizing avian species for their risk of population-level consequences from wind energy development. PLoS One 11. https://doi.org/10.1371/journal.pone.0150813

Bevanger, K., 1998. Biological and conservation aspects of bird mortality caused by electricity power lines: A review. Biol Conserv 86, 67–76. https://doi.org/10.1016/S0006-3207(97)00176-6

Bevanger, K., 1994. Bird interactions with utility structures: collision and electrocution, causes and mitigating measures. Ibis 136, 412–425. https://doi.org/10.1111/j.1474-919X.1994.tb01116.x

Boivin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlandson, J.M., Denhami, T., Petraglia, M.D., 2016. Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. Proc Natl Acad Sci U S A 113, 6388–6396. https://doi.org/10.1073/pnas.1525200113

Carrete, M., Sánchez-Zapata, J.A., Martínez, J.E., Sánchez, M.Á., Calvo, J.F., 2002. Factors influencing the decline of a Bonelli's eagle *Hieraaetus fasciatus* population in southeastern Spain: Demography, habitat or competition? Biodivers Conserv 11, 975–985. https://doi.org/10.1023/A:1015856924451

Chevallier, C., Hernández-Matías, A., Real, J., Vincent-Martin, N., Ravayrol, A., Besnard, A., 2015. Retrofitting of power lines effectively reduces mortality by electrocution in large birds: An example with the endangered Bonelli's eagle. Journal of Applied Ecology 52, 1465–1473. https://doi.org/10.1111/1365-2664.12476

Frouz, J., Kindlmann, P., 2015. Source-sink colonization as a possible strategy of insects living in temporary habitats. PLoS One 10, 1–10. https://doi.org/10.1371/journal.pone.0127743

González, L.M., Margalida, A., Mañosa, S., Sánchez, R., Oria, J., Molina, J.I., Caldera, J., Aranda, A., Prada, L., 2007. Causes and spatio-temporal variations of non-natural mortality in the Vulnerable Spanish imperial eagle *Aquila adalberti* during a recovery period. Oryx 41, 495–502. https://doi.org/10.1017/S0030605307414119

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1, e1500052. https://doi.org/10.1126/sciadv.1500052

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

IPBES, 2019. The global assessment report on biodiversity and ecosystem services, Population and Development Review.

Janss, G.F.E., 2000. Avian mortality from power lines: A morphologic approach of a species-specific mortality. Biol Conserv 95, 353–359. https://doi.org/10.1016/S0006-3207(00)00021-5

Lobermeier, S., Moldenhauer, M., Peter, C.M., Slominski, L., Tedesco, R.A., Meer, M. Ver, Dwyer, J.F., Harness, R.E., Stewart, A.H., 2015. Mitigating avian collision with power lines: A proof of concept for installation of line markers via unmanned aerial vehicle. J Unmanned Veh Syst 3, 252–258. https://doi.org/10.1139/juvs-2015-0009

López-López, P., Ferrer, M., Madero, A., Casado, E., McGrady, M., 2011. Solving man-induced large-scale conservation problems: The Spanish Imperial Eagle and power lines. PLoS One 6. https://doi.org/10.1371/journal.pone.0017196

Loss, S.R., Will, T., Marra, P.P., 2015. Direct Mortality of Birds from Anthropogenic Causes. Annu Rev Ecol Evol Syst 46, 99–120. https://doi.org/10.1146/annurev-ecolsys-112414-054133

Lourie, E., 2016. Drivers of habitat selection: Investigating behaviours and movement for the study of GPS tracked animal habitat selection (MSc Thesis). University of East Anglia (United Kingdom).

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

Marcelino, J., Moreira, F., Mañosa, S., Cuscó, F., Morales, M.B., García de la Morena, E., Bota, G., Palmeirim, J.M., Silva, J.P., 2017. 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

Marques, A.T., Batalha, H., Rodrigues, S., Costa, H., Pereira, M.J.R., Fonseca, C., Mascarenhas, M., Bernardino, J., 2014. Understanding bird collisions at wind farms: An updated review on the causes and possible mitigation strategies. Biol Conserv 179, 40–52. https://doi.org/10.1016/j.biocon.2014.08.017

Martínez, J.E., Zuberogoitia, I., Jiménez-Franco, M. V., Mañosa, S., Calvo, J.F., 2016. Spatio-temporal variations in mortality causes of two migratory forest raptors in Spain. Eur J Wildl Res 62, 109–118. https://doi.org/10.1007/s10344-015-0981-x

Mojica, E.K., Dwyer, J.F., Harness, R.E., Williams, G.E., Woodbridge, B., 2018. Review and synthesis of research investigating golden eagle electrocutions. Journal of Wildlife Management 82, 495–506. https://doi.org/10.1002/jwmg.21412

Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., Faure, D., Garnier, E., Gimenez, O., Huneman, P., Jabot, F., Jarne, P., Joly, D., Julliard, R., Kéfi, S., Kergoat, G.J., Lavorel, S., Le Gall, L., Meslin, L., Morand, S., Morin, X., Morlon, H., Pinay, G., Pradel, R., Schurr, F.M., Thuiller, W., Loreau, M., 2015. Predictive ecology in a changing world. Journal of Applied Ecology 52, 1293–1310. https://doi.org/10.1111/1365-2664.12482

Pennekamp, F., Adamson, M.W., Petchey, O.L., Poggiale, J.C., Aguiar, M., Kooi, B.W., Botkin, D.B., DeAngelis, D.L., 2017. The practice of prediction: What can ecologists learn from applied, ecology-related fields? Ecological Complexity 32, 156–167. https://doi.org/10.1016/j.ecocom.2016.12.005

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

Pulliam, R., 1988. Sources, sinks, and population regulation. Am Nat 132, 652–661.

Quintero, S., Abrahams, M.I., Beirne, C., Blake, J., Carvalho, E., Costa, H.C.M., de Paula, M.J., Endo, W., Haugaasen, T., Lima, M.G.M., Michalski, F., Mosquera, D., Norris, D., Oliveira, T., Paemelaere, E., Peres, C.A., Pezzuti, J., Romero, S., Santos, F., Sillero-Zubiri, C., Whitworth, A., Zwicker, S., Maffei, L., Sahley, C., Tuesta, C., Valdez, F., Macdonald, D.W., Tan, C.K.W., 2023. Effects of human-induced habitat changes on site-use patterns in large Amazonian Forest mammals. Biol Conserv 279. https://doi.org/10.1016/j.biocon.2023.109904

Rayner, J.M. V., 1988. Form and Function in Avian Flight, in: Current Ornithology. Springer US, Boston, MA, pp. 1–66. https://doi.org/10.1007/978-1-4615-6787-5_1

Reif, J., Vermouzek, Z., 2019. Collapse of farmland bird populations in an Eastern European country following its EU accession. Conserv Lett 12, 1–8. https://doi.org/10.1111/conl.12585

Reigada, C., Schreiber, S.J., Altermatt, F., Holyoak, M., 2015. Metapopulation dynamics on ephemeral patches. American Naturalist 185, 183–195. https://doi.org/10.1086/679502

Schwartz, M.W., Cook, C.N., Pressey, R.L., Pullin, A.S., Runge, M.C., Salafsky, N., Sutherland, W.J., Williamson, M.A., 2018. Decision Support Frameworks and Tools for Conservation. Conserv Lett 11, 1–12. https://doi.org/10.1111/conl.12385

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., Santos, M., Queirós, L., Leitão, D., Moreira, F., Pinto, M., Leqoc, M., Cabral, J.A., 2010. Estimating the influence of overhead transmission power lines and landscape context on the density of little bustard *Tetrax tetrax* breeding populations. Ecol Modell 221, 1954–1963. https://doi.org/10.1016/j.ecolmodel.2010.03.027

Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., Packer, C., 2017. Future threats to biodiversity and pathways to their prevention. Nature 546, 73–81. https://doi.org/10.1038/nature22900

van Vliet, J., de Groot, H.L.F., Rietveld, P., Verburg, P.H., 2015. Manifestations and underlying drivers of agricultural land use change in Europe. Landsc Urban Plan 133, 24–36. https://doi.org/10.1016/j.landurbplan.2014.09.001

Zurell, D., König, C., Malchow, A.K., Kapitza, S., Bocedi, G., Travis, J., Fandos, G., 2022. Spatially explicit models for decision-making in animal conservation and restoration. Ecography 2022, 1–16. https://doi.org/10.1111/ecog.05787

Supplementary Materials

Supplementary Material for Chapter 2

Appendix A - ODD Protocol

Model Description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al. 2006), as updated by (Grimm et al. 2020). The model was implemented in NetLogo (Wilensky 1999). All simulation runs for testing and analysing the model, were performed using the "*NLRX*" package (Salecker et al. 2019) for program R (R Core Team 2021).

1. Purpose and patterns

The overall purpose of our model is to recreate the post-colonization demography of the Cabrera vole (*Microtus cabrerae*) within a single short-lived habitat patch amid a hostile matrix, with the characteristics of the habitat patch, including its size, internal quality, and connectivity, varying based on documented biological and ecological traits specific to the species (e.g. Fernández-Salvador et al. 2001, 2005a; Pita et al. 2010; Proença-Ferreira et al. 2019).

The ultimate purpose of the model is to assess, in a context of high habitat turnover, the role of patch spatial attributes (size, internal quality and connectivity) and time to disturbance in emergent demographic parameters and metrics quantifying local population self-sustainability and contribution to other patches.

Specifically, we used a pattern-oriented modelling (POM) strategy (Grimm 2005; Grimm and Railsback 2012) to simulate individual-level processes and determine post-colonization emergent demographic parameters and metrics quantifying internal recruitment from births, immigration inflow, and emigration outflow, while evaluating our model by its capacity to replicate individual-level patterns and behaviours, including spatial organization, breeding behaviour, parental care, migration, and survival.

To infer the source-sink status of local populations, we opt to use two simple metrics that can be extracted for relatively short-interval time periods along transient population dynamics. Specifically, we measured the imbalance between births and immigration (hereafter, B-I index) in persisting local populations (i.e. where overall recruitment apparently compensates deaths) calculated as the difference between net births and net immigration divided by the total number of recruits every three months. This index measures the role of births and immigration in overall local population gains, varying between -1 and 1. Positive values in the B-I index indicate a higher proportion of births over immigration (i.e., self-sustaining through reproduction), with negative values indicating the opposite pattern (i.e. persistence via immigration). We also quantified the imbalance between immigration and emigration (hereafter I-E index) as the difference between net immigration and net emigration divided by the total number of migrants every three months (Christensen and Walters 2004; Stoffels et al. 2016). This index also varies between -1 and 1, with positive values indicating higher net immigration (hence limited demographic contribution to the overall metapopulation) and negative values indicating higher net emigration (i.e. increased demographic contribution).

2. Entities, state variables, and scales

The model includes the following entities: habitat cells (1x1m2), Cabrera vole individuals (agents) and their home-ranges (collectives), and the global environment (referred to as “Observer” in NetLogo; the only entity at the system level, controlling the submodels and defining the simulation date). The state variables characterizing these entities are listed in Table 2.1 from the main text.

Cabrera vole individuals were included in the model to represent each individual and their spatial location in an individual and explicit way. Each Cabrera Vole's home-range is represented by a collective that aggregates the different individual agents (home-range agents) that are created in each habitat cell situated inside the Cabrera Vole's specific home-range buffer area. Home-range agents are created or eliminated whenever the respective individual enters, leaves, or moves within the habitat patch. They have been included in the model in order to allow a realistic spatial distribution of individuals in the local patch, according to empirical data on size and overlap between home-ranges.

Habitat cells are arranged in a circular pattern around the centre of the model world, forming a single habitat patch. The habitat patch may vary in size (according to the number of cells included in the simulation, which determine patch carrying capacity), internal quality, and connectivity relative to other virtual neighbouring patches (not explicitly represented in the model).

Each simulation was run for two years (104 weeks; ca. 6 vole generation times), where a single time step in the model corresponded to one week. This weekly time scale is sufficient to properly recreate individual behaviours and post-colonization fine-scale demography of the species, while the temporal extent is adequate to understand transient dynamics of local population in short-lived patches, as those typically found in highly managed farmland (e.g. Pita et al. 2007).

3. Process overview and scheduling

The model was developed to represent a local population of Cabrera voles (on a single short-lived habitat patch amid a hostile matrix), covering all aspects of the species' life cycle considered relevant for an adequate and realistic response to the model's purpose. In this sense, it is structured in 11 processes (submodels, see Section 7): One related to the update of the variables (variables updating), nine concerning Cabrera voles (ageing, maternal nest leaving, breeding status updating, mate searching, reproduction, birthing, emigration, immigration and survival) and one concerning data collection (outputs collection).

The update of variables (*reproduction_prob, emigration_prob,* and *immigration_prob*) occurs monthly except for *sim_date*, which is updated every time step over the whole simulation. Cabrera voles perform each process every timestep and the model was designed to collect data on the population of the habitat patch every three months intervals of the simulations.

The different processes are executed in the following predetermined order:

1. The variables are updated.
2. Cabrera voles update their age.
3. Juvenile Cabrera voles leave their mother's home-range and try to establish their own home-range in the patch.
4. Cabrera voles update their breeding status.
5. Adult Cabrera voles, without a defined mate, search within the patch for an available mate.
6. Adult Cabrera voles reproduce according to the probability of reproduction.
7. In the week a pregnant female reaches the date to give birth, it generates between 3 and 5 pups.
8. Individuals older than the defined age of dispersal, with no defined mate and, in the case of females, with no lactating pups, decide whether they will emigrate or not.
9. Immigrants can enter the patch and try to establish a home-range if predefined overlapping requirements are met.
10. Cabrera voles face a survival trial.
11. Model outputs are collected.

The model uses "asynchronous updating", in which the agents update the state variables one at a time as they execute a submodel that uses the variable. There is no hierarchy among agents of the same type (i.e. the order in which agents conduct each process is random and varies each time step), to avoid artefacts of execution order.

4. Design concepts

The design concepts *Objectives, Learning* and *Prediction* do not apply to this model.

Basic principles – The model assumes that Cabrera vole populations are patchily distributed, with individuals typically grouped into distinct local populations restricted to small habitat patches (Pita et al. 2006; Do Rosário and Mathias 2007). It's also assumed that Cabrera's reproduction follows a k-selection strategy (Fernández-Salvador et al. 2001), with monogamy being the predominant social and mating system, with possible deviations to facultative polygyny and cooperative breeding strategies (Fernández-Salvador et al. 2005b; Pita et al. 2010, 2011, 2014), as suggested by cases of high spatial overlap among females and male home-ranges containing several female home-ranges (Pita et al. 2010; Rosário 2012). These principles are represented in the model through the "reproduction" submodel and overlapping rules (see Table A.4).

Cabrera voles are also assumed to have a metapopulation-like dynamics, in which annual extinction and colonization rates are highly related to the size and connectivity of local habitat patches (Pita et al. 2007). An opportunistic reproductive pattern associated with habitat quality is also assumed, with a positive response to green grass availability (Fernández-Salvador et al. 2005a). These assumptions were very important to the way we conceptualised and built our model, as it is meant to test how patch characteristics affect the short-term sink-to-source transition potential of newly established local populations.

Emergence – The model's primary results (number of births, net immigration, and net emigration) as well as the output patterns used to validate the model (density, sex-ratio, residence times, and extinction rates) emerge from the dynamical interaction between the individuals, the local habitat patch attributes (size, internal quality, and connectivity), and the seasonality of migration and reproduction probabilities.

Adaptation – Individual settlement within a patch is a key adaptive behaviour such that they attempt to set their home-ranges according to spatial overlapping rules with other individuals' home-ranges (see Table A.4), while considering the availability of sexual partners, so as to minimize competition and maximize reproductive success (see “nest leaving” and “mate searching” submodels, below).

Another adaptative behaviour is emigration, when individuals without a defined mate decide to emigrate to another patch, trying to increase their reproductive success. This behaviour is simulated through a defined emigration probability value (*emigration_prob*) (see “nest leaving” and “emigration” submodels, below).

Sensing – Cabrera voles can sense the *location*, *sex*, *age*, *breeding_status* and *home_range* of other individuals in the local population, and whether they are relatives or not. They are also assumed to sense the *size* and *quality* of the patch.

Interaction – There are two kinds of interactions in this model. An indirect interaction exists among Cabrera voles when they try to define their home-range according to the overlapping rules (see Table A.4), which restricts the locations where they can be established. On the other hand, a direct interaction occurs among Cabrera voles during reproduction.

Stochasticity – Stochasticity is incorporated into the model through several processes. The initial location (*location*) of founders and the age (*age*) of immigrants are randomly assigned (see Section 5 and “immigration” submodel, below). The probability of selecting a sexual partner is also stochastic and increases with the amount of overlap between potential partners' home-ranges (see “reproduction” submodel, below).

Bernoulli trials are used to assess when reproduction, emigration, and immigration occur and to define the survival of Cabrera voles. Poisson distributions are used to assess values for litter size (*litter_size*) (see “birthing” submodel, below) and home-range size (*home_range_size*) (see “nest leaving” submodel, below).

Collectives – Each Cabrera Vole's home-range is represented by a collective that aggregates the different individual agents (home-range agents) that are created in each habitat cell situated inside the Cabrera Vole's specific home-range buffer area. Home-range agents are created or eliminated whenever the respective individual enters, leaves, or moves within the habitat patch. They have been included in the model in order to allow a realistic spatial distribution of individuals in the habitat patch, according to empirical data on size and overlap between home-ranges (see Table A.4).

Observation – The model was designed to collect demographic data at every three-month interval of the simulations (at each 13 time step interval, eight times along the full simulation), roughly corresponding to the end of the four main seasons in the Mediterranean basin (autumn, from October to December; winter, from January to March; spring, from April to June; and summer, from July to September). On each of these occasions, the model's primary results (number of births, net immigration, and net emigration) as well as the output patterns used to test the model (density, sex-ratio, residence times, and extinction rates) are recorded.

5. Initialization

The model is initialized to represent a recently formed breeding pair in a recently colonized habitat patch. For this, the simulations start at the beginning of October (when investment in reproduction starts to increase, (Ventura et al. 1998; Pita et al. 2014) with one male and one female founding voles. The home-range sizes are randomly generated according to $N(X, \sigma)$ as recorded in Pita et. al. (2011).

The values of habitat size, internal quality, and connectivity are defined at the initialization phase and kept constant throughout the simulation. Patch size may vary between 500 m^2 and 5000 m^2, which is the typical range of habitat patches occupied by the species in fragmented landscapes (Pita et al. 2014). Patch internal quality and connectivity were formulated as single synthetic measures ranging from 0 (minimum) to 1 (maximum), implicitly reflecting different biotic and abiotic conditions affecting habitat suitability at the patch (e.g. vegetation and soil properties) and landscape scales (e.g. proximity to surrounding habitat patches and degree of matrix hostility). Patch internal quality directly influences individual probability of reproduction (see *"reproduction"* submodel, below). Patch connectivity directly influences the probability of immigration, and therefore the amount of immigrant individuals that can colonize the focal patch (see "*immigration*" submodel, below). Connectivity also influences the probability of emigration and thus the number of individuals that may leave the patch (see "*emigration*" submodel, below). Model dynamics are driven by input data and minimum and maximum monthly probabilities of reproduction and migration, estimated based on empirical data (see Section 6).

6. Input data

Two input data files from external sources are used in the model: 1) Weekly reproduction probability; 2) Weekly immigration probability.

6.1. Weekly Reproduction probability

The first data file refers to reproduction probabilities. This file contains, for each month of the year, a minimum and maximum probability of a female becoming pregnant by week. These values are estimated from the data collected by Fernández-Salvador et al. (2005b) (2 years) and Rosário (2012) (1 year) (see 6.1.1., for a detailed description of the calculations). These estimates implicitly assume that empirically-based variations recorded for the same month result from the interannual fluctuations in habitat quality. These values are assumed to reflect the weekly probability of reproduction (*reproduction_prob*) of each female in each month of the simulation, which is weighted by the value attributed to habitat internal quality (*quality*) (see "variables updating" submodel, below).

6.1.1. Weekly Reproduction probability - Calculations

The calculations were based on data from Fernández-Salvador et al. (2005b. Table 2 - Number of pregnant females and total females between April 1997 and April 1999) and Rosário (2012. Page 92; Fig. 6 - Percentage of sexually active females from January to December 2004), following the steps below:

- First, the percentage of non-pregnant females was calculated for each month of the three years of data (Table A.1). The weekly reproduction probability (WRP) per month was then derived using equation (1).

(Eq. 1)

$$\text{WRP} = 1 - \left(\%\ \text{non\_pregnant\_female}^{\left(1/_{4.3}\right)}\right)$$

NOTE: 4.3 is the average number of weeks per month

Table A.1 Data used to calculate the weekly reproduction probability. A - Fernández-Salvador et al. (2005b); B - Rosário (2012); PF - pregnant females; AF - adult females; N-PF - non-pregnant females; WRP - weekly reproduction probability.

Month	Study	N PF	N AF	% PF	% N-PF	WRP
Apr	A	1	1	1	0	1
May	A	0	2	0	1	0
Jun	A	2	4	0,5	0,5	0,149
Jul	A	3	4	0,75	0,25	0,276
Aug	A	1	7	0,143	0,857	0,035
Sep	A	1	7	0,143	0,857	0,035
Oct	A	4	7	0,571	0,429	0,179
Nov	A	1	6	0,167	0,833	0,042
Dec	A	0	5	0	1	0
Jan	A	0	4	0	1	0
Feb	A	5	5	1	0	1
Mar	A	4	5	0,8	0,2	0,312
Apr	A	0	5	0	1	0
May	A	1	2	0,5	0,5	0,149
Jun	A	1	4	0,25	0,75	0,065
Jul	A	0	2	0	1	0
Aug	A	0	2	0	1	0
Sep	A	0	2	0	1	0
Oct	A	2	2	1	0	1
Nov	A	2	2	1	0	1
Dec	A	0	3	0	1	0
Jan	A	3	4	0,75	0,25	0,276
Feb	A	2	6	0,333	0,667	0,090
Mar	A	2	6	0,333	0,667	0,090
Apr	A	3	6	0,5	0,5	0,149
Jan	B	-	-	0,4	0,6	0,112
Feb	B	-	-	1	0	1
Mar	B	-	-	1	0	1
Apr	B	-	-	1	0	1
May	B	-	-	1	0	1
Jun	B	-	-	0,25	0,75	0,065
Jul	B	-	-	0	1	0
Aug	B	-	-	0	1	0
Sep	B	-	-	0	1	0
Oct	B	-	-	1	0	1
Nov	B	-	-	0,3	0,7	0,080
Dec	B	-	-	1	0	1

- Subsequently, from the total of the three years of data used, the minimum and maximum values recorded for each month were selected, defining the range used in the model (Figure A.1).

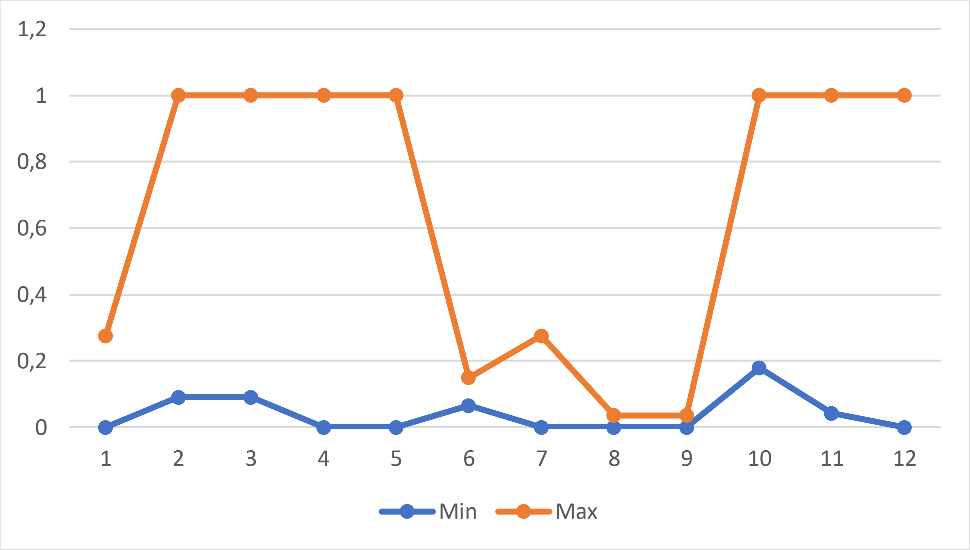


Figure A.1 Minimum and maximum weekly reproduction probability by month.

6.2. Weekly immigration probability

The second data file refers to immigration probabilities, containing for each month a maximum value of the weekly probability of an immigrant entering the local patch (*entering_prob*). These probabilities were calculated from the data collected in "NetPersist" project (Proença-Ferreira et al. 2019), assuming that the probability of an immigrant entering a patch is related to its connectivity to other patches (see 6.2.1., for a detailed description of the calculations). These values are used in the model to define the weekly probability of an immigrant entering the patch in each month of simulation (*immigration_prob*), while considering the value attributed to habitat connectivity (*connectivity*) (see "variables updating" submodel, below).

6.2.1. Weekly immigration probability - Calculations

The probability of immigration was calculated based on the data collected in the "NetPersist" project (Proença-Ferreira et al. 2019), according to the following steps:

1. Calculation of the percentage of the population that migrated (PM) per sampling session using equation (2), where N_movements = number of identified movements between

different patches per sampling session; and N_individuals = number of identified individuals per sampling session.

(Eq. 2)

$$\% \text{ PMpss } = \frac{\text{N\_movements}}{\text{N\_individuals}}$$

2. Calculation of the percentage of the population that migrated to a particular patch (PMPP) per sampling session using equation (3), where % PMpps = percentage of the population that migrated per sampling session (equation 2); and N_patches = number of favourable habitat patches per sampling session.

(Eq. 3)

$$\% \text{ PMPPpss} = \frac{\% \text{ PMpps}}{\text{N\_patches}}$$

3. Calculation of the percentage of the population that migrated to a particular patch (PMPP) per week (pw) using equation (4), where % PMPPpss = percentage of the population that migrated to a particular patch per sampling session (equation 3); and N_weeks = number of weeks between samples.

(Eq. 4)

$$\% \text{ PMPPpw} = \frac{\% \text{ PMPPpss}}{\text{N\_weeks}}$$

NOTE: N_weeks = 13 (approximately 3 months)

4. Calculation of the percentage of favourable habitat (PFH) per sampling session (pss) in the NetPersist project using equation (5), where favourable_area = area of favourable habitat sampled per sampling session; and total_area = total area sampled per sampling session.

(Eq. 5)

$$\text{PFHpss } = \frac{\text{favourable\_area}}{\text{total\_area}}$$

5. Calculation of the expected area of favourable habitat in the 2 km buffer (FHB) per sampling session using equation (6), where buffer_area = area of a buffer with 2km radius (assumed

as the median distance an individual is likely to travel during dispersal, Mestre et al. 2017), equivalent to an area of 1,256.64 ha.; and PFHpss = percentage of favourable habitat per sampling session (equation 5)

(Eq. 6)

$$\mathrm{FHBpss} = \mathrm{buffer\_area} \times \mathrm{PFHpss}$$

6. Calculation of the number of expected individuals in the 2km buffer (NEIB) per sampling session using equation (7), where % FHBpss = expected area of favourable habitat in the 2 km buffer per sampling session; and density_recorded = density of individuals recorded per sampling session.

(Eq. 7)

$$\mathrm{NEIBpss} = \frac{\%\ \mathrm{FHBpss}}{\mathrm{density\_recorded}}$$

NOTE: Density estimates given by the capwire ECM estimator (Miller et al. 2005; Pennell et al. 2013).

7. Calculation of the immigration probability to a particular patch (NEIMPP) per week, in each season (ind/week) (Table A.2) using equation (8), where NEIBpss = number of expected individuals in the 2km buffer per sampling session (equation 7); and % PMPPpw = percentage of the population that migrated to a particular patch per week (equation 4).

(Eq. 8)

$$\mathrm{NEIMPPpw} = \frac{\mathrm{NEIBpss}}{\%\ \mathrm{PMPPpw}}$$

Table A.2 Weekly immigration probability, in each month.

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
0,096	0,376	0,376	0,376	0,309	0,309	0,309	0,067	0,067	0,067	0,096	0,096

7. Submodels

The model includes 11 submodels or processes, and their description follows the fixed scheduling presented in Section 3 (Process overview and scheduling). Model parameters used in the submodels are listed in Table A.3 according to the processes they are involved in: environment, home-range, reproduction, survival, and movement.

Table A.3 Key parameters, values and references.

Parameter name	Description (units)	Value	Reference
Environment			
size	Habitat patch size (m^2)	500 – 5000	(Pita et al. 2014)
quality	Habitat patch internal quality (-)	0 – 1	-
connectivity	Habitat patch connectivity (-)	0 – 1	-
Home-range			
home_range_M	Average male home-range size (m^2)	Mean 535,64 (123,6 – 1075,6)	(Pita et al. 2010)
home_range_F	Average female home-range size (m^2)	Mean 355,44 (39,3 – 991,5)	(Pita et al. 2010)
Reproduction			
maturation_age	Maturation age (weeks)	8	(Fernández-Salvador et al. 2001, 2005a)
reproduction_prob	Reproduction probability (week^{-1})	0 – 1	Calculated from (Fernández-Salvador et al. 2005a; Rosário 2012)
gestation_length	Length of gestation period (week)	3	(Fernández-Salvador et al. 2001)
litter_size	Litter size (number of pups)	4 (3 – 5)	(Ventura et al. 1998; Fernández-Salvador et al. 2001)
sex_ratio	Sex ratio at birth (M:F)	1:1	(Fernández-Salvador et al. 2001)
lactation_length	Length of lactation period (weeks)	2	(Fernández-Salvador et al. 2001)
Survival			
juvenile_mortality	Weekly juvenile (< 8 weeks) mortality rate (week^{-1})	0,123	Calculated from (Fernández-Salvador et al. 2005b)
adult_mortality	Weekly adult (> = 8 weeks) mortality rate (week^{-1})	0,020	Adapted from (Topping et al. 2012; Radchuk et al. 2016)
Movement			
nest_leave_age	Maternal nest leaving age (weeks)	6	Guesstimated
emigration_prob	Weekly individual probability of emigration (week^{-1})	0,075 – 0,177	Calculated from (Proença-Ferreira et al. 2019)
immigration_prob	Weekly probability of immigration (week^{-1})	0,050 – 0,376	Pita et al. unpublished data; Proença-Ferreira et al. (2019)
max_immigration_age	Maximum age of an immigrant (weeks)	77	Guesstimated

7.1. Variables updating

The simulation date (*sim_date*) is updated each time step, by adding a further week.

Each month, the reproduction probability (*reproduction_prob*) is updated, using the input data referent to the minimum and maximum weekly reproduction probability by month (WRP) (see Section 6) and the habitat quality (*quality*) parameter, using equation (9).

(Eq. 9)

$$reproduction\_prob \; = \; \big((\mathrm{max\_WRP} - \mathrm{min\_WRP}) \; \times \; quality\big) + \; \mathrm{min\_WRP}$$

The immigration probability (*immigration_prob*) is also updated monthly, using the input data referent to the minimum (defined as 0.05 for all months) and maximum weekly immigration probability by month (WIP) (see Section 6) and the habitat connectivity parameter (*connectivity*), using equation (10).

(Eq. 10)

$$immigration\_prob \; = \; \big((\mathrm{max\_WIP} - \mathrm{min\_WIP}) \; \times \; connectivity\big) + \; \mathrm{min\_WIP}$$

The emigration probability (*emigration_prob*) is calculated only in the first time step, as it remains constant throughout the rest of the simulation, since there were no changes in apparent survival (mortality + emigration) throughout the year (Fernández-Salvador et al. 2005b; Proença-Ferreira et al. 2019). For this, the minimum and maximum values of the weekly individual probability of emigration (WIPE) (see "emigration" submodel, below) and the habitat connectivity parameter (*connectivity*) are used in equation (11).

(Eq. 11)

$$emigration\_prob \; = \; \big((\mathrm{max\_WIPE} - \mathrm{min\_WIPE}) \; \times \; connectivity\big) + \; \mathrm{min\_WIPE}$$

7.2. Ageing

One week is added to each Cabrera vole age (*age*) and residence time (*residence_time*) at each time step.

7.3. Nest leaving

In the week a Cabrera vole reaches the maternal nest leaving age (*nest_leave_age*), it moves out his mother's home-range, and tries to establish its own home-range in the patch. If insufficient space is available within the patch, that individual is forced to emigrate.

Before starting the search for the new home-range in the local patch, the home-range size (*home_range_size*) is defined, according to a normal distribution following the values observed in (Pita et al. 2010) for the 95% Kernel. In order to establish a home-range in the patch, it is necessary to fulfil the following rules (see Table A.4):

- The entire home-range must be included within the habitat patch;

- In the case of males, they cannot overlap more than 10% of their home-range with any other male;

- In the case of females, they should not overlap more than 10% of their home-range with any other female. If there is no location in the patch with these characteristics, they can overlap up to 80% of their home-range with a related female (mother or sisters from the same litter), as long as they never overlap more than 10% with any unrelated female. Such females may concur to the likely presence of cooperative breeding in some Cabrera vole populations (Fernández-Salvador 2007), and therefore their breeding status was classified as 'helpers'. However, because the net contribution of possible helpers to litter survival or success is unknown, no such effect was explicitly included in the model.

The overlapping rules are implemented by counting the percentage of habitat cells, located within the buffer area of the home-range, with home-range agents referring to a particular individual.

If there is more than one location in the patch that meets the requirements mentioned above, the Cabrera vole chooses one at random and moves to it and updates the variable breeding status (*breeding_status*). One home-range agent is created in each habitat cell located within the buffer area (*home_range_size*) of the Cabrera vole home-range, being characterized by the Cabrera vole ID.

In case there is no location in the patch with these requirements, the Cabrera vole is obliged to emigrate to a hypothetical neighbour patch (in practice these individuals are removed from the simulation), being therefore added to the number of emigrants recorded along the simulation (*N_emigrants*).

Table A.4 Home-range overlap constraints (based on Pita et al. 2010).

	Unrelated Males	Related Males	Unrelated Females	Related Females	Mate
Unpaired Males	< 10%	< 10%	Up to 100%	Up to 100%	-
Paired Males	< 10%	< 10%	Up to 100%	< 10% (paired)	> 80%
Unpaired Females	Up to 100%	Up to 100%	< 10%	< 80% *	-
Paired Females	Up to 100%	< 10% (paired)	< 10%	< 10% (paired) or < 80% (unpaired)	> 80%

* Up to 80% if there is no place with < 10%. If there is > 10% overlap (with mother or sister) it is classified as "helper".

7.4. Breeding status updating

Updates the Cabrera voles breeding status variable (*breeding_status*). Checks whether all individuals aged or over the maturation age (*maturation_age*), without a “link-neighbour” (see “Mate searching” submodel, below), and not classified as "helper", are defined as "no-mate", hence correcting the status of individuals who were left without a mate in the previous time step (week). It also checks whether the conditions that lead females to be considered as "helper" remain, if not, it defines them as "no-mate", correcting possible changes in breeding status due to movements or death of other individuals.

Note: Maturation age estimated based on Fernández-Salvador et al. (2005a), where individuals over 39 g are considered as adults, and Fernández-Salvador et al. (2001), where, through the analysis of Fig. 1, it is verified that the individuals begin to reach a weight of ≈ 39 g around the 50th day (≈ 7 weeks). Therefore, it was considered that maturation of Cabrera voles occurs in the eighth week of life.

7.5. Mate searching

Adult Cabrera voles without a defined mate search within the patch for an available mate. To do so, the Cabrera vole must have reach the maturation age (*maturation_age*), must have a breeding status (*breeding_status*) of “no-mate”, and, in the case of being a female, cannot be pregnant or have lactating pups (*lactation_duration*). The potential mate also must be aged over the maturation age (*maturation_age*), have a breeding status (*breeding_status*) of “no-mate”, and be genetically unrelated (i.e. neither parent, pup, or full sibling). In the case of males, the possible mate must not be classified as "helper".

If there are one or more possible mates, the individual who started the search, evaluates if there is any place in the patch where:

- Their entire home-range is included within the patch;

- At least 80% of their home-range overlap with the one of the possible mates;

- A maximum of 10% overlap with related individuals with a mate;

- A maximum of 10% overlap with individuals of the same sex, with females being able to overlap up to 80% with related females without a mate (passing these to be classified as "overlapper"). What differentiates an "overlaper" female from a "helper" is the fact that a "helper" overlaps her home-range with her father's home-range and overlaps more than 10% with her mother's home-range. "Helper" females can never reproduce. On the other hand, "overlapper" females are classified as such because they overlap their home-range by more than 10% with the home-range of any related female that has a mate. In this case, females cannot form pairs but can reproduce.

In case there are places with these characteristics, the individual who started the search, chooses one of these places at random and moves there. The previous home-range is vacated and, in each habitat cell located within the new Cabrera vole home-range are (*home_range_size*), a home-range agent is added, characterized by the Cabrera vole ID.

The Cabrera voles that moved, create a “link-neighbour” (a NetLogo primitive) with the selected mate and both update their breeding status (*breeding_status*) to the respective mate’s ID.

7.6. Reproduction

Cabrera voles can reproduce throughout the year, however the probability of reproducing has fluctuations during the year, being linked to the internal quality of the habitat. Therefore, each week, all females older than the maturation age (*maturation_age*), who are not classified as "helpers" and who are not pregnant or have lactating pups (*lactation_duration*), can reproduce. For this, a Bernoulli trial with p = *reproduction_prob* is used to check if such females will try to reproduce in the current week. If so, they define as possible sexual partners, unrelated males, older than the maturation age (*maturation_age*) and that overlap their own home-range.

For females with a defined mate, extra pair mating may occur whenever there is a further possible sexual partner besides their mate. This is supported by the fact that this species likely presents a social monogamous mating system (see Section 4 “Basic principles”). Extra-pair mate selection is defined using a probability equivalent to the percentage of overlap of each one of the males with their home-range.

In the case of females without a defined mate, they may possibly mate with a nearby male (except with their parent, offspring, or full siblings, for which perfect kin recognition was assumed). This was defined as a probability given by the percentage of home-range overlap. For this, a Bernoulli trial with p = “percentage of overlap with possible sexual partners” is used. This represents a lower probability of reproduction compared to females with a defined partner.

The overlap percentages are defined by counting the percentage of habitat cells, located within the buffer area (*home_range_size*) of the female home-range, with home-range agents referring to a particular male.

Once chosen the sexual partner, the current week will be defined as the date of last reproduction (*last_reproduction*) for the female, as well as the time step it will give birth (*give_birth*) and the ID of the sexual partner (*father’s_ID*).

Since eventual differences in litter survival and success between mating systems is unknown, no such effects were explicitly included in the model.

7.7. Birthing

Pregnant Cabrera voles, who have the current time step set to give birth (*give_birth*), generate between 3 and 5 pups, that will be added to the model in the same habitat cell as the mother. The exact number of pups is defined according to a Poison distribution (*litter_size* – mean 4 and SD 0.89). The sex ratio at birth is assumed to be 1:1.

After giving birth, females change their variables *father’s_ID* and *give_birth* to “n.a.”.

7.8. Emigration

Emigration events can occur through 2 different processes, when juveniles leave the nest and there is no space for them to settle in the patch, being forced to emigrate (see “Nest leaving” submodel, above); or when adult or sub-adult individuals without a defined mate decide to leave the patch.

In this last scenario, Cabrera voles older than the defined nest leaving age (*nest_leave_age*), who have no defined mate, and, in the case of females, don´t have lactating pups (*lactation_duration*), decide whether to emigrate in the current time step or not. This decision is made through a Bernoulli trial with p = *emigration_prob*.

In case of emigration, the individual is removed from the simulation and accounted to the total number of emigrants (N_emigrants), independently of individual costs associated to movement. The individual's home-range is eliminated.

7.8.1. Weekly individual probability of emigration - Calculations

- The weekly individual probability of emigration (WIPE), minimum (0.075) and maximum (0.177), was calculated using the equation (12).

(Eq. 12)

$$\mathrm{WIPE} = \mathrm{WAM} - \mathrm{weekly\_mortality\_rate}$$

Note: For the weekly mortality rate (0.02), see "Survival" submodel, below.

- The minimum and maximum values of apparent monthly survival (0.39 and 0.65) were taken from Proença-Ferreira et al. (2019), and used to calculate the weekly apparent mortality (WAM) with the equation (13).

(Eq. 13)

$$\mathrm{WAM} = 1 - \left(\mathrm{monthly\_apparent\_survival}^{\left(1/_{4.3}\right)}\right)$$

7.9. Immigration

At each time step, an immigrant can enter and try to establish a home-range in the local patch. The decision of whether or not to allow entry by an immigrant is defined according to a Bernoulli trial with p = *immigration_prob*.

The immigrant Cabrera voles only establish a home-range in the habitat patch if predefined overlapping requirements are met (see Table A.4). If the minimum requirements are not met, the individual is eliminated from the model, simulating his departure in search of another patch.

If an immigrant enters the local population successfully, a Cabrera vole is added to the model, its sex is randomly defined, as well as its age, which can vary between the nest leaving age (*nest_leave_age*) and maximum age to immigrate (*max_immigration_age*). The size of their home-range is defined according to a normal distribution, following the values observed in Pita et al. (2010) for the 95% Kernel. In this case, the individual is accounted for the total number of immigrants (*N_immigrants*) and in each habitat cell located within their home-range area (*home_range_size*), a home-range agent is added, characterized by the immigrant's ID.

7.10. Survival

At each time step, each Cabrera vole challenges its survival by means of a Bernoulli trial. For that, two age classes are considered: under the age of maturation – juveniles, and aged or over the maturation age – adults (*maturation_age*). In the first case, for the Bernoulli trial, a p = *juvenile_mortality* is used and, in the second case, a p = *adult_mortality*. If the death of a Cabrera vole is defined, it is eliminated from the simulation, as well as the corresponding home-range.

In the case a female with lactating pups (*lactation_duration*) dies, its pups also die, since at this life stage they are assumed to be highly dependent on their progenitors.

7.10.1. Weekly juvenile mortality rate - Calculations

- The weekly juvenile mortality rate (WJMR), 0.123, was calculated based on Fernández-Salvador et al. (2005b), which estimates that only 40% of individuals reach the adult stage, using the equation (14).

(Eq. 14)

$$\mathrm{WJMR} = 1 - \left(\mathrm{probability\_reach\_adult\_stage}^{\left(1/_{\mathrm{N\ of\ weeks}}\right)}\right)$$

NOTE: N of weeks of the juvenile phase = 7

7.10.2. Weekly adult mortality rate (> = 8 weeks) - Calculations

- The weekly mortality rate (0.02) was defined based on Topping et al. (2012) (*Microtus agrestis*; daily unattributed mortality probability = 0.003) and from Radchuk et al. (2016) (*Microtus oeconomus*; baseline survival rate in summer (week^{-1}) = 0.98).

7.11. Outputs collection

After the start of the simulation, every three-month interval of the simulations (at each 13 time step interval, eight times along the full simulation), 6 population outputs are collected (see Table 2.2 in main text for more details). For the calculation of these outputs only Cabrera voles over the lactation age (*lactation_duration*) were counted, making these data comparable with empirical data, since individuals under this age are seldom sampled in the field.

References

Christensen V, Walters CJ (2004) Ecopath with Ecosim: Methods, capabilities and limitations. Ecol Modell 172:109–139. https://doi.org/10.1016/j.ecolmodel.2003.09.003

Do Rosário IT, Mathias M da L (2007) Post-fire recolonisation of a montado area by the endangered Cabrera vole (*Microtus cabrerae*). Int J Wildland Fire 16:450–457. https://doi.org/10.1071/WF06096

Fernández-Salvador R (2007) Biología y ecología de *Microtus cabrerae* Thomas, 1906 (Rodentia: Cricetidae). Ph.D. dissertation, Universitat Autònoma de Barcelona, Barcelona, Spain

Fernández-Salvador R, García-Perea R, Ventura J (2001) Reproduction and postnatal growth of the Cabrera vole, *Microtus cabrerae*, in captivity. Can J Zool 79:2080–2085. https://doi.org/10.1139/cjz-79-11-2080

Fernández-Salvador R, García-Perea R, Ventura J (2005a) Effect of climatic fluctuations on body mass of a Mediterranean vole, *Microtus cabrerae*. Mammalian Biology 70:73–83. https://doi.org/10.1016/j.mambio.2004.06.002

Fernández-Salvador R, Ventura J, García-Perea R (2005b) Breeding patterns and demography of a population of the Cabrera vole, *Microtus cabrerae*. Animal Biology 55:147–161. https://doi.org/10.1163/1570756053993497

Grimm V (2005) Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology. Science (1979) 310:987–991. https://doi.org/10.1126/science.1116681

Grimm V, Berger U, Bastiansen F, et al (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, Railsback SF (2012) Pattern-oriented modelling: A “multi-scope” for predictive systems ecology. Philosophical Transactions of the Royal Society B: Biological Sciences 367:298–310. https://doi.org/10.1098/rstb.2011.0180

Grimm V, Railsback SF, Vincenot CE, et al (2020) The ODD protocol for describing agent-based and other simulation models: A second update to improve clarity, replication, and structural realism. Jasss 23:. https://doi.org/10.18564/jasss.4259

Mestre F, Risk BB, Mira A, et al (2017) A metapopulation approach to predict species range shifts under different climate change and landscape connectivity scenarios. Ecol Modell 359:406–414. https://doi.org/10.1016/j.ecolmodel.2017.06.013

Miller CR, Joyce P, Waits LP (2005) A new method for estimating the size of small populations from genetic mark-recapture data. Mol Ecol 14:1991–2005. https://doi.org/10.1111/j.1365-294X.2005.02577.x

Pennell MW, Stansbury CR, Waits LP, Miller CR (2013) Capwire: A R package for estimating population census size from non-invasive genetic sampling. Mol Ecol Resour 13:154–157. https://doi.org/10.1111/1755-0998.12019

Pita R, Beja P, Mira A (2007) Spatial population structure of the Cabrera vole in Mediterranean farmland: The relative role of patch and matrix effects. Biol Conserv 134:383–392. https://doi.org/10.1016/j.biocon.2006.08.026

Pita R, Mira A, Beja P (2010) Spatial segregation of two vole species (*Arvicola sapidus* and *Microtus cabrerae*) within habitat patches in a highly fragmented farmland landscape. Eur J Wildl Res 56:651–662. https://doi.org/10.1007/s10344-009-0360-6

Pita R, Mira A, Beja P (2006) Conserving the Cabrera vole, *Microtus cabrerae*, in intensively used Mediterranean landscapes. Agric Ecosyst Environ 115:1–5. https://doi.org/10.1016/j.agee.2005.12.002

Pita R, Mira A, Beja P (2011) Circadian activity rhythms in relation to season, sex and interspecific interactions in two Mediterranean voles. Animal Behaviour 81:1023–1030. https://doi.org/10.1016/j.anbehav.2011.02.007

Pita R, Mira A, Beja P (2014) *Microtus cabrerae* (Rodentia: Cricetidae). Mammalian Species 46:48–70. https://doi.org/10.1644/912.1

Proença-Ferreira A, Ferreira CM, Leitão I, et al (2019) Drivers of survival in a small mammal of conservation concern: An assessment using extensive genetic non-invasive sampling in fragmented farmland. Biol Conserv 230:131–140. https://doi.org/10.1016/j.biocon.2018.12.021

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/.

Radchuk V, Ims RA, Andreassen HP (2016) From individuals to population cycles: The role of extrinsic and intrinsic factors in rodent populations. Ecology 97:720–732. https://doi.org/10.1890/15-0756.1

Rosário IT (2012) Towards a conservation strategy for an endangered rodent, the Cabrera vole (*Microtus cabrerae* Thomas). Insights from ecological data. PhD Thesis, University of Lisbon, Lisbon, Portugal

Salecker J, Sciaini M, Meyer KM, Wiegand K (2019) The NLRX R package: A next-generation framework for reproducible NetLogo model analyses. Methods Ecol Evol 10:1854–1863. https://doi.org/10.1111/2041-210X.13286

Stoffels RJ, Rehwinkel RA, Price AE, Fagan WF (2016) Dynamics of fish dispersal during river-floodplain connectivity and its implications for community assembly. Aquatic Sciences 78:355–365. https://doi.org/10.1007/s00027-015-0437-0

Topping CJ, Dalkvist T, Grimm V (2012) Post-Hoc Pattern-Oriented Testing and Tuning of an Existing Large Model: Lessons from the Field Vole. PLoS ONE 7:e45872. https://doi.org/10.1371/journal.pone.0045872

Ventura J, Lopez-Fuster MJ, Cabrera-Millet M (1998) The Cabrera vole, *Microtus cabrerae*, in Spain: A biological and a morphometric approach. Netherlands Journal of Zoology 48:83–100. https://doi.org/10.1163/156854298X00237

Wilensky U (1999) NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling. Northwestern University, Evanston, Illinois, U.S.

Supplementary Material for Chapter 2

Appendix B - Supplementary results

Table B.1 Summary results of linear regressions describing the general trends in emergent validation outputs, matching expectations from general ecological theory (see Figure 2.3 and main text for details). Data used to build these relationships were derived from the original Sobol estimator simulations. The very low R^2 values (<0.026) likely reflect the strong interaction effects among patch attributes on voles' demography, thus resulting in large unexplained variance in single-variable regressions (see main text).

Demographic Indices	**Intercept**	**Slope**	R^2
Extinction rate – Size	0.33	-4. 8e-05	0.017
Extinction rate – Connectivity	0.25	-0.093	0.0032
Extinction rate – Quality	0.23	-0.051	0.00098
Density – Time	16	0.0077	0.00026
Density – Quality	12	7.9	0.026

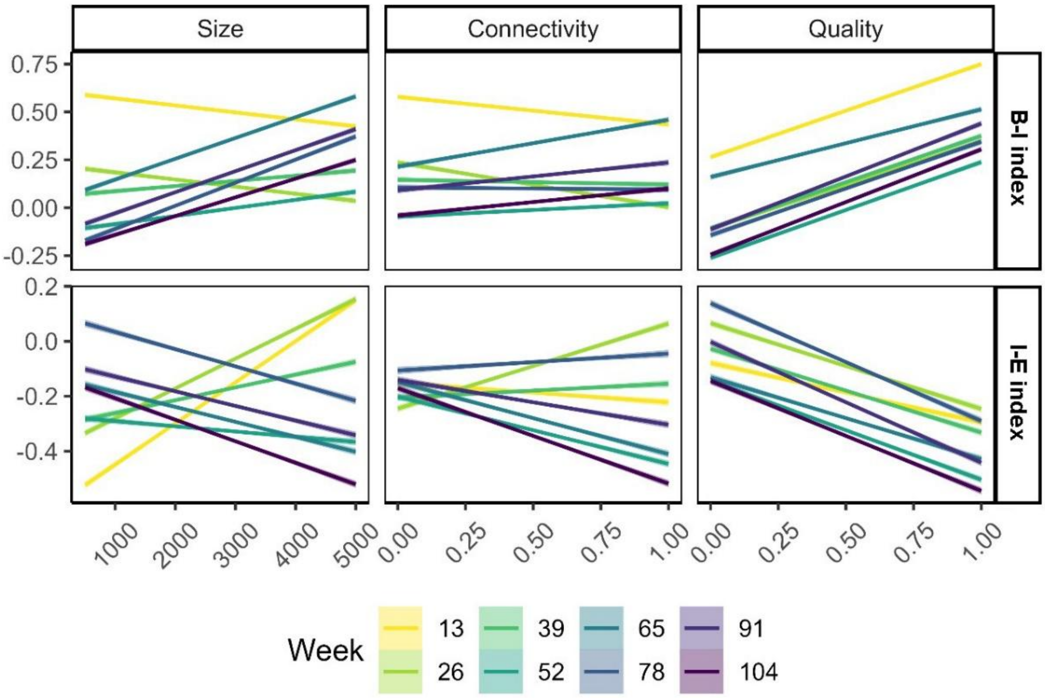


Figure B.1 Fitted single-variable linear regression lines (and their narrow 95% confidence interval bands) showing the relationships between focal demographic indices (rows) and local patch attributes (columns), over the simulation period. Data used to represent these relationships were derived from the original Sobol estimator simulations (see main text and Table B.2).

Table B.2 Summary results of linear regressions build to illustrate single-variable effects of patch attributes on B-I and I-E indexes across time. The very low R2 values (<0.10) likely reflect the strong interaction effects among patch attributes, thus resulting in large unexplained variation in single-variable regression models (see main text).

Demographic Indices	Local Patch Attributes	Week	Intercept	Slope	R^2
B-I index	Size	13	0.61	-3.7e-05	0.00616
		26	0.22	-3.7e-05	0.00469
		39	0.059	2.7e-05	0.00243
		52	-0.13	4.2e-05	0.00684
		65	0.038	0.00011	0.0438
		78	-0.23	0.00012	0.0443
		91	-0.14	0.00011	0.0387
		104	-0.24	9.8e-05	0.0349
	Connectivity	13	0.58	-0.14	0.00475
		26	0.24	-0.23	0.00908
		39	0.15	-0.024	9.94e-05
		52	-0.046	0.07	0.00092
		65	0.21	0.25	0.011
		78	0.11	-0.011	1.7e-05
		91	0.091	0.15	0.00334
		104	-0.041	0.14	0.00356
	Quality	13	0.26	0.49	0.0538
		26	-0.11	0.46	0.0347
		39	-0.11	0.48	0.0388
		52	-0.26	0.5	0.0473
		65	0.16	0.35	0.0229
		78	-0.14	0.49	0.0358
		91	-0.11	0.55	0.0483
		104	-0.25	0.55	0.0546
I-E Index	Size	13	-0.6	0.00015	0.0946
		26	-0.39	0.00011	0.0557
		39	-0.31	4.7e-05	0.0107
		52	-0.27	-1.9e-05	0.00177
		65	-0.13	-5.4e-05	0.0136
		78	0.096	-6.3e-05	0.0165
		91	-0.075	-5.3e-05	0.0131
		104	-0.13	-7.8e-05	0.0291
	Connectivity	13	-0.15	-0.07	0.00103
		26	-0.24	0.31	0.0224
		39	-0.2	0.05	0.000618
		52	-0.2	-0.25	0.0146
		65	-0.15	-0.26	0.0156
		78	-0.11	0.061	0.000782
		91	-0.14	-0.16	0.0061
		104	-0.17	-0.35	0.0282
	Quality	13	-0.079	-0.22	0.00974
		26	0.066	-0.31	0.0228
		39	-0.027	-0.3	0.0225
		52	-0.14	-0.36	0.0316
		65	-0.13	-0.3	0.0202
		78	0.14	-0.43	0.0381
		91	-0.0024	-0.44	0.0439
		104	-0.14	-0.4	0.0375

Supplementary Material for Chapter 3

Appendix C - ODD Protocol

Model Description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2006), as updated by (Grimm et al., 2020). The model was implemented in NetLogo (Wilensky, 1999). All simulation runs for testing and analysing the model, were performed using the "*NLRX*" package (Salecker et al., 2019) for program R (R Core Team, 2021).

The code is available here:

https://github.com/TCrispimMendes/IBM_Anthropogenic_Mortality_on_Territorial_Predators

1. Purpose and patterns

The overall purpose of our model was to understand how exposure to additional mortality from anthropogenic sources impacts long-lived raptors species with territorial behaviour. We specified an IBM framework considering a generalisation of the spatial and social structures of the Bonelli's eagle (*Aquila fasciata*), which is akin of that of many other territorial birds of prey. Specifically, we used a pattern-oriented modelling (POM) strategy (Grimm, 2005; Grimm and Railsback, 2012) to simulate individual level patterns and behaviours, and determine emergent demographic responses across multiple scenarios of exposure to additional mortality. For this, we combined different percentages of territories exposed to additional mortality (25%, 50% and 75% of territories), with different levels of additional mortality probability (10% to 100%, at 10% intervals), and affecting either Patches occupied by territorial birds, non-territorial birds, or both. This simulation design was used to estimate thresholds above which the exposure to additional mortality could exert population-level have population effects, conditional on territorial status.

2. Entities, state variables, and scales

The model includes three entities, characterised by the state variables listed in Table C.1: grid cells representing spatial units used by Bonelli’s eagles (i.e., Patches), agents representing individual Bonelli’s eagles (i.e., Birds), and the Global Environment (i.e., “Observer” in NetLogo), the only entity at the system level, which controls the submodels and additional mortality parameters, and keep track of simulated time. The model spatial extent simulates the geographical context of the population, including 131 Patches potentially used by territorial birds (type “A“ Patches), and another 50 Patches that can only be used by non-territorial individuals (type “B” Patches). We limited the breeding population to a total of 131 pairs (i.e., carrying capacity), corresponding to 110% of the breeding population of southern Portugal 2019, which was considered close to saturation (Dias et al., 2017). As we lack detailed empirical data about the range and settlement areas used by the non-territorial birds of the Bonelli’s’ eagle population in southern Portugal, we chose a number of patches type “B” sufficient to accommodate the non-breeding birds predicted for a population with a stable age distribution of 131 pairs (the maximum possible value in the model). This calculation was conducted assuming a delay in recruitment as a density-dependent mechanism, which occurs when the carrying capacity of patches occupied by territorial individuals (type “A”) is reached. In this scenario, we assumed that recruitment only takes place in the 4th year of life, rather than being able to occur in the 2nd and 3rd years. In this case, considering the basal recruitment probability of 0.93 for individuals of 4 years, for a population of 262 territorial individuals (131 pairs) with a stable age distribution, it is anticipated that there will be 236 non-territorial individuals. Given our model's carrying capacity of 5 non-territorial individuals per Patch, this suggests the need for at least 48 type “B” Patches to accommodate all non-territorial individuals. Additionally, considering the potential reduction in recruitment probability for individuals aged = 4, we chose to conservatively include 50 “B” Patches in the model to ensure adequate space for the maximum expected population when the carrying capacity of “A” Patches is reached.

Each Patch is also characterised by the absence or presence of exposure to different probabilities of additional mortality. Birds are classified according to their territoriality/ breeding status and by their sex and age class, which defines the corresponding values of the demographic parameters. The model runs at 1-year time-steps, representing the annual life cycle of the species. The temporal extent is 50 years, which is considered long enough to analyse the demographic consequences of exposure to additional mortality.

Table C.1 List of entities intervening in the model, with their state variables and corresponding range of possible values.

Entity/State Variable	Description	Unit (Values)
Patches		
type	Patch type (suitable or not for breeding territories)	Categoric (“A”; “B”)
additional_mortality	Define the presence of additional mortality sources	Boolean (True; False)
occupied_M	Define if a breeding male occupies the Patch	Boolean (True; False)
occupied_F	Define if a breeding female occupies the Patch	Boolean (True; False)
non_territorial	Number of non-territorial birds in the Patch	Integer (0 - 5)
Birds		
ID	Unique identification code	Integer (-)
sex	Individual’s sex	Categoric (“F”; “M”)
age	Individual’s age	Integer (1 - 20)
age_class	Individual’s age class	Ordinal categoric (“Fledgling”; “Juvenile”; “Immature”; “Subadult”; “Adult”)
territorial	Define if the individual is territorial (breeder) or not	Boolean (True; False)
patch_type	Type of current Patch	Categoric (“A”; “B”)
Global Environment		
sim_year	Current year of simulation	Integer (1 - 50)
patches_AM	Percentage of Patches with additional mortality sources	Integer (0 - 100)
mortality_AM_NT	Yearly death probability from additional mortality sources to non-breeders	Integer (0 - 100)
mortality_AM_T	Yearly death probability from additional mortality sources to breeders	Integer (0 - 100)

3. Process overview and scheduling

The model is structured in seven processes or submodels, two performed by the Environment: (i) time update and (ii) outputs update and collection; and five concerning Birds: (iii) *survival*, (iv) *ageing*, (v) *reproduction*, (vi) *territorial recruitment*, and (vii) *dispersal*. Individuals perform each process at each time-step, and the model was designed to collect outputs on the population, namely the annual population growth rate, the number of breeding pairs in year 50, the number of years of population persistence, the mean annual survival, the proportion of Birds dying in Patches with exposure to additional mortality, and the proportion of Birds in those patches at the end of the simulation.

The different processes are executed in the following predetermined order:

1. The Observer executes the "Time Update" submodel, which updates its state variable *sim_year*.
2. Each Bird executes the "Survival" submodel, where individuals aged 20 years die (due to having reached the maximum life span) and the remaining individuals face a survival trial due to stochastic mortality and additional mortality from anthropogenic origin.
3. Each Bird executes the "Ageing" submodel, which updates their age.
4. The non-breeding Birds execute the "territorial recruitment" submodel, in which they define if they will become territorials/breeders or remain non-territorials/non-breeders.
5. The territorial birds execute the "Reproduction" submodel, in which they try to reproduce with their pair, and, in case of success, females give birth between one and three chicks.
6. Birds who are in their first year of life run the "Dispersal" submodel, in which they leave the Patch of their parents to a Patch that is not occupied by territorial birds, starting their floater phase.
7. At last, the Observer executes the "Outputs Update and Collection" submodel, where, at the end of each timestep, various metrics about the current state of the population are updated and, at the end of the simulation (year 50), the metrics of interest for analysis are collected.

The model uses asynchronous updating, in which the agents update the state variables one at a time as they execute a submodel that uses the variable. To avoid artefacts of execution order, there was no hierarchy among agents of the same type (i.e., age or sex), and so the order in which agents conduct each process is random and varies at each time-step.

4. Design concepts

The design concepts Objectives, Learning, Prediction and Collectives do not apply to this model.

Basic principles **–** This model addresses the problematic of additional mortality from anthropogenic sources in long-lived avian territorial raptors. By differentiating Patches suitable for breeding territories (type "A" Patches) from others only usable by non-breeding individuals (type “B” Patches) and, by differentiating exposures to additional mortality that can, with different degrees of probability, differentially impact breeding and non-breeding individuals, this model allows answering questions such as: What are the priority locations (breeding territories or settlement areas used by non-territorial birds) for intervention and minimization of the impacts of additional mortality sources? Which fraction of the population, when exposed to additional mortality sources, causes the greatest impact on the population as a whole? What is the maximum exposure and probability of additional sources of mortality that a population can withstand? Such questions are especially important when trying to design an action plan to mitigate this type of impact.

At the agent level, this model is based on the population viability analysis (PVA) developed by Hernández-Matías et al. (2013) for the Bonelli’s eagle. In particular, we implemented the same life cycle in our model and used the estimated vital rates for the population of southern Portugal. Compared with the previous PVA model, our model is not simply a population-level model but instead, it explicitly represents lower levels of organization within the population. Furthermore, it is highly stochastic (see Stochasticity, below) and, the explicit representation of individuals and Patches, allows the existence of adaptive behaviours within the population (see Adaptation, below).

At the system level, the spatial representation is not fully explicit (the location of Patches and the distance between them is not intended to be realistic), as it is considered that during the period of a time step (1 year) an individual can easily cross the entire study area (i.e., can access any Patch; Hernández-Matías et al. 2010), and it is irrelevant to the objective of the model to know the exact geographic location and movements of each individual.

***Emergence* –** The key outcomes of the model are the annual population growth rate, the number of breeding pairs, and the year of population extinction. These outcomes emerge from the interaction between the models’ stochastic processes and how Birds respond to the additional mortality features.

Intermediate results, such as occupation of Patches emerges from the interaction between the number of Birds and their breeding status, and the percentage of Patches with additional mortality and their death probability.

***Adaptation* –** The primary adaptive behaviour of Birds is whether or not to become territorial (see “Territorial recruitment” submodel, below). This behaviour is modelled using indirect fitness seeking with stochastic rules that take the individual to select each alternative with a frequency similar to the frequency observed in real populations by class age.

Patch selection is also an adaptive behaviour of Birds. It is modelled via an indirect objective-seeking using a stochastic process dependent on the type and availability of free Patches. This behaviour can occur in three distinct occasions: when non-breeders leave the nest (see "Dispersal" submodel, below); when the Patch where a non-breeder stay is occupied by a breeding male; or when non-breeders become breeders (see "Territorial recruitment" submodel, below).

***Sensing* –** Birds are assumed able to sense its own sex and age class. Non-breeders are assumed able to perfectly sense the type and occupation (occupied_M; occupied_F; and non_breeders) of all Patches in the study area, since it is expected that during the period of a time-step (1 year) an individual will be able to cover the entire study area.

***Interaction* –** Birds interact directly with Patches and with other Birds. With Patches, interaction involves their occupation, and limiting its availability to other Birds. Interaction whit other Birds occurs when a male establishes his territory and forces non-breeders in that Patch to switch to another Patch and, between breeding pairs through the sharing of territory and the reproduction.

***Stochasticity* –** Stochasticity is incorporated in the model through several processes. When initializing the model (Initialization, below), stochasticity is used by randomly assign the sex and location of each Bird, and in the pairing of breeding individuals. Stochasticity is also used in initialization to randomly assign the location of additional mortality sources. This initialization stochasticity makes the model unsegregated at the beginning of a simulation, producing different results in each run. During the simulation, when a Bird move to another Patch, its choice of the new location is stochastic, but not completely random (see "Dispersal" and "Territorial recruitment" submodels, below). The new locations are stochastic because modelling the details of movement is unnecessary for this model.

Stochasticity is also used to make model events or behaviours occur with the same frequency as in real populations. Specifically, Bernoulli trials are used to assess when Birds become breeders and to define the Bird's survival, and a Poisson distribution is used to assess the clutch size for each pair, with the sex of the chicks being randomly assigned (see "Reproduction" submodel, below).

***Observation* –** The model was designed to collect data on the population at the end of the simulation (year 50). The key output is the annual population growth rate (λ), estimated as:

$$\lambda = \left(\frac{present}{past}\right)^{\frac{1}{n}}$$

Where “past” is the number of individuals at the beginning of the simulation, “present“ is the number of individuals at the end of the simulation and “n“ the number of years of simulation. In case the population goes extinct, the number of individuals in the last year before extinction is considered as “present”, and as “n” the number of years that passed until extinction. Values <1 indicate a population decline, while values >1 indicate a population growth.

Other populational outputs include the number of breeding pairs at the end of the simulation, the population persistence (number of years that the population persisted until its extinction, if it occurs), the mean annual survival, the proportion of Birds dying in Patches with exposure to additional mortality, and the proportion of Birds in those patches at the end of the simulation.

The average annual survival is independently calculated for both territorial and non-territorial birds. This is computed for each simulation as the mean survival rate over each year of the simulation, extending until its conclusion or the extinction of the population. In every year of the simulation, the survival rate for each territorial state is determined by dividing the number of individuals in that territorial state after running the survival submodel (where individual mortality occurs) by the number of individuals in that territorial state before running the survival submodel (N_post-survival / N_pre-survival).

5. Initialization

The percentage of Patches exposed to additional mortality (patches_AM), and the additional mortality probability to non-territorial (mortality_AM_NT) and territorial (mortality_AM_T) birds, are defined at the initialization phase and kept constant throughout the simulation. At the beginning of the simulation, all the type “A” and “B” Patches are randomly distributed across the study area. The Patches are empty, with state variables occupied_M and occupied_F set to “false”, and the non_territorial state variable set to “0”. The state variable additional_mortality is defined according to the state variable patches_AM. If a non-null percentage of Patches of each type is defined for patches_AM, then additional mortality is randomly set to “true” in some Patches and accordingly to the proportion of Patches affected, remaining “false” in the others.

Then, 66 territorial and 42 non-territorial birds are randomly assigned to the Patches. Initially, the model incorporates territorial males, as they play a pivotal role in establishing territories in Patches of type “A”, executing the “Set_Territory” component of the “Territorial_recruitment” submodel (see “Territorial recruitment” submodel, below). Subsequently, breeding females are introduced to the model, forming pairs with the already established males. Finally, non-territorial individuals are incorporated and execute the "Dispersal" submodel (see "Dispersal" submodel, below), evaluating available Patches and expressing a preference for those of type "A" whenever they are unoccupied. The breeding population size was chosen considering the 33 Bonelli's eagles pairs breeding in southern Portugal in 1991. The number of non-territorials was chosen after calculating the stable age-structure and identifying the number of non-breeders that would exist if the population were in equilibrium with a Leslie matrix analyses (Caswell, 2001), using the "popbio" package (Stubben et al., 2020). Birds ages are defined by the stable age structure. The sex of non-territorial birds is randomly assigned with a probability of 50/50, while in territorial birds a 1:1 sex ratio is defined.

6. Input data

The model does not use input data to represent time-varying processes.

7. Submodels

7.1 Survival

At each time-step, each Bird survives or dies following a Bernoulli trial, with a mortality probability conditional on its age class (Table C.2) and the exposure to additional anthropogenic mortality. The probability of mortality is calculated as:

$$Probability\ of\ mortality = 1 - (S \times (1 - AM))$$

Where S stands for survival of the individual's age class and AM stands for the annual additional mortality probability for the individual's breeding status (mortality_AM_NT or mortality_AM_T). A survival of 0 is assigned to individuals aged 20 years, corresponding to the maximum age recorded in the nature (DelHoyo et al., 1992). When a non-territorial individual dies, the non-territorial value of the Patch it occupied is subtracted by one. When a territorial individual dies, the state variable occupied_M or occupied_F of the territory it occupied is updated to "false", in the case of males and females, respectively. When one element of a breeding pair dies, the other remains as territorial in the same Patch and becomes available to form a new pair.

7.2 Ageing

One year is added to each Birds' age, and its age_ class is updated according to the terminology presented in Table C.2.

Table C.2 Summary of parameter information used in the model. Values correspond to empirical data from the Southern Portuguese population. * Parameters inferred from other populations.

Parameter	Values	Source
Age-classes		Hernández-Matías et al. (2013)
Fledgling	Age 1	
Juvenile	Age 2	
Immature	Age 3	
Subadult	Age 4	
Adult	Age >=5	
Survival		Hernández-Matías et al. (2013)
S1 (fledgling)	0.662946	
S23 (juvenile and immature)	0.719976	
S4 (subadult)	0.874833	
SA (adult)	0.937492	
Maximum age individuals can reach	20 years	delHoyo et al. (1992)
Recruitment		Hernández-Matías et al. (2013)
R1 (fledgling)	0	
R2 (juvenile)	0.160763*	
R3 (immature)	0.679674*	
R4 (subadult)	0.934197*	
RA (adult)	1*	
Fertility		Hernández-Matías et al. (2013)
F1 (fledgling)	0	
F2 (juvenile)	0.285714*	
F3 (immature)	0.5	
F4 (subadult)	0.830328	
FA (adult)	0.830328	

7.3 Territorial recruitment

At each time-step, non-territorial birds have a probability of recruiting to the breeding population (i.e., becoming territorial), which varies according to the recruitment probability of each age class (see Recruitment in Figure 3.1 of the main text and Table C.2). However, given the predominant role of male raptors in establishing and maintaining territories (Newton, 1979), effective recruitment occurs only under one of two conditions: 1) the availability of an unpaired territorial birds of the opposite sex; or 2) for males, the availability of a type 'A' Patch unoccupied by any territorial individual, allowing the establishment of a new territory (which could be shared with up to 4 non-territorial birds).

In the first scenario, a breeding pair is formed, resulting in the displacement of all non-territorial birds from the Patch that perform the "Dispersal" submodel (see “Dispersal” submodel, below). In this case, one unit is subtracted from the value of the state variable *non_territorial* of the Patch where the Bird was. Also, the state variable *occupied_M* or *occupied_F* (depending on the Bird's sex) of the new Patch is updated to "true". The Bird also updates its *patch_type* and *territory* state variables.

In the second scenario, if a type “A“ Patch is unavailable, the male remains non-territorial in its current location, anticipating a future recruitment opportunity. The same occurs with females in the absence of an unpaired territorial male (first scenario).

7.4 Reproduction

At each time-step, each paired breeding female produces from 0 to 3 offspring, with probabilities varying according to its age (Table C.2). Specifically, the number of offspring produced is drawn from a Poisson distribution truncated to 3 fledglings, with a mean corresponding to the fertility rate of the female’s age class. Each offspring remains until fledgling in the territory where it was born. Offspring sex is randomly assigned following a 1:1 sex ratio and age is set to 1 (first year of life).

7.5 Dispersal

At each time step, fledglings disperse out of the territories where they were born. Then, these individuals search for a Patch not occupied by any territorial Bird and occupied by up to other 4 non-territorial Birds. If type “A” Patches meeting these conditions are available, the non-territorial individual is randomly assigned to one of them and stops dispersing. If not, the individual settles in a type “B” Patch randomly selected, unless there are no longer any Patch meeting the required conditions, in which case it disperses out of the study area and is excluded from the system. At each time step, the patch_type state of each Bird and the non-territorial state of each Patch are updated. We have not considered dispersal into the study system from external populations.

Additionally, this submodel can also be performed by non-territorial birds that need to move out of Patches that have been occupied by a new breeding pair (see “Territorial Recruitment” submodel, above).

References

Caswell, H., 2001. Matrix population models: construction, analysis, and interpretation, Second edi. ed. Sinauer, Sunderland, Massachusetts, USA.

DelHoyo, J., Elliot, A., Sargatal, J., 1992. Handbook of Birds of the World, Vol. 1. Barcelona: Lynx Edicions.

Dias, A., Palma, L., Carvalho, F., Neto, D., Real, J., Beja, P., 2017. The role of conservative versus innovative nesting behavior on the 25-year population expansion of an avian predator. Ecol Evol 7, 4241–4253. https://doi.org/10.1002/ece3.3007

Grimm, V., 2005. Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology. Science (1979) 310, 987–991. https://doi.org/10.1126/science.1116681

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe’er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, 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., Railsback, S.F., 2012. Pattern-oriented modelling: A “multi-scope” for predictive systems ecology. Philosophical Transactions of the Royal Society B: Biological Sciences 367, 298–310. https://doi.org/10.1098/rstb.2011.0180

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. Jasss 23. https://doi.org/10.18564/jasss.4259

Hernández-Matías, A., Real, J., Moleón, M., Palma, L., Sánchez-Zapata, J.A., Pradel, R., Carrete, M., Gil-Sánchez, J.M., Beja, P., Balbontín, J., Vincent-Martin, N., Ravayrol, A., Benítez, J.R., Arroyo, B., Fernández, C., Ferreiro, E., García, J., 2013. From local monitoring to a broad-scale viability assessment: a case study for the Bonelli's Eagle in western Europe. Ecol Monogr 83, 239–261. https://doi.org/10.1890/12-1248.1

Hernández-Matías, A., Real, J., Pradel, R., Ravayrol, A., Vincent-Martin, N., Bosca, F., Cheylan, G., 2010. Determinants of Territorial Recruitment in Bonelli's Eagle (*Aquila fasciata*) Populations. Auk 127, 173–184. https://doi.org/10.1525/auk.2009.09143

Newton, I., 1979. Population ecology of raptors, T & A D Po. ed. Berkhamsted, England.

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/.

Salecker, J., Sciaini, M., Meyer, K.M., Wiegand, K., 2019. The NLRX R package: A next-generation framework for reproducible NetLogo model analyses. Methods Ecol Evol 10, 1854–1863. https://doi.org/10.1111/2041-210X.13286

Stubben, C., Milligan, B., Nantel, P., 2020. Package 'popbio'. Construction and Analysis of Matrix Population Models. Version, 2.7.

Wilensky, U., 1999. NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling. Northwestern University, Evanston, Illinois, U.S.

Supplementary Material for Chapter 3

Appendix D - Supplementary results

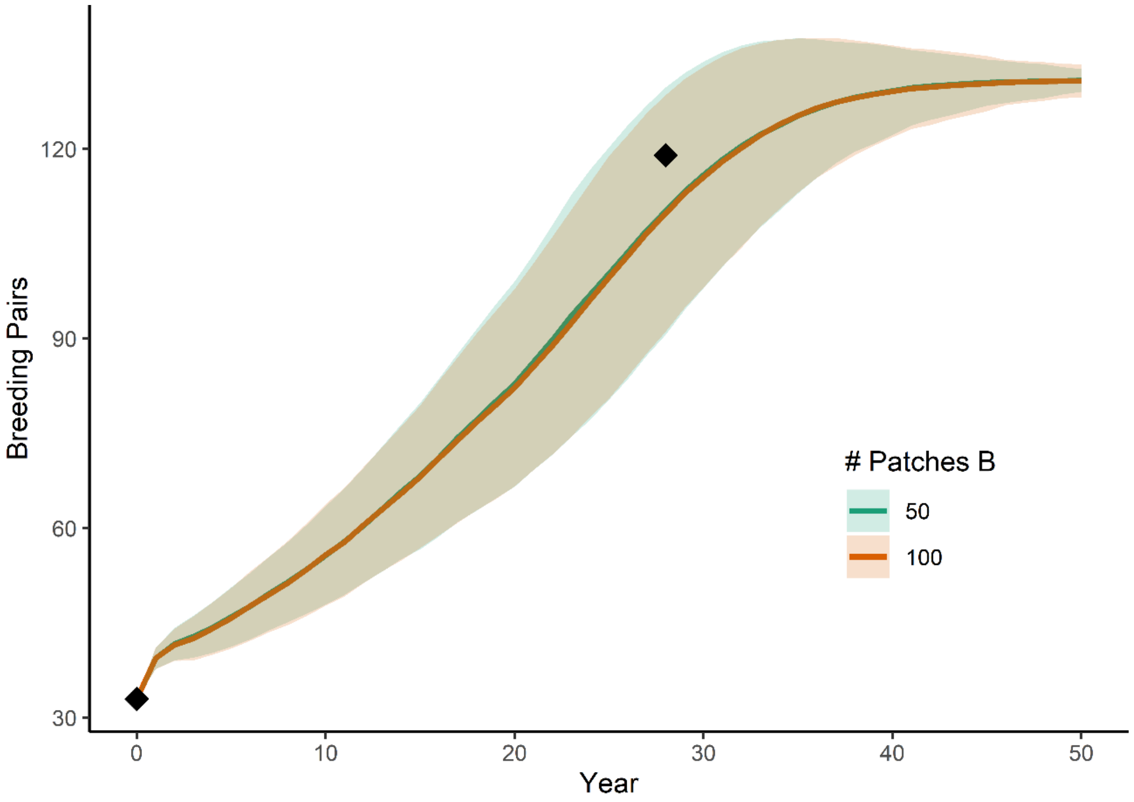


Figure D.1 Estimated growth of the Bonelli's eagle population of southern Portugal during a 50-year period, considering two scenarios for the number of type "B" Patches: 50 (baseline scenario) or 100 Patches. The lines and shadowed areas represent the mean number of breeding pairs and the standard deviation. The black diamonds represent the empirical value for the number of breeding pairs in 1991 and 2019 (28 years apart).

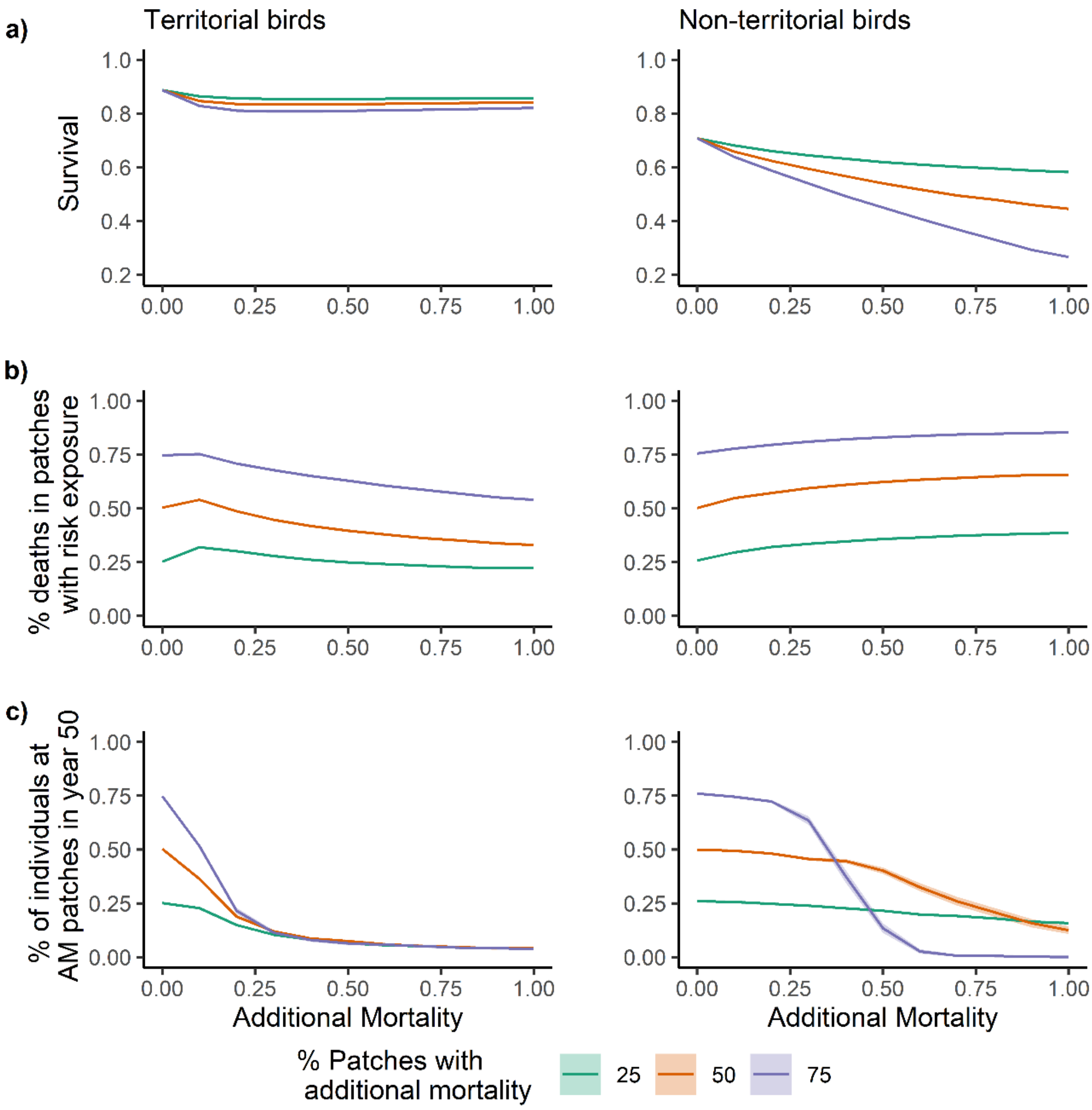


Figure D.2 Impact of exposure to additional mortality in 25%, 50% and 75% of the Patches on the a) mean annual survival of territorial of territorial and non-territorial birds, b) proportion of deaths in Patches exposed to additional mortality during the 50-year simulation, and c) proportion of individuals in Patches exposed to additional mortality at the end of the 50-year simulation period, when affecting only territorial or non-territorial birds. Additional mortality values represent a percentage increase in the mortality probability. Lines are mean values, and the shadowed areas represent the 95% confident-interval.

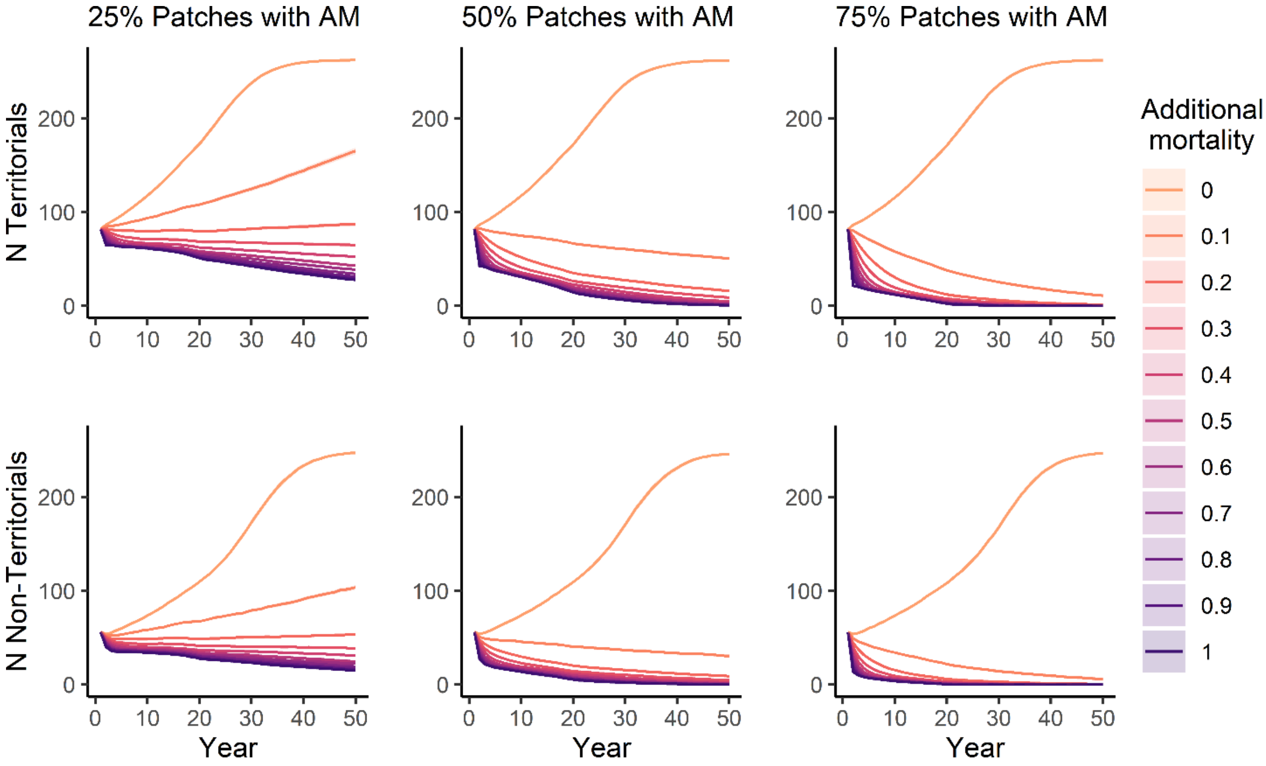


Figure D.3 Impact of exposure to additional mortality in 25%, 50% and 75% of the Patches exposed to additional mortality on the number of territorial (top) and non-territorial (bottom) birds across the 50-year simulation period. Additional mortality values represent a percentage increase in the mortality probability. Lines are mean values, and the shadowed areas represent the 95% confident-interval.

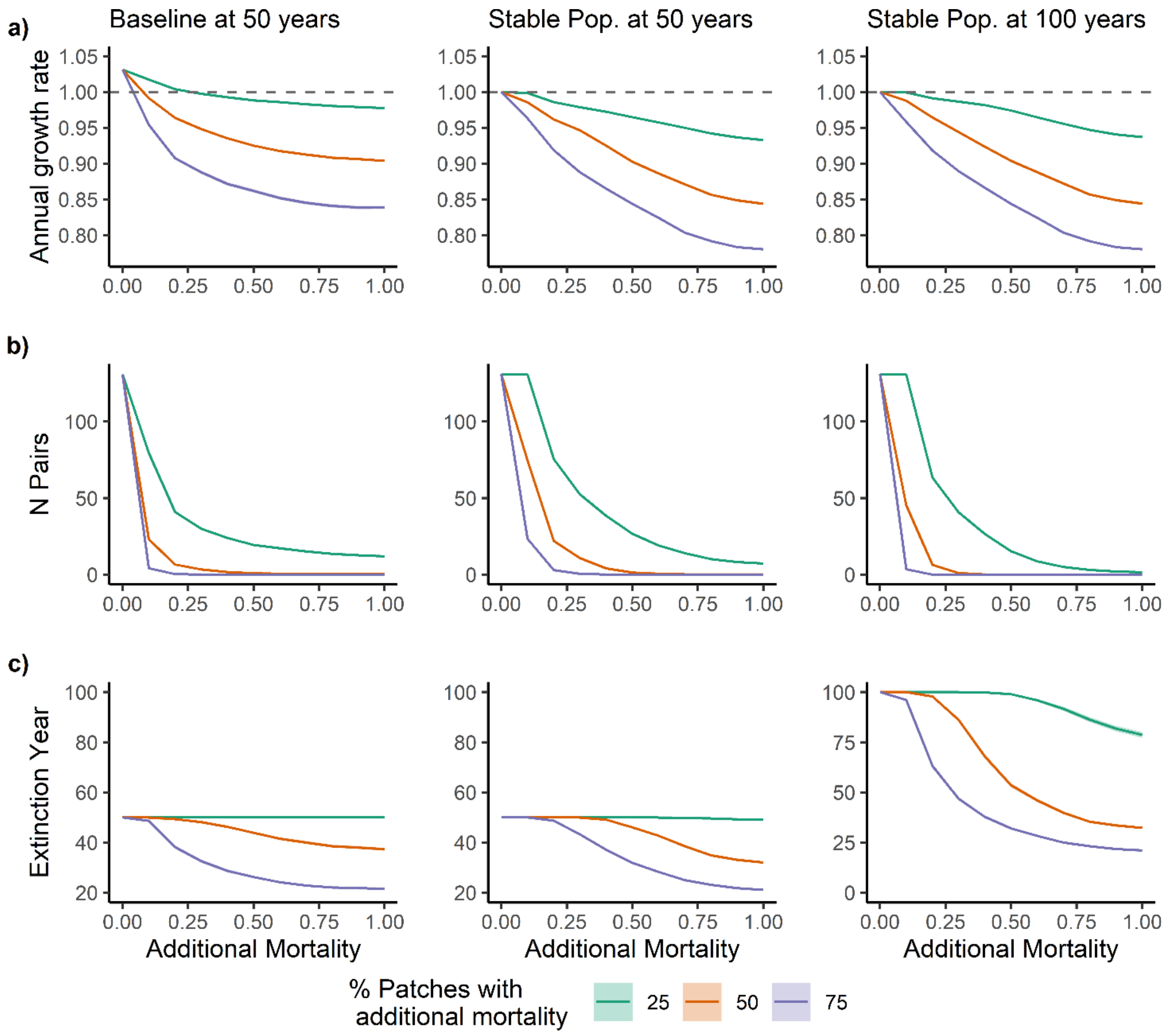
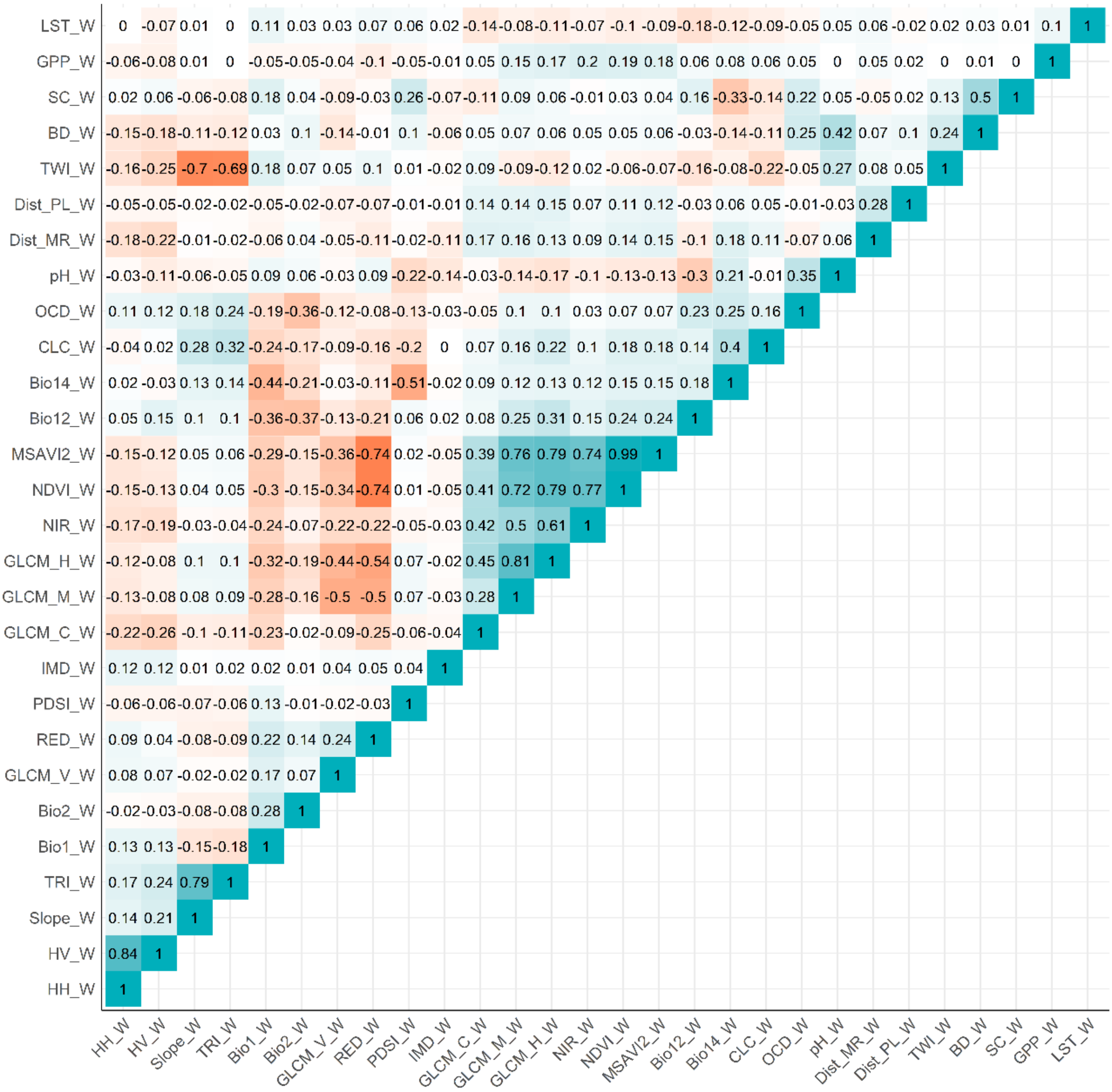


Figure D.4 Impact of exposure to additional mortality in 25%, 50% and 75% of the Patches on the a) annual growth rate (λ = 1 represents the population trend threshold: if λ > 1 the population increases and if λ < 1 the population declines), b) number of breeding pairs in year 50 and c) number of years of population persistence (number of years that the population persisted until eventual its extinction), when both territorial and non-territorial birds are affected, within three scenarios: (i) baseline model of an initial population of 33 breeding pairs during a 50-year simulation, (ii) model of an initial stable population of 131 breeding pairs during a 50-year simulation, and (iii) model of an initial stable population of 131 breeding pairs during a 100-year simulation. Additional mortality values represent a percentage increase in the mortality probability. Lines are mean values and the shadowed areas represent the 95% confident-interval.

Supplementary Material for Chapter 4

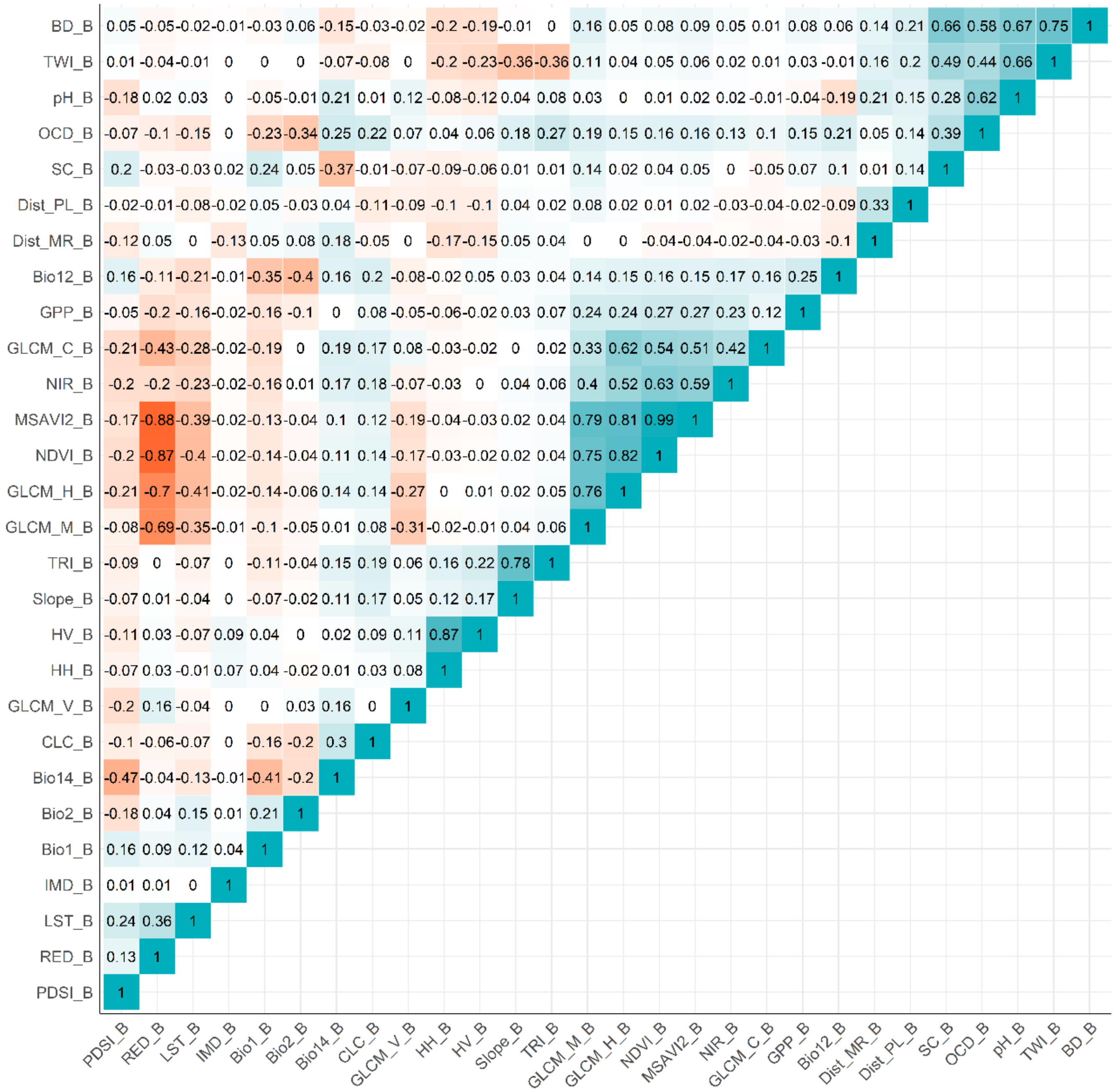
Appendix E - Supplementary results

Pairwise Pearson correlation matrix



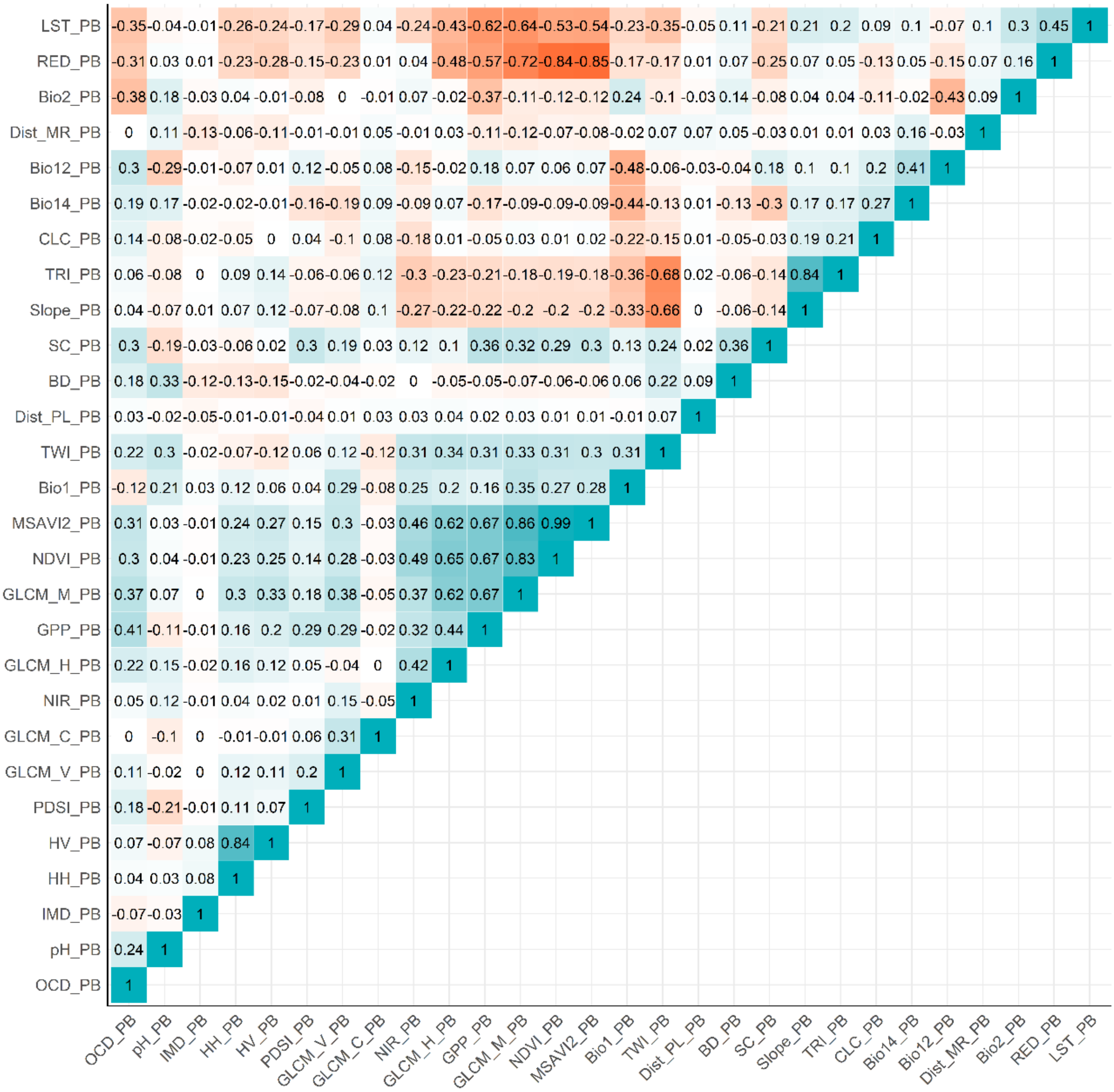
	HH_W	HV_W	Slope_W	TRI_W	Bio1_W	Bio2_W	GLCM_V_W	RED_W	PDSI_W	IMD_W	GLCM_C_W	GLCM_M_W	GLCM_H_W	NIR_W	NDVI_W	MSAVI2_W	Bio12_W	Bio14_W	CLC_W	OCD_W	pH_W	Dist_MR_W	Dist_PL_W	TWI_W	BD_W	SC_W	GPP_W	LST_W
LST_W	0	-0.07	0.01	0	0.11	0.03	0.03	0.07	0.06	0.02	-0.14	-0.08	-0.11	-0.07	-0.1	-0.09	-0.18	-0.12	-0.09	-0.05	0.05	0.06	-0.02	0.02	0.03	0.01	0.1	1
GPP_W	-0.06	-0.08	0.01	0	-0.05	-0.05	-0.04	-0.1	-0.05	-0.01	0.05	0.15	0.17	0.2	0.19	0.18	0.06	0.08	0.06	0.05	0	0.05	0.02	0	0.01	0	1	
SC_W	0.02	0.06	-0.06	-0.08	0.18	0.04	-0.09	-0.03	0.26	-0.07	-0.11	0.09	0.06	-0.01	0.03	0.04	0.16	-0.33	-0.14	0.22	0.05	-0.05	0.02	0.13	0.5	1		
BD_W	-0.15	-0.18	-0.11	-0.12	0.03	0.1	-0.14	-0.01	0.1	-0.06	0.05	0.07	0.06	0.05	0.05	0.06	-0.03	-0.14	-0.11	0.25	0.42	0.07	0.1	0.24	1			
TWI_W	-0.16	-0.25	-0.7	-0.69	0.18	0.07	0.05	0.1	0.01	-0.02	0.09	-0.09	-0.12	0.02	-0.06	-0.07	-0.16	-0.08	-0.22	-0.05	0.27	0.08	0.05	1				
Dist_PL_W	-0.05	-0.05	-0.02	-0.02	-0.05	-0.02	-0.07	-0.07	-0.01	-0.01	0.14	0.14	0.15	0.07	0.11	0.12	-0.03	0.06	0.05	-0.01	-0.03	0.28	1					
Dist_MR_W	-0.18	-0.22	-0.01	-0.02	-0.06	0.04	-0.05	-0.11	-0.02	-0.11	0.17	0.16	0.13	0.09	0.14	0.15	-0.1	0.18	0.11	-0.07	0.06	1						
pH_W	-0.03	-0.11	-0.06	-0.05	0.09	0.06	-0.03	0.09	-0.22	-0.14	-0.03	-0.14	-0.17	-0.1	-0.13	-0.13	-0.3	0.21	-0.01	0.35	1							
OCD_W	0.11	0.12	0.18	0.24	-0.19	-0.36	-0.12	-0.08	-0.13	-0.03	-0.05	0.1	0.1	0.03	0.07	0.07	0.23	0.25	0.16	1								
CLC_W	-0.04	0.02	0.28	0.32	-0.24	-0.17	-0.09	-0.16	-0.2	0	0.07	0.16	0.22	0.1	0.18	0.18	0.14	0.4	1									
Bio14_W	0.02	-0.03	0.13	0.14	-0.44	-0.21	-0.03	-0.11	-0.51	-0.02	0.09	0.12	0.13	0.12	0.15	0.15	0.18	1										
Bio12_W	0.05	0.15	0.1	0.1	-0.36	-0.37	-0.13	-0.21	0.06	0.02	0.08	0.25	0.31	0.15	0.24	0.24	1											
MSAVI2_W	-0.15	-0.12	0.05	0.06	-0.29	-0.15	-0.36	-0.74	0.02	-0.05	0.39	0.76	0.79	0.74	0.99	1												
NDVI_W	-0.15	-0.13	0.04	0.05	-0.3	-0.15	-0.34	-0.74	0.01	-0.05	0.41	0.72	0.79	0.77	1													
NIR_W	-0.17	-0.19	-0.03	-0.04	-0.24	-0.07	-0.22	-0.22	-0.05	-0.03	0.42	0.5	0.61	1														
GLCM_H_W	-0.12	-0.08	0.1	0.1	-0.32	-0.19	-0.44	-0.54	0.07	-0.02	0.45	0.81	1															
GLCM_M_W	-0.13	-0.08	0.08	0.09	-0.28	-0.16	-0.5	-0.5	0.07	-0.03	0.28	1																
GLCM_C_W	-0.22	-0.26	-0.1	-0.11	-0.23	-0.02	-0.09	-0.25	-0.06	-0.04	1																	
IMD_W	0.12	0.12	0.01	0.02	0.02	0.01	0.04	0.05	0.04	1																		
PDSI_W	-0.06	-0.06	-0.07	-0.06	0.13	-0.01	-0.02	-0.03	1																			
RED_W	0.09	0.04	-0.08	-0.09	0.22	0.14	0.24	1																				
GLCM_V_W	0.08	0.07	-0.02	-0.02	0.17	0.07	1																					
Bio2_W	-0.02	-0.03	-0.08	-0.08	0.28	1																						
Bio1_W	0.13	0.13	-0.15	-0.18	1																							
TRI_W	0.17	0.24	0.79	1																								
Slope_W	0.14	0.21	1																									
HV_W	0.84	1																										
HH_W	1																											

Figure E.1a Winter – Pairwise Pearson correlation matrix for all predictor variables. See Table E.1 for description of the predictor's acronyms.



	PDSI_B	RED_B	LST_B	IMD_B	Bio1_B	Bio2_B	Bio14_B	CLC_B	GLCM_V_B	HH_B	HV_B	Slope_B	TRI_B	GLCM_M_B	GLCM_H_B	NDVI_B	MSAVI2_B	NIR_B	GLCM_C_B	GPP_B	Bio12_B	Dist_MR_B	Dist_PL_B	SC_B	OCD_B	pH_B	TWI_B	BD_B
BD_B	0.05	-0.05	-0.02	-0.01	-0.03	0.06	-0.15	-0.03	-0.02	-0.2	-0.19	-0.01	0	0.16	0.05	0.08	0.09	0.05	0.01	0.08	0.06	0.14	0.21	0.66	0.58	0.67	0.75	1
TWI_B	0.01	-0.04	-0.01	0	0	0	-0.07	-0.08	0	-0.2	-0.23	-0.36	-0.36	0.11	0.04	0.05	0.06	0.02	0.01	0.03	-0.01	0.16	0.2	0.49	0.44	0.66	1	
pH_B	-0.18	0.02	0.03	0	-0.05	-0.01	0.21	0.01	0.12	-0.08	-0.12	0.04	0.08	0.03	0	0.01	0.02	0.02	-0.01	-0.04	-0.19	0.21	0.15	0.28	0.62	1		
OCD_B	-0.07	-0.1	-0.15	0	-0.23	-0.34	0.25	0.22	0.07	0.04	0.06	0.18	0.27	0.19	0.15	0.16	0.16	0.13	0.1	0.15	0.21	0.05	0.14	0.39	1			
SC_B	0.2	-0.03	-0.03	0.02	0.24	0.05	-0.37	-0.01	-0.07	-0.09	-0.06	0.01	0.01	0.14	0.02	0.04	0.05	0	-0.05	0.07	0.1	0.01	0.14	1				
Dist_PL_B	-0.02	-0.01	-0.08	-0.02	0.05	-0.03	0.04	-0.11	-0.09	-0.1	-0.1	0.04	0.02	0.08	0.02	0.01	0.02	-0.03	-0.04	-0.02	-0.09	0.33	1					
Dist_MR_B	-0.12	0.05	0	-0.13	0.05	0.08	0.18	-0.05	0	-0.17	-0.15	0.05	0.04	0	0	-0.04	-0.04	-0.02	-0.04	-0.03	-0.1	1						
Bio12_B	0.16	-0.11	-0.21	-0.01	-0.35	-0.4	0.16	0.2	-0.08	-0.02	0.05	0.03	0.04	0.14	0.15	0.16	0.15	0.17	0.16	0.25	1							
GPP_B	-0.05	-0.2	-0.16	-0.02	-0.16	-0.1	0	0.08	-0.05	-0.06	-0.02	0.03	0.07	0.24	0.24	0.27	0.27	0.23	0.12	1								
GLCM_C_B	-0.21	-0.43	-0.28	-0.02	-0.19	0	0.19	0.17	0.08	-0.03	-0.02	0	0.02	0.33	0.62	0.54	0.51	0.42	1									
NIR_B	-0.2	-0.2	-0.23	-0.02	-0.16	0.01	0.17	0.18	-0.07	-0.03	0	0.04	0.06	0.4	0.52	0.63	0.59	1										
MSAVI2_B	-0.17	-0.88	-0.39	-0.02	-0.13	-0.04	0.1	0.12	-0.19	-0.04	-0.03	0.02	0.04	0.79	0.81	0.99	1											
NDVI_B	-0.2	-0.87	-0.4	-0.02	-0.14	-0.04	0.11	0.14	-0.17	-0.03	-0.02	0.02	0.04	0.75	0.82	1												
GLCM_H_B	-0.21	-0.7	-0.41	-0.02	-0.14	-0.06	0.14	0.14	-0.27	0	0.01	0.02	0.05	0.76	1													
GLCM_M_B	-0.08	-0.69	-0.35	-0.01	-0.1	-0.05	0.01	0.08	-0.31	-0.02	-0.01	0.04	0.06	1														
TRI_B	-0.09	0	-0.07	0	-0.11	-0.04	0.15	0.19	0.06	0.16	0.22	0.78	1															
Slope_B	-0.07	0.01	-0.04	0	-0.07	-0.02	0.11	0.17	0.05	0.12	0.17	1																
HV_B	-0.11	0.03	-0.07	0.09	0.04	0	0.02	0.09	0.11	0.87	1																	
HH_B	-0.07	0.03	-0.01	0.07	0.04	-0.02	0.01	0.03	0.08	1																		
GLCM_V_B	-0.2	0.16	-0.04	0	0	0.03	0.16	0	1																			
CLC_B	-0.1	-0.06	-0.07	0	-0.16	-0.2	0.3	1																				
Bio14_B	-0.47	-0.04	-0.13	-0.01	-0.41	-0.2	1																					
Bio2_B	-0.18	0.04	0.15	0.01	0.21	1																						
Bio1_B	0.16	0.09	0.12	0.04	1																							
IMD_B	0.01	0.01	0	1																								
LST_B	0.24	0.36	1																									
RED_B	0.13	1																										
PDSI_B	1																											

Figure E.1b Breeding – Pairwise Pearson correlation matrix for all predictor variables. See Table E.1 for a description of the predictor's acronyms.



	OCD_PB	pH_PB	IMD_PB	HH_PB	HV_PB	PDSI_PB	GLCM_V_PB	GLCM_C_PB	NIR_PB	GLCM_H_PB	GPP_PB	GLCM_M_PB	NDVI_PB	MSAVI2_PB	Bio1_PB	TWI_PB	Dist_PL_PB	BD_PB	SC_PB	Slope_PB	TRI_PB	CLC_PB	Bio14_PB	Bio12_PB	Dist_MR_PB	Bio2_PB	RED_PB	LST_PB
LST_PB	-0.35	-0.04	-0.01	-0.26	-0.24	-0.17	-0.29	0.04	-0.24	-0.43	-0.62	-0.64	-0.53	-0.54	-0.23	-0.35	-0.05	0.11	-0.21	0.21	0.2	0.09	0.1	-0.07	0.1	0.3	0.45	1
RED_PB	-0.31	0.03	0.01	-0.23	-0.28	-0.15	-0.23	0.01	0.04	-0.48	-0.57	-0.72	-0.84	-0.85	-0.17	-0.17	0.01	0.07	-0.25	0.07	0.05	-0.13	0.05	-0.15	0.07	0.16	1	
Bio2_PB	-0.38	0.18	-0.03	0.04	-0.01	-0.08	0	-0.01	0.07	-0.02	-0.37	-0.11	-0.12	-0.12	0.24	-0.1	-0.03	0.14	-0.08	0.04	0.04	-0.11	-0.02	-0.43	0.09	1		
Dist_MR_PB	0	0.11	-0.13	-0.06	-0.11	-0.01	-0.01	0.05	-0.01	0.03	-0.11	-0.12	-0.07	-0.08	-0.02	0.07	0.07	0.05	-0.03	0.01	0.01	0.03	0.16	-0.03	1			
Bio12_PB	0.3	-0.29	-0.01	-0.07	0.01	0.12	-0.05	0.08	-0.15	-0.02	0.18	0.07	0.06	0.07	-0.48	-0.06	-0.03	-0.04	0.18	0.1	0.1	0.2	0.41	1				
Bio14_PB	0.19	0.17	-0.02	-0.02	-0.01	-0.16	-0.19	0.09	-0.09	0.07	-0.17	-0.09	-0.09	-0.09	-0.44	-0.13	0.01	-0.13	-0.3	0.17	0.17	0.27	1					
CLC_PB	0.14	-0.08	-0.02	-0.05	0	0.04	-0.1	0.08	-0.18	0.01	-0.05	0.03	0.01	0.02	-0.22	-0.15	0.01	-0.05	-0.03	0.19	0.21	1						
TRI_PB	0.06	-0.08	0	0.09	0.14	-0.06	-0.06	0.12	-0.3	-0.23	-0.21	-0.18	-0.19	-0.18	-0.36	-0.68	0.02	-0.06	-0.14	0.84	1							
Slope_PB	0.04	-0.07	0.01	0.07	0.12	-0.07	-0.08	0.1	-0.27	-0.22	-0.22	-0.2	-0.2	-0.2	-0.33	-0.66	0	-0.06	-0.14	1								
SC_PB	0.3	-0.19	-0.03	-0.06	0.02	0.3	0.19	0.03	0.12	0.1	0.36	0.32	0.29	0.3	0.13	0.24	0.02	0.36	1									
BD_PB	0.18	0.33	-0.12	-0.13	-0.15	-0.02	-0.04	-0.02	0	-0.05	-0.05	-0.07	-0.06	-0.06	0.06	0.22	0.09	1										
Dist_PL_PB	0.03	-0.02	-0.05	-0.01	-0.01	-0.04	0.01	0.03	0.03	0.04	0.02	0.03	0.01	0.01	-0.01	0.07	1											
TWI_PB	0.22	0.3	-0.02	-0.07	-0.12	0.06	0.12	-0.12	0.31	0.34	0.31	0.33	0.31	0.3	0.31	1												
Bio1_PB	-0.12	0.21	0.03	0.12	0.06	0.04	0.29	-0.08	0.25	0.2	0.16	0.35	0.27	0.28	1													
MSAVI2_PB	0.31	0.03	-0.01	0.24	0.27	0.15	0.3	-0.03	0.46	0.62	0.67	0.86	0.99	1														
NDVI_PB	0.3	0.04	-0.01	0.23	0.25	0.14	0.28	-0.03	0.49	0.65	0.67	0.83	1															
GLCM_M_PB	0.37	0.07	0	0.3	0.33	0.18	0.38	-0.05	0.37	0.62	0.67	1																
GPP_PB	0.41	-0.11	-0.01	0.16	0.2	0.29	0.29	-0.02	0.32	0.44	1																	
GLCM_H_PB	0.22	0.15	-0.02	0.16	0.12	0.05	-0.04	0	0.42	1																		
NIR_PB	0.05	0.12	-0.01	0.04	0.02	0.01	0.15	-0.05	1																			
GLCM_C_PB	0	-0.1	0	-0.01	-0.01	0.06	0.31	1																				
GLCM_V_PB	0.11	-0.02	0	0.12	0.11	0.2	1																					
PDSI_PB	0.18	-0.21	-0.01	0.11	0.07	1																						
HV_PB	0.07	-0.07	0.08	0.84	1																							
HH_PB	0.04	0.03	0.08	1																								
IMD_PB	-0.07	-0.03	1																									
pH_PB	0.24	1																										
OCD_PB	1																											

Figure E.1c Post-breeding – Pairwise Pearson correlation matrix for all predictor variables. See Table E.1 for a description of the predictor's acronyms.

List of predictors

Table E.1 List of predictors included in the SDMs of the little bustard in Extremadura, Spain, including the biological rationale for their selection and the data source or the formula or model utilised in their calculus.

Predictor name	Biological rationale	Formula, Model, or Data source	Reference
Slope	The species is associated with plains and areas with gentle slopes.	$arctan * \frac{(-H)}{(-G)}$	(Zevenbergen & Thorne, 1987)
TRI	-	$\ln(sqr(\text{ssdiff}))$ Where ssdiff = temporary scalar, square feet	(Riley et al., 1999)
TWI	-	$\ln(a/\tan\beta)$ Where a = upslope contributing area per unit contour; $\tan\beta$ = local slope angle	(Quinn et al., 1995)
Altitude	-	Global Elevation Model	(Crippen et al., 2016)
Dist_MR	The species distribution is known to be affected by human infrastructures as roads and powerlines, in particular during the breeding season.	Open-StreetMap contributors	(Haklay & Weber, 2008)
Dist_PL		Open-StreetMap contributors and authors' data	
OCD	-	World Soil Information Service Models	(Hengl et al., 2017)
pH	-		
SC	-		
BD	-		
Bio1	Predictors derived from the climatological normal can be used as a climatological fingerprint of each location and the conditions that influenced the species' historical distribution.	Global Circulation Models	(Fick & Hijmans, 2017)
Bio2			
Bio12			
Bio14			
RED	The RED and NIR bands are crucial for monitoring vegetation health and productivity. They correspond to the wavelengths of light that are absorbed and reflected by chlorophyll, the pigment responsible for photosynthesis in plants. The spectral information in these bands can indicate the presence and vitality of vegetation, which is a fundamental resource for many species. Moreover, Red and NIR bands can help discriminate between different habitat types and vegetation classes based on their spectral signatures.	-	-
NIR		-	-

Predictor name	Biological rationale	Formula, Model, or Data source	Reference
NDVI	NDVI is a measure of the "greenness" or vegetation density in a given area. NDVI serves as an indicator of vegetation quality and quantity. Higher NDVI values often correlate with greater primary productivity, which supports a more diverse community of plant species.	C$\frac{(NIR-RED)}{(NIR+RED)}$	(Huete et al., 2002)
MSAVI2	The same as NDVI but improved for better characterization of semi-arid environments where bare areas are a common element across the landscape.	$\frac{(2*NIR+1-\sqrt{(2*NIR+1)^2-8*(NIR-RED)}}{2}$	(Richardson & Wiegand, 1977)
GLCM_M	Descriptive statistics derived from GLCM provide summary statistics of texture patterns, such as mean and variance. These statistics can offer insights into the landscape's complexity and can be biologically relevant in quantifying the complexity of habitat structures.	Textural variables calculated using the first Normalized Difference Vegetation Index (NDVI) with a 3 × 3 pixels spatial moving window in all directions (0°, 45°, 90°, and 135°)	(Haralick et al., 1973)
GLCM_V			
GLCM_H	Contrast metrics derived from GLCM, such as homogeneity and contrast, provide information about the sharpness of transitions between different image features, which can be indicative of heterogeneity or abrupt changes in the landscape. For example, high contrast values in GLCM may indicate the presence of habitat edges, which are ecologically important for edge-dwelling species.		
GLCM_C			
GPP	-	https://lpdaac.usgs.gov/products/mod17a2hv006	-
PDSI	-	https://www.climatologylab.org/gridmet.html	-
LST	Provides insights into temperature variations across the landscape, which can be useful to assess species' microclimate preferences.	https://lpdaac.usgs.gov/products/mod11a2v061/	-
HH	HH and HV polarizations can reveal details about the structure and composition of habitats. These polarizations respond differently to the scattering properties of various objects in the landscape, including vegetation, water, and soil. This information can be used to distinguish between different vegetation types, such as forests, wetlands, and open grasslands, which are critical for understanding species habitat preferences. Both polarizations can capture information about the vertical structure and moisture content of vegetation. For example, HV is sensitive to the volume scattering from vegetation, making it useful for discriminating between different forest types and tree densities.	-	(Shimada et al., 2014)
HV		-	
CLC	-	-	Copernicus Land Monitoring Service
IMD	-	-	

Variance Inflation Factor (VIF)

Table E.2a Winter – Variance Inflation Factor (VIF) for each of the predictor variables. See Table E.1 for a description of the predictor's acronyms.

Variable	VIF
GLCM_C_W	1.590515
HV_W	1.363306
SC_W	1.830307
OCD_W	1.813115
TRI_W	2.276368
TWI_W	2.248382
Bio12_W	1.759193
PDSI_W	1.561406
Bio1_W	1.700829
GLCM_V_W	1.412891
Bio2_W	1.417867
Bio14_W	2.366495
GLCM_M_W	2.229435
pH_W	2.033075
Dist_MR_W	1.589146
GPP_W	1.079797
LST_W	1.098377
NIR_W	1.626452
Dist_PL_W	1.459111
BD_W	1.909122
CLC_W	1.363936
RED_W	1.409383
IMD_W	1.054428

Table E.2b Breeding – Variance Inflation Factor (VIF) for each of the predictor variables. See Table E.1 for a description of the predictor's acronyms.

Variable	VIF
GLCM_V_B	1.144370
NIR_B	1.203215
RED_B	1.253758
GPP_B	1.171964
LST_B	1.353628
PDSI_B	1.726684
Bio1_B	1.524176
Bio2_B	1.561495
Bio14_B	2.303053
TRI_B	1.845192
TWI_B	3.732355
Dist_MR_B	1.281093
Dist_PL_B	1.235996
OCD_B	3.123322
pH_B	3.566011
SC_B	2.196063
HV_B	1.195672
IMD_B	1.029656
Bio12_B	1.802278
CLC_B	1.243968

Table E.2c Post-breeding – Variance Inflation Factor VIF) for each of the predictor variables. See Table E.1 for a description of the predictor's acronyms.

Variable	**VIF**
GLCM_V_PB	1.483815
NIR_PB	1.304491
GLCM_C_PB	1.213120
GPP_PB	2.353993
LST_PB	1.990320
PDSI_PB	1.252250
Bio1_PB	1.973201
Bio2_PB	1.782087
Bio14_PB	2.271079
TRI_PB	2.360615
TWI_PB	2.605133
Dist_MR_PB	1.110610
Dist_PL_PB	1.058772
BD_PB	1.780942
OCD_PB	2.104946
pH_PB	2.299806
SC_PB	1.928795
HV_PB	1.197286
IMD_PB	1.051006
Bio12_PB	2.219643
CLC_PB	1.355882

Boruta results

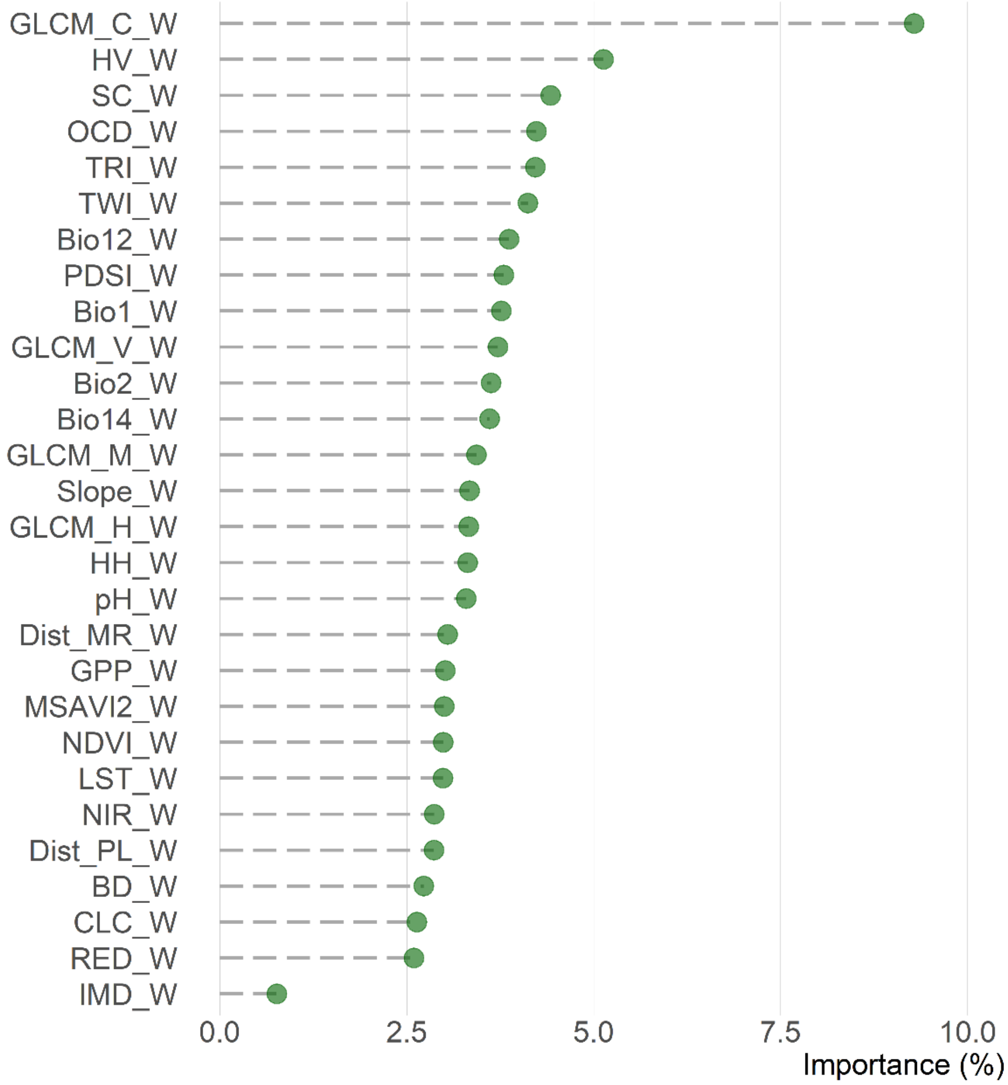


Figure E.2a Winter - Variable explanation power during the variables screening procedure, calculated by the Boruta feature selection algorithm. See Table E.1 for a description of the variable's acronyms.

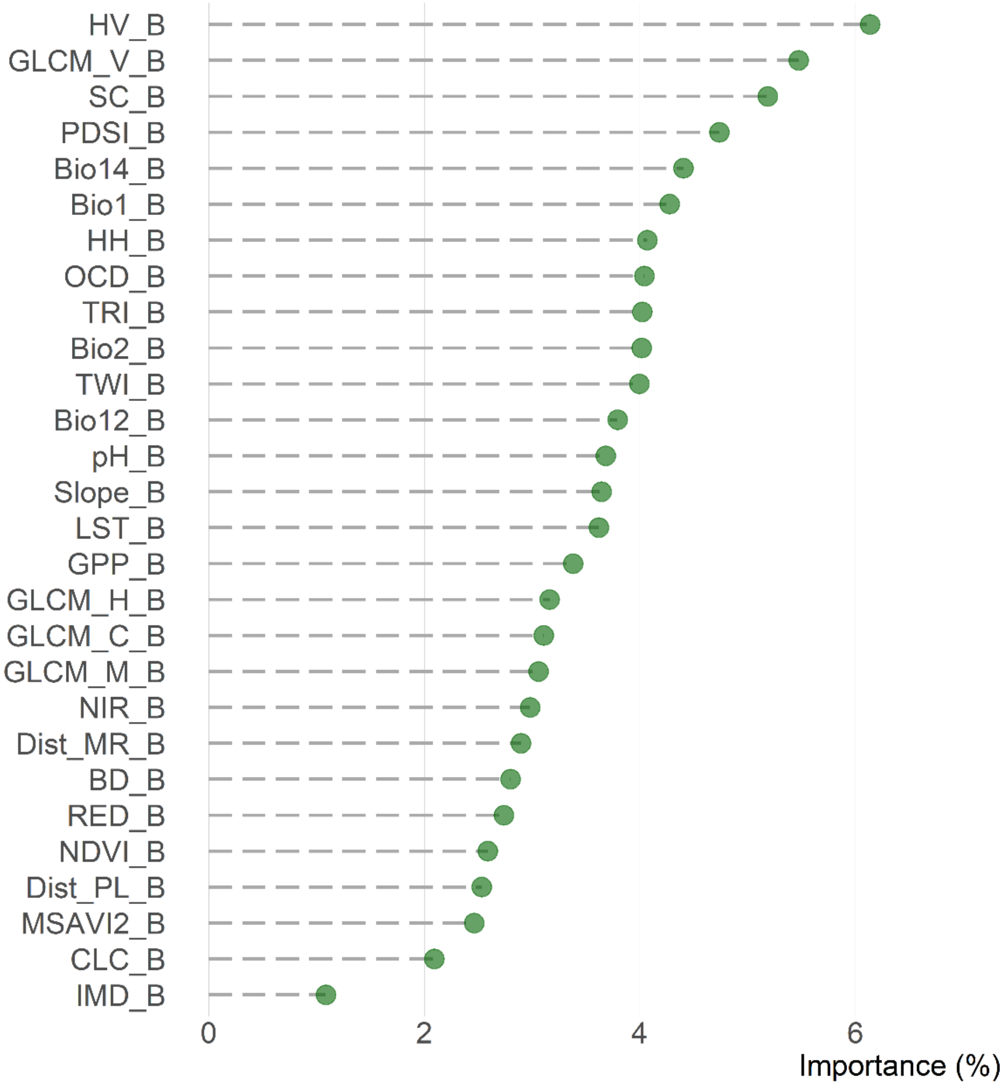


Figure E.2b Breeding - Variable explanation power during the variables screening procedure, calculated by the Boruta feature selection algorithm. See Table E.1 for a description of the variable's acronyms.

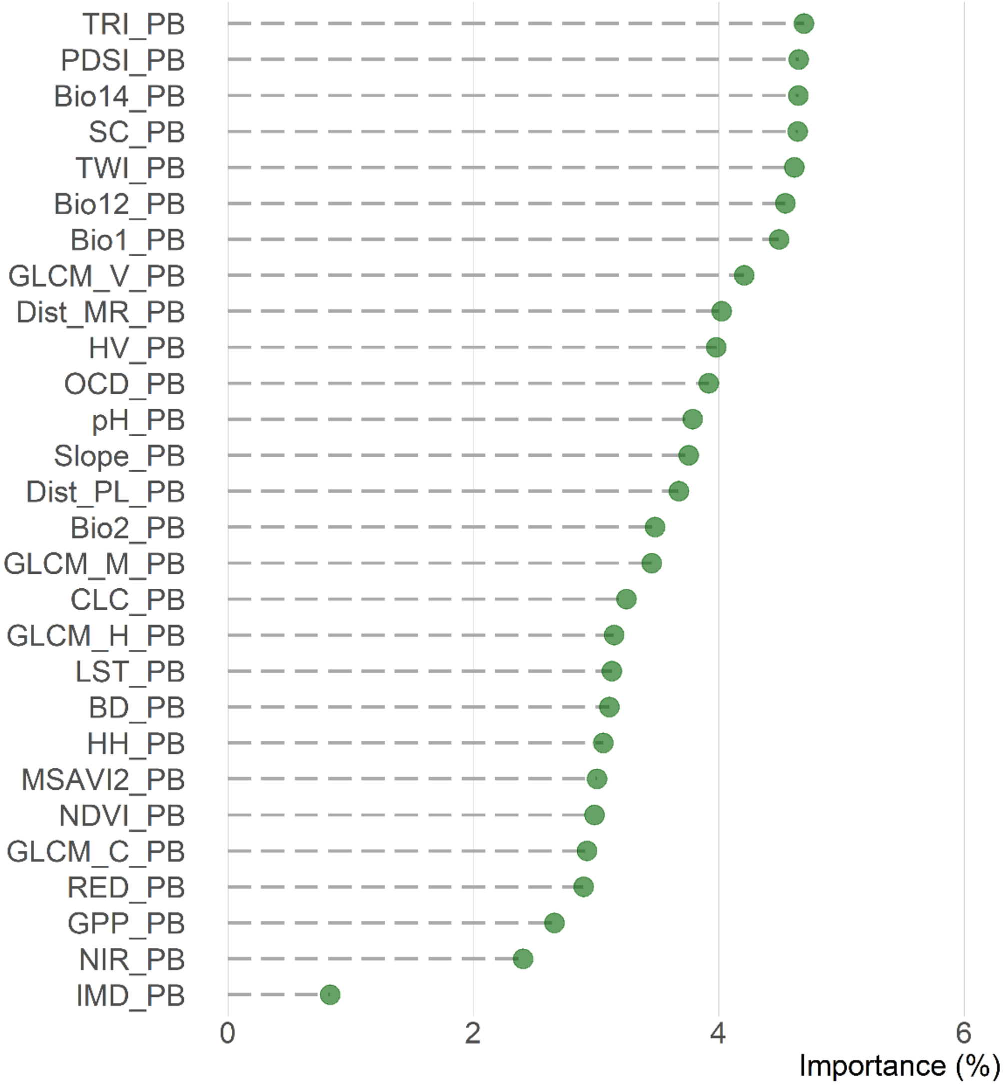


Figure E.2c Post- Breeding - Variable explanation power during the variables screening procedure, calculated by the Boruta feature selection algorithm. See Table E.1 for a description of the variable's acronyms.

Response curves

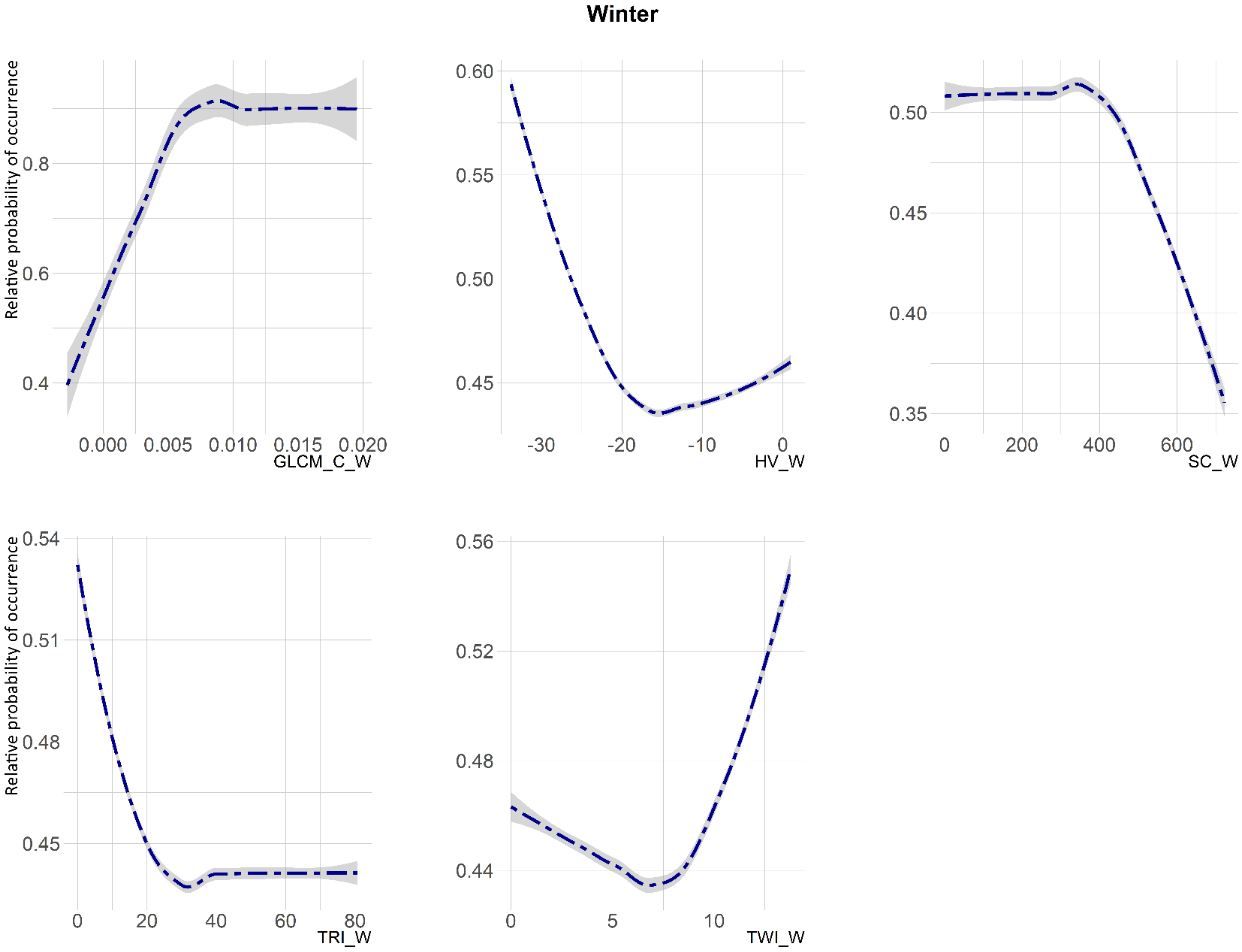
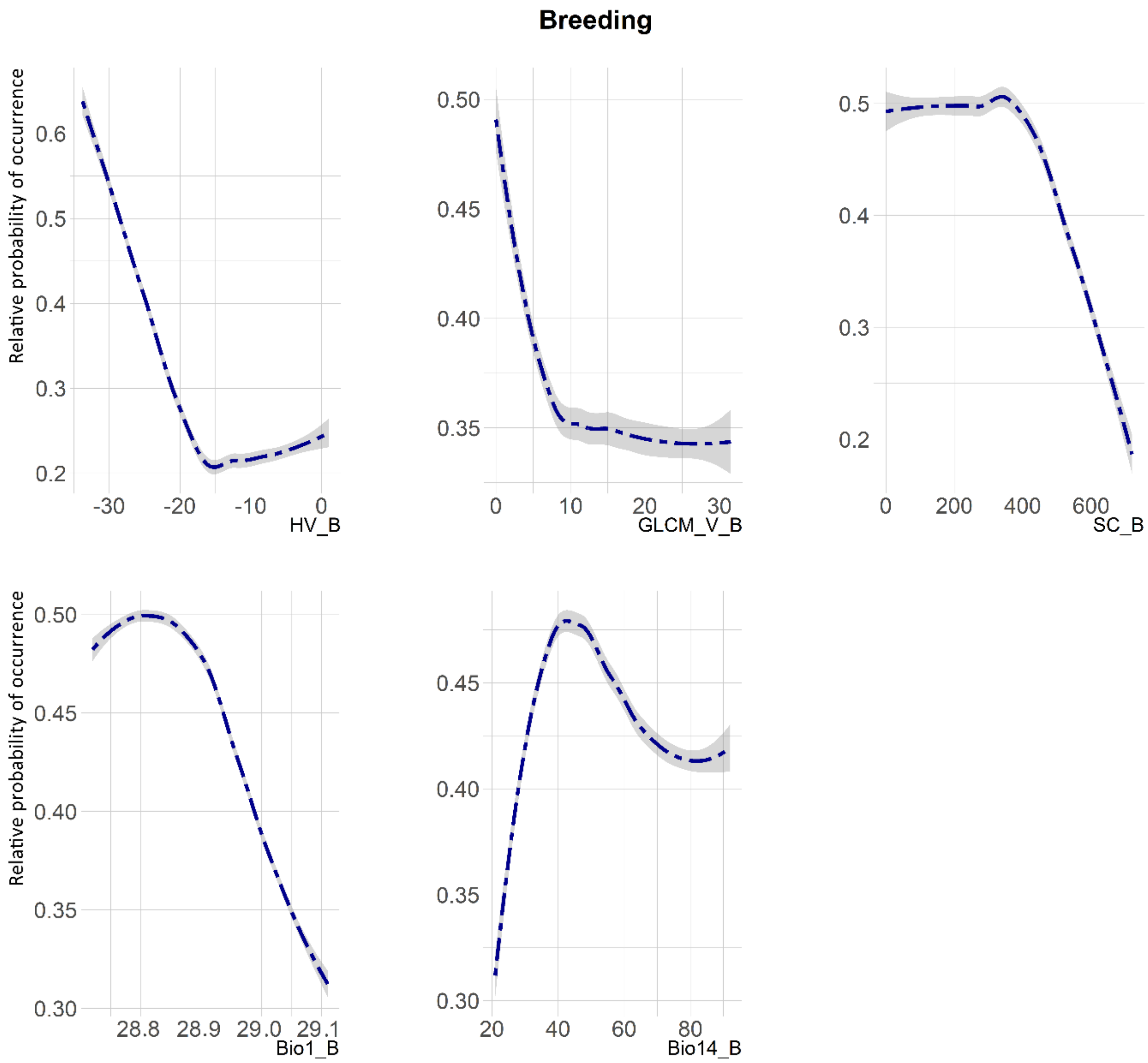


Figure E.3a Partial response plots (partial dependence curves) of top-5 variables during the winter phase. The average 10-fold cross-validation results are depicted by the blue lines. The grey area limits ± standard error. GLCM_C - NDVI-based texture contrast; HV - HV polarization; SC - Sand content; TRI - Terrain Ruggedness Index; TWI - Terrain Water Index.



Breeding

Figure E.3b Partial response plots (partial dependence curves) of top-5 variables during the breeding phase. The average 10-fold cross-validation results are depicted by the blue lines. The grey area limits ± standard error. HV - HV polarization; GLCM_V - NDVI-based texture variance; SC - Sand content; Bio1 - Annual Mean Temperature; Bio14 - Precipitation of Driest Month.

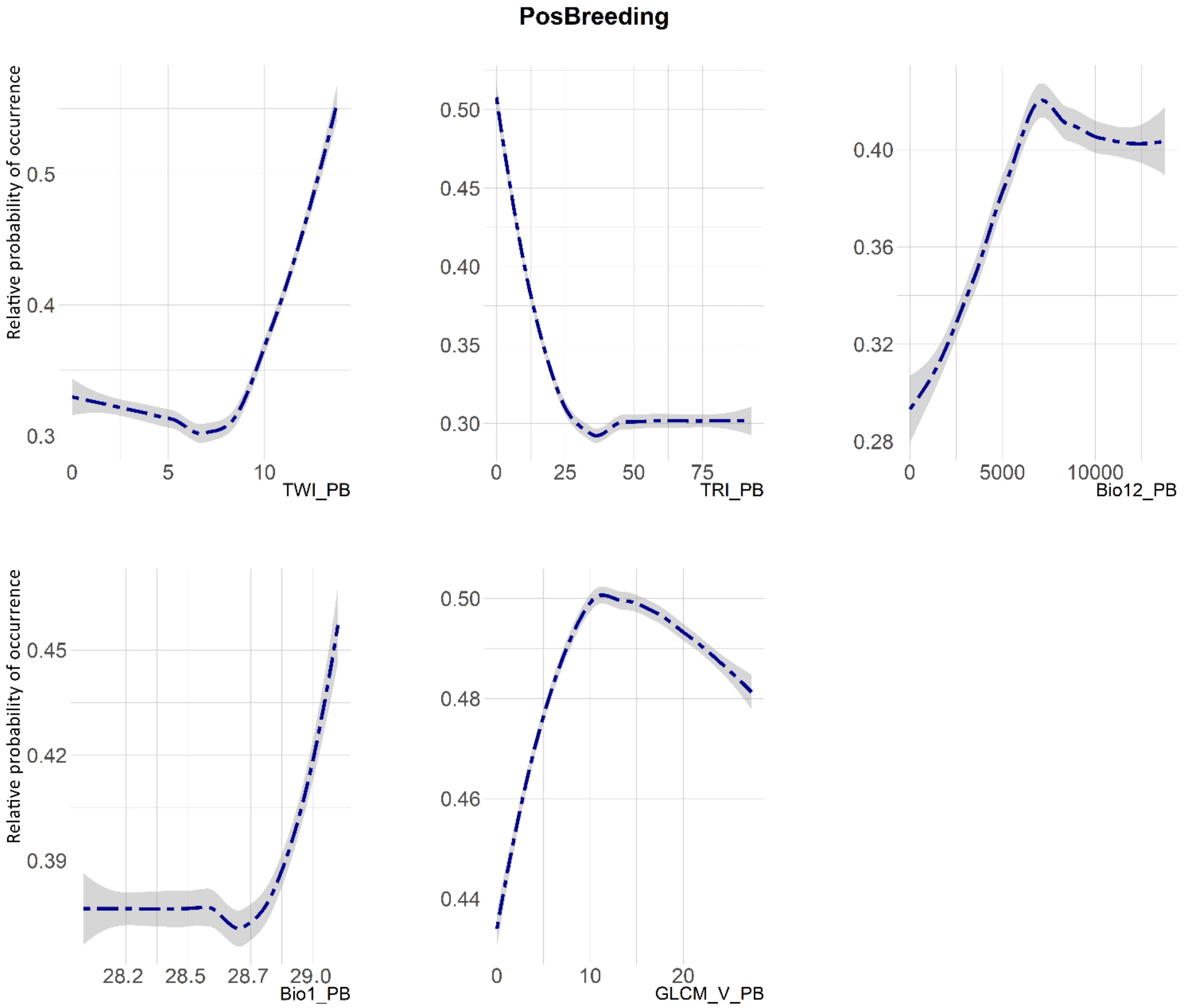


Figure E.3c Partial response plots (partial dependence curves) of top-5 variables during the post-breeding phase. The average 10-fold cross-validation results are depicted by the blue lines. The grey area limits ± standard error. TWI - Terrain Water Index; TRI - Terrain Ruggedness Index; Bio12 - Annual Precipitation; Bio1 - Annual Mean Temperature; GLCM_V - NDVI-based texture variance

Results for different threshold selection methods and average cutoff

Table E.3 Results for different threshold selection methods and average cutoffs for each phenological phase. Threshold selection methods: SeSpeql - Equalize sensitivity and specificity; SeSpmax - Maximize sum of sensitivity and specificity; PredPrev = Obs - Predicted prevalence same as observed; AvgProb - Average probability. The Average Cutoff, utilised for model binarization, was calculated as the average of the four different threshold selection methods.

Threshold	Winter	Breeding	Post-Breeding
SeSpeql	0,605	0,503	0,455
SeSpmax	0,500	0,500	0,500
PredPrev = Obs	0,500	0,501	0,500
AvgProb	0,490	0,496	0,512
Average Cutoff	0,524	0,500	0,492

Average nearest neighbour index (NNI)

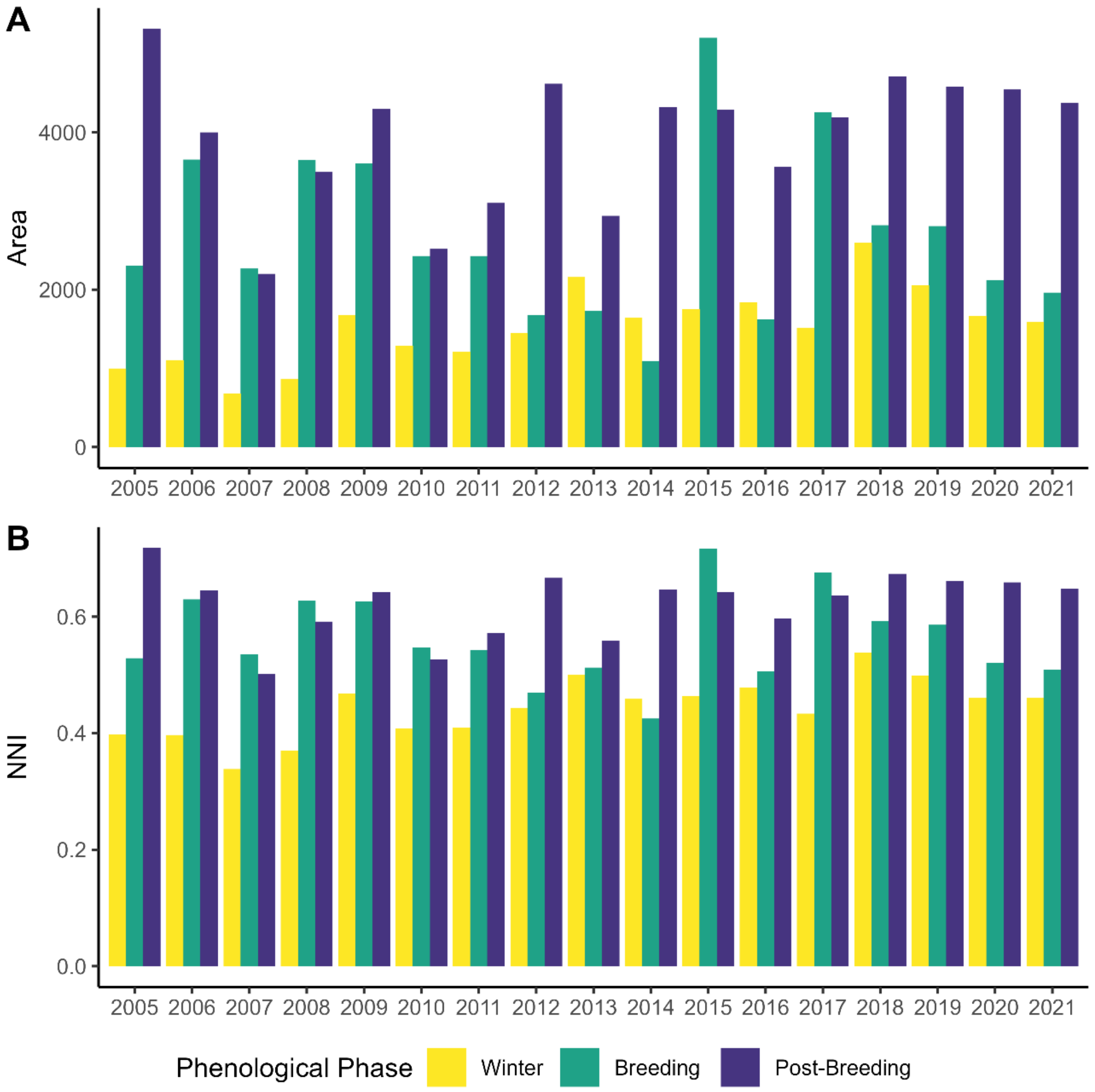


Figure E.4 (**a**) Area extent (km2) of predicted suitable habitat for each phenological phase over the period 2005 – 2021. Calculated as the area of all pixels with HS values >cutoff. (**b**) Average nearest neighbour index (NNI) for all pixels with predicted habitat suitability values >cutoff. A NNI <1 indicates spatial clustering of suitable habitat, whereas a NNI >1 suggests dispersion.

The nearest neighbour index (NNI) was calculated for suitable pixels (HS >cutoff), as a measure of clustering or dispersion, using the R package ‘spatialEco’ (Evans & Murphy, 2021). The NNI is written as the ratio of the distance between the observed nearest neighbour and the distance that would be expected, where the expected distance is the average distance between neighbours in a random distribution.

Interannual and spatial variability

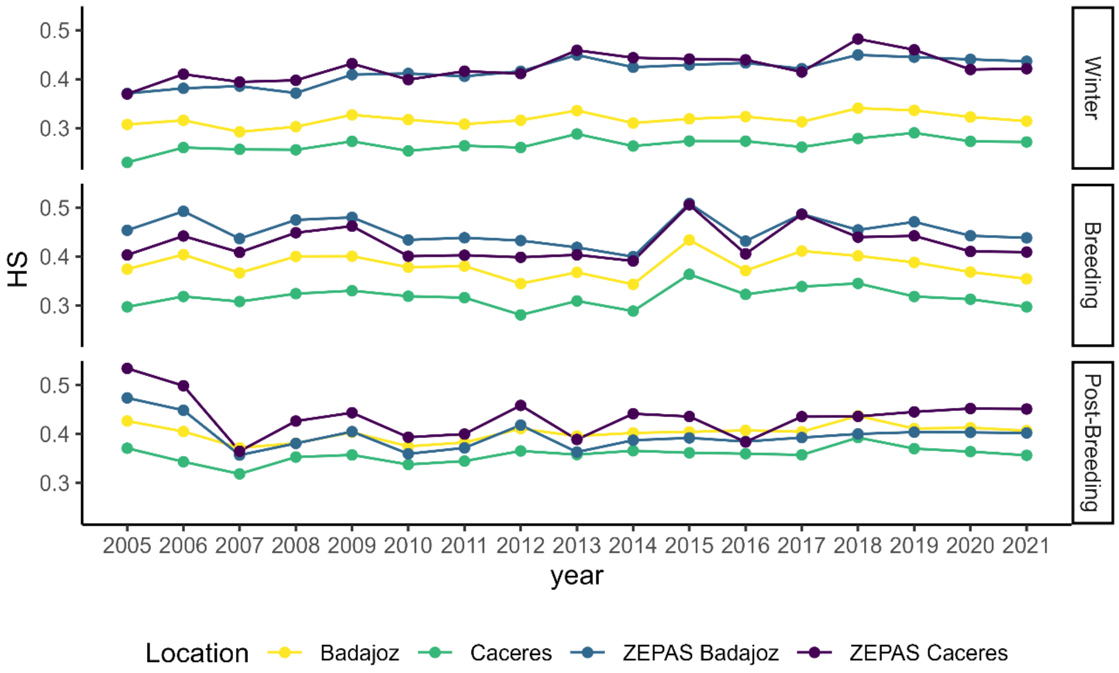


Figure E.5a Interannual and spatial variability in the habitat suitability (HS) over the period 2005 - 2021. Calculated as the HS average per phase and year, from 2005 to 2021, for the interior and exterior of the SPAs of both provinces (Cáceres and Badajoz).

For the winter and breeding phases, the interannual and spatial variability in habitat suitability (Figure E5a) showed similar average suitability values within the SPAs of both provinces, which were always higher than in the areas outside the SPAs. When compared to the province of Caceres, Badajoz's average suitability values were higher in both phases. In the post-breeding phase, after an unusual beginning in which high average suitability values were observed, the values stabilised (Figure E5a). In this phase, there is no obvious distinction between the average suitability inside and outside the SPAs, in contrast to what happens in the other phases. Despite being also the areas that exhibit greater fluctuation over time, the zones inside the Cáceres SPAs typically present higher values. On the other hand, the areas of the Caceres province located outside the SPAs are the ones with the lowest average suitability.

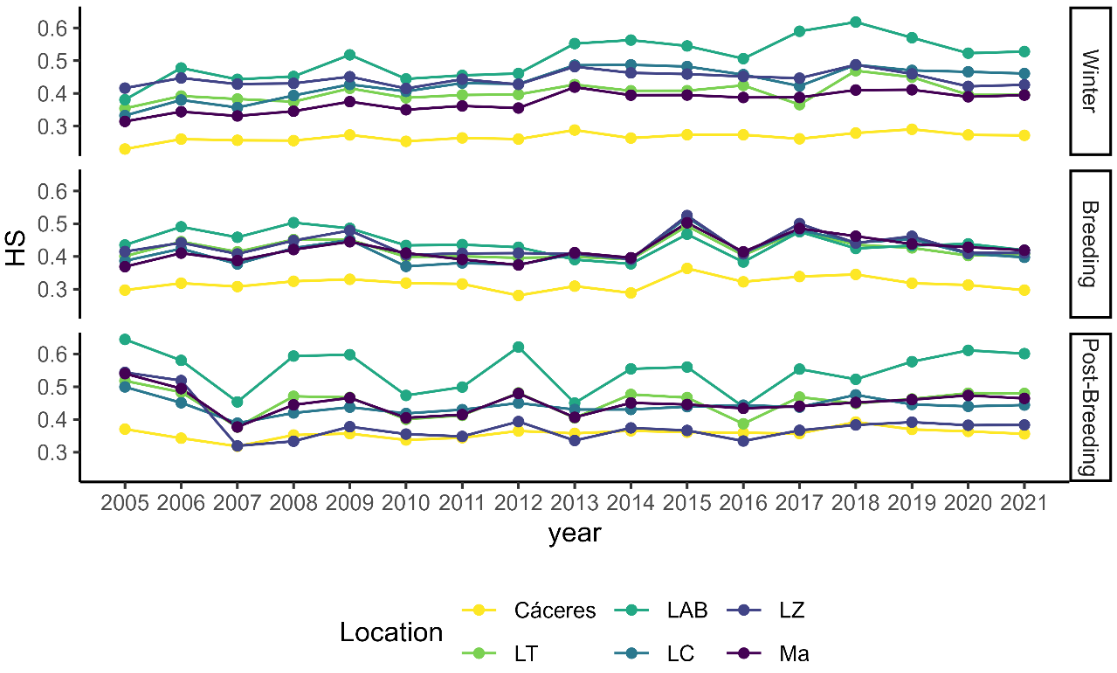


Figure E.5b Interannual variability in the habitat suitability (HS) over the period 2005 – 2021. Calculated for each Caceres SPA and for the area outside the SPAs of this region. See Figure 4.1 (main text) to consult the denomination of SPAs their location.

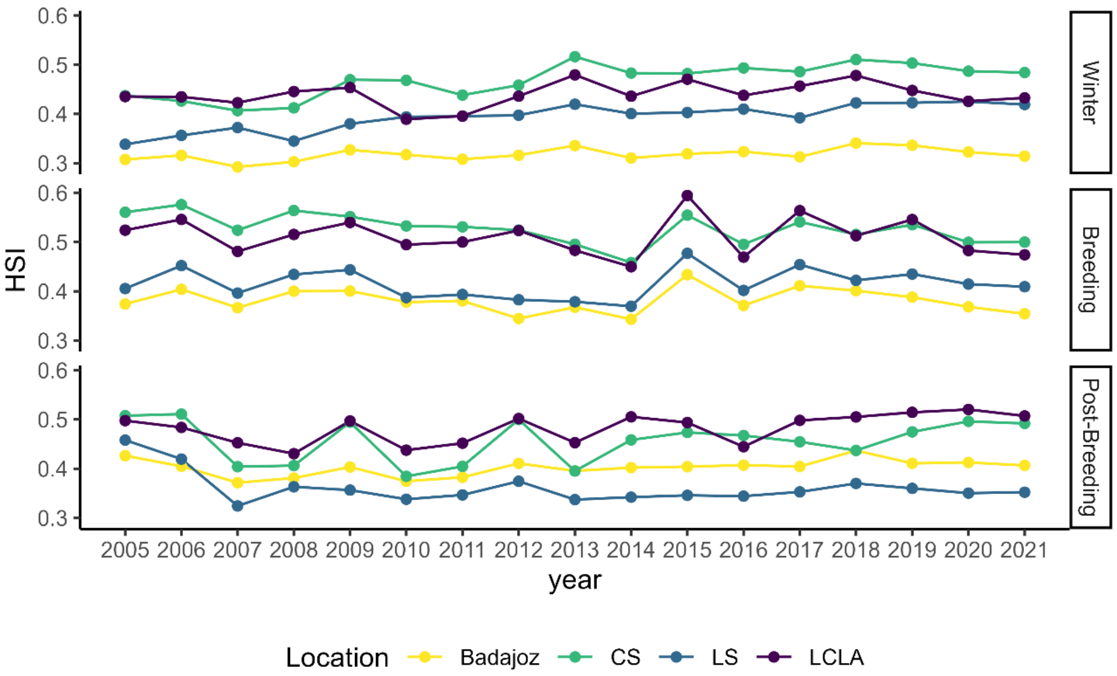


Figure E.5c Interannual variability in the habitat suitability (HS) over the period 2005 – 2021. Calculated for each Badajoz SPA and for the area outside the SPAs of this region. See Figure 4.1 (main text) to consult the denomination of SPAs their location.

Predict maps for all years and phenological phases

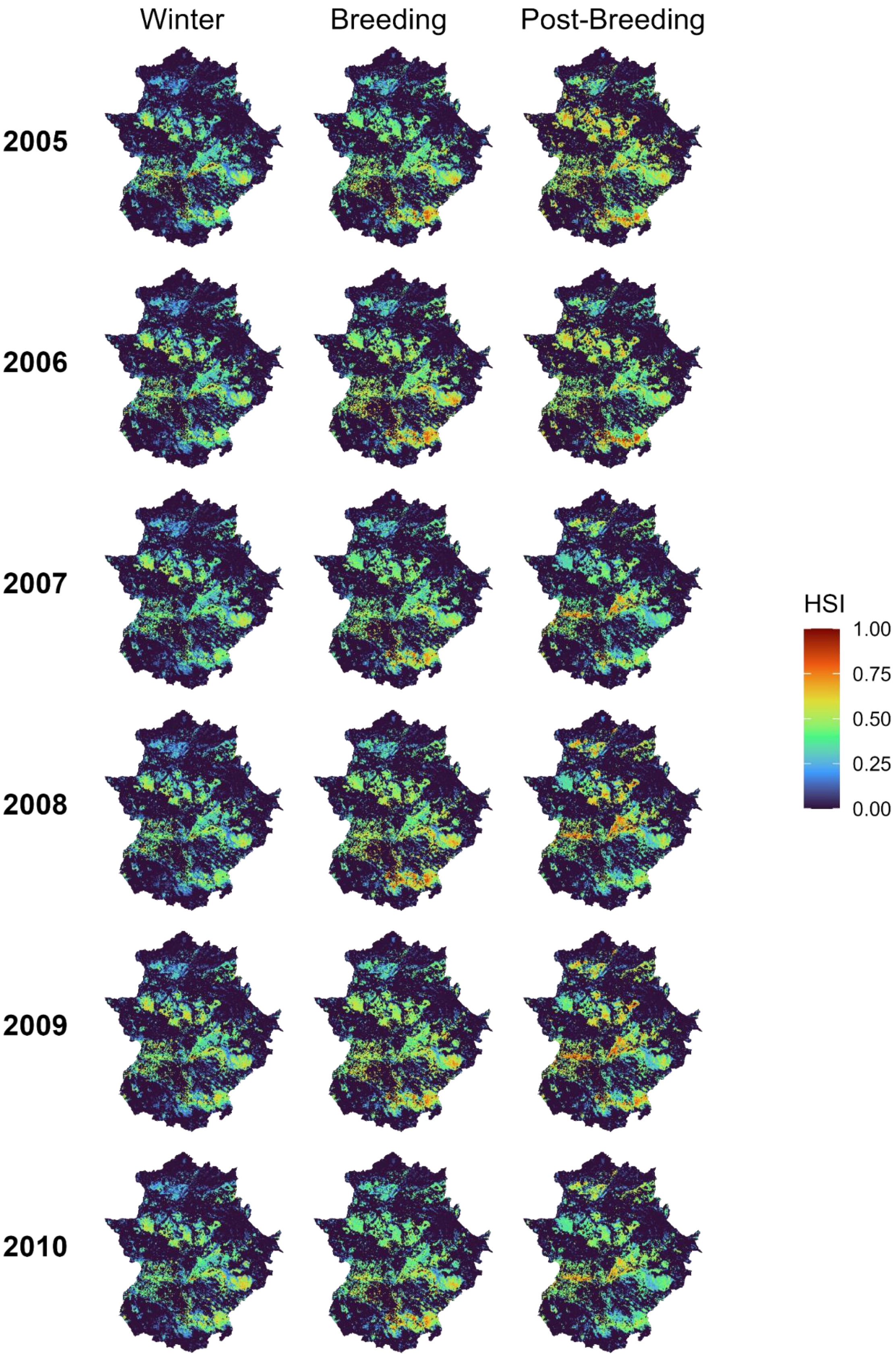


Figure E.6 Habitat suitability (HS) model predict maps for each phenological phase of each year, over the period 2005 – 2021, and a median of all years.

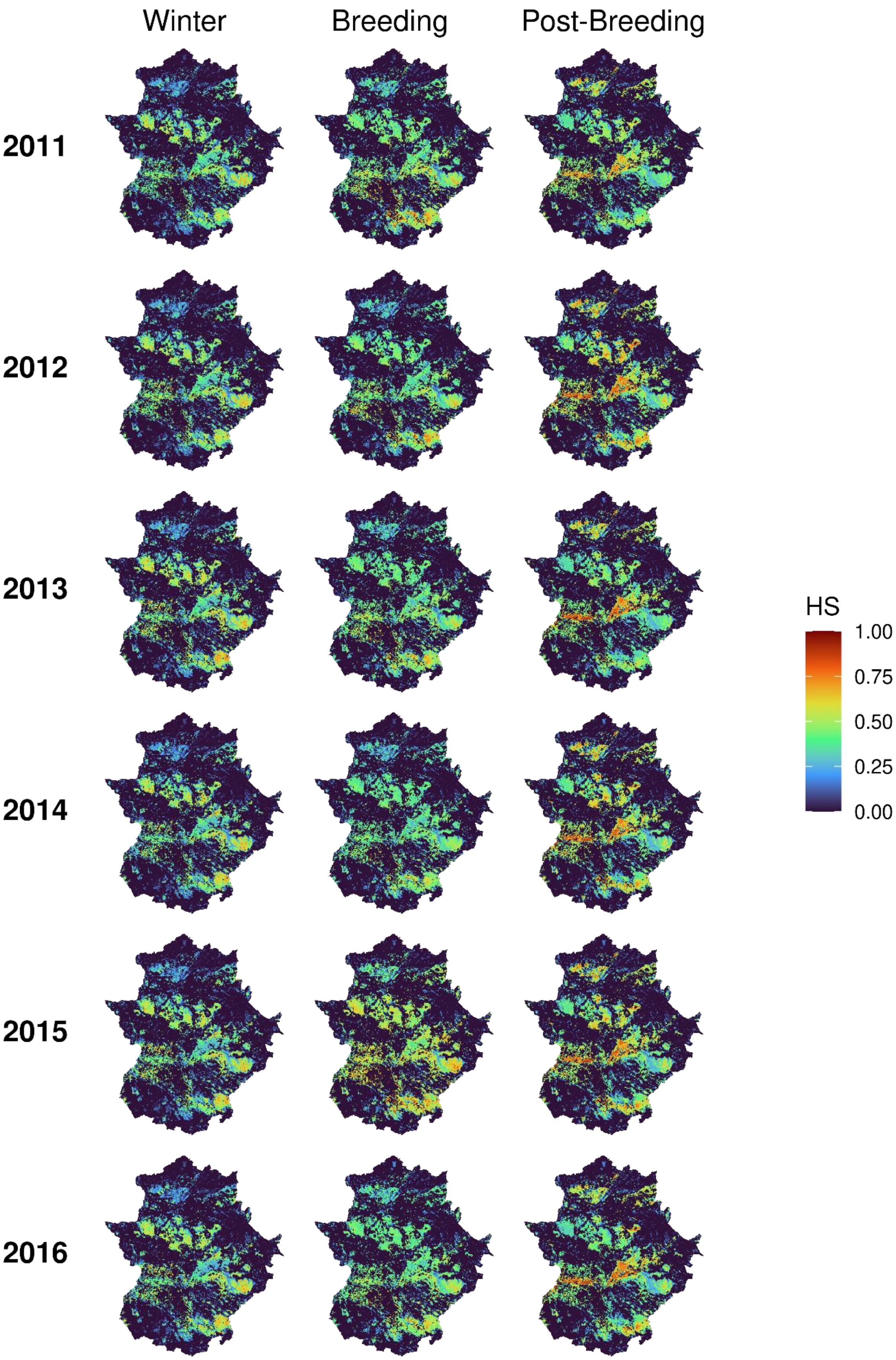


Figure E.6 (Continuation)

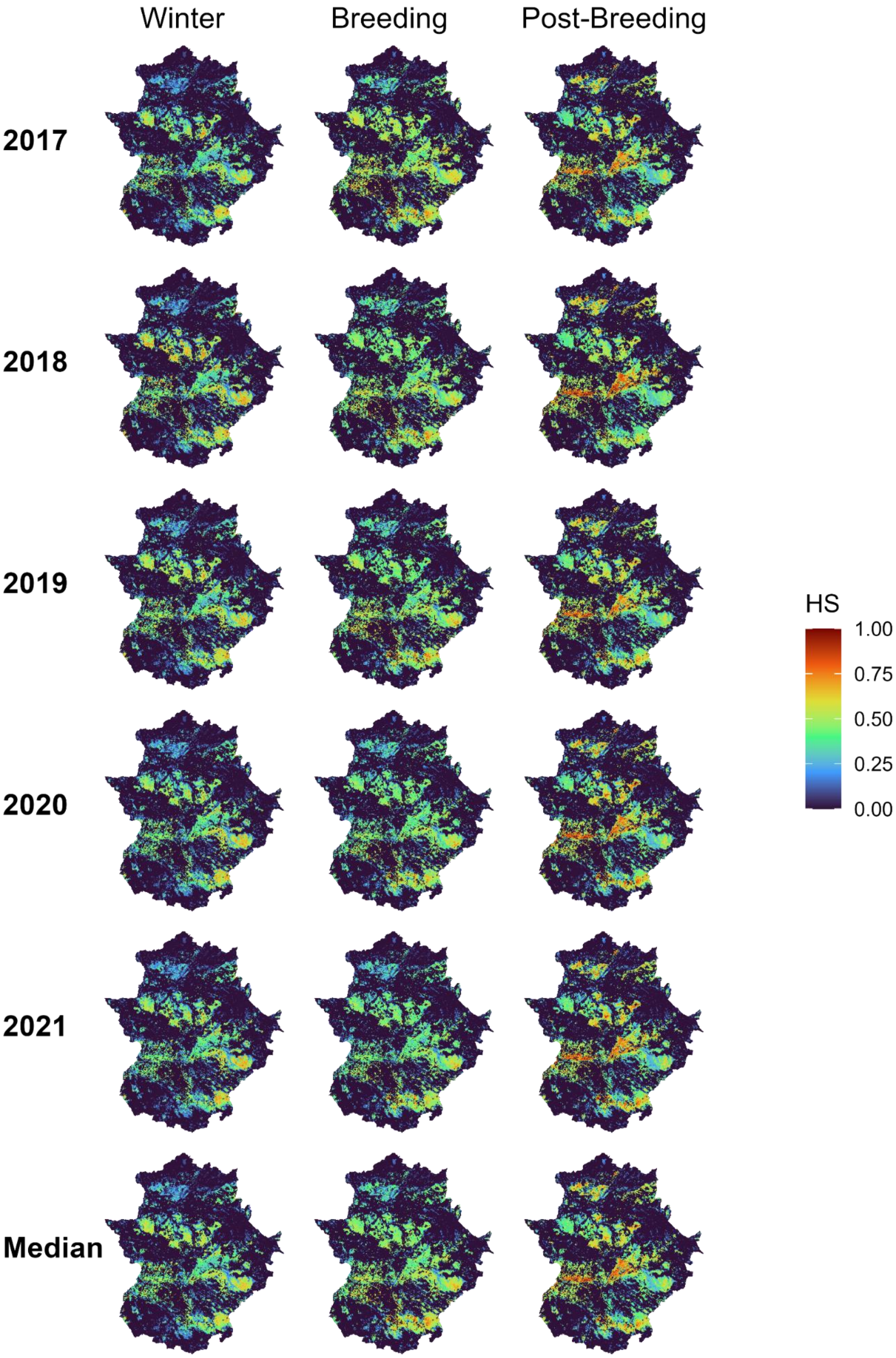


Figure E.6 (Continuation)

Supplementary Material for Chapter 4

Appendix F – ODMAP Protocol

Overview

Authorship

Contact: tfcm@uevora.pt (Tiago Crispim-Mendes)

Model objective

Model objective: Mapping and interpolation

Target output: Continuous habitat suitability and suitable vs. unsuitable habitat

Focal Taxon

Focal Taxon: *Tetrax tetrax* (Linnaeus, 1758), Otididae (Bustards), Otidiformes, Aves

Location

Location: Extremadura, Spain

Scale of Analysis

Spatial extent: Longitude 7.31° W – 4.43° W; Latitude 40.30° N – 37.53° N

Spatial resolution: 250m

Temporal extent: 2009 - 2021

Temporal resolution: Phenological phases: breeding (April 1–May 15), post-breeding (July 15–September 15), and winter (December 15–February 15).

Boundary: political

Biodiversity data

Observation type: GPS tracking

Response data type: Presence and pseudo-absences

Predictors

Predictor types: biophysical, topographic, anthropogenic

Hypotheses

Hypotheses: We hypothesize that the little bustard exhibits varying habitat preferences over different phenological phases, with interannual habitat modifications driven by environmental changes.

Assumptions

Model assumptions:

1 - The annual cycle of the little bustard was subdivided into three distinct phenological phases: breeding (April 1–May 15), post-breeding (July 15–September 15), and winter (December 15–February 15);

2 - We assumed that species are at pseudo-equilibrium with the environment;

3 -Relevant ecological drivers (or proxies) of species distributions are included;

4 - Sampling is adequate and representative (and any biases are accounted for/corrected).

Algorithms

Modelling techniques: Random Forest

Model complexity: Random forests models were built with 2000 trees and square root of total number of predictors included in the analysis to determine the number of variables randomly sampled as candidates at each node split.

Model averaging: Ensemble modelling was performed to combine species distribution model predictions.

Workflow

Model workflow: Only low correlated predictors were retained in the analysis. Ten cross-validation were repeated for each of the ten selected runs for a total of 100 models. Accuracy was based on AUC, Boyce Index, Sensitivity, Specificity and MCC. We therefore compared our predictions within years and across years to derive metrics of habitat variation.

Software

Software: R and the Google Earth Engine to prepare predictors

Data

Biodiversity data

Taxon names: Single species: *Tetrax tetrax*

Ecological level: Species

Data sources: Survey data collected in the field between January 2009 and December 2021.

Sampling design: The presence data used to train the species distribution models (SDMs) was obtained from a 12-year GPS telemetry data set of 91 male little bustards. Individuals were captured in Extremadura (distributed throughout the region) and Alentejo (in Castro Verde and Vila Fernando, Portugal) between 2009 and 2020 and fitted with highly precise GPS solar ARGOS Platform Transmitter Terminals (https://www.microwavetelemetry.com/) and solar GPS/GSM tags from Movetech Telemetry (https://movetech-telemetry.com/), E-Obs (https://e-obs.de/) and Ornitela OT (https://www.ornitela.com/) (e.g. Gudka et al., 2019).

Sample size: Overall, 2214 locations of 41 individuals were used to model the winter phase, 2225 locations of 82 individuals were used to model the breeding phase, and 2877 locations of 59 individuals were used to model the post-breeding phase, with 45.9% of these locations being in southern Portugal.

Clipping: Political boundary of Extremadura (Spain) and Alentejo (Portugal)

Scaling: Telemetry data was temporally thinned (within 1 day)

Cleaning: The dataset was temporally filtered in order to obtain locations for the core periods of the three distinct phases of the little bustard yearly cycle: breeding (April 1 - May 15), post-breeding (July 15 - Sep 15) and winter (Dec 15 - Feb 15). The definition of these core periods ensures that the locations used to characterize each biological phase, correspond to the phase of interest, regardless of the interannual variations in the yearly cycle. First, all records in flight (speed > 3 m/s) or outside the geographical limits of Extremadura and Alentejo were excluded (locations from Alentejo were kept to better inform the models). Then, to standardise the contribution of all the available individuals and avoid overrepresentation of some locations, for each bird, a single biological phase per year was selected and, within this phase, only a single location per day. Since captures were conducted mainly during the breeding phase, if there were several years of data for the same individual, data from the first year were used for post-breeding or winter, and data from the second year for breeding, in order to ensure a complete breeding period.

Absence data: We generated the same number of pseudoabsences as presences for each phenological phase (prevalence = 0.5; Barbet-Massin et al., 2012). A mask was created within the study area to represent the appropriate geographical space for generating random pseudo-absences, using specific land-use classes extracted from the European CORINE Land Cover (CLC; European Commission, 1994), namely 211 - Non-irrigated arable land; 212 - Permanently irrigated land; 213 - Rice fields; 321 - Vineyards and 231 – Pastures; as they represent a potential suitable habitat for little bustards. The patch sizes of CLC classes were converted into percentage values within the mask, which in turn were subjected to an inverse normalisation analysis. This allowed these values to be defined as probability weights for the generation of pseudo-absences, throughout the function “randomPoints” (prob argument set to TRUE) in the R package ‘dismo’ (Version 1.3-9; Hijmans et al., 2022). Specifically, a higher chance of generating pseudo-absences on less represented pixels was required to counterbalance those pertaining to most large patches and abundant CLC classes, hence, to sample the entire species’ environmental range (Barbet-Massin et al., 2012; VanDerWal et al., 2009). Two CLC products were used: the 2012 product represented the years between 2009 and 2015, and the 2018 product represented the years between 2016 and 2021. For each presence, a pseudo-absence within the mask was repeatedly generated by considering a minimum and maximum distance range. Indeed, it is recommended to set a minimum distance exclusion buffer, here corresponding to 250 m from known presences, to soften false absence error rates (Iturbide et al., 2015). Furthermore, a maximum geographical extent (i.e., maximum distance from presences) may be necessary to deal with possible inflated results (e.g. over-predictions) (Iturbide et al., 2015; VanDerWal et al., 2009). As maximum distance, the little bustard’s movement capability was considered, resulting in 50 km for the breeding phase or 80 km for the post-breeding and winter phases (average distance of movements by phenological phase; Silva et al., 2014).

Background data: We generated the same number of pseudoabsences as presences for each phenological phase (prevalence = 0.5).

Errors and biases: Telemetry locations were identified with high spatio-temporal precision from time-stamped GPS tracks.

Data partitioning

Training data: Tenfold cross-validations using 70% of the dataset as training and 30% as validation

Validation data: See Training data

Predictor variables

Predictor variables: Our study included several products, referred to as bioclimatic, anthropogenic, and topographic predictors, all prepared at different scales (Table 4.1 of main text). Based on multispectral corrected optical imageries (Moderate Resolution Imaging Spectroradiometer MODIS), several remote sensing metrics were computed (Table 4.1 of main text), reflecting telemetry surveys along little bustard phenological phases. In detail, within the Google Earth Engine (GEE) cloud platform (Gorelick et al., 2017), satellite imageries were aggregated, corrected, and analysed, and the spatio-temporal concordance was addressed between calculated predictors and telemetry observations. This step aimed to extract sound high-quality data, while providing an overview of the biophysical characteristics of agricultural and steppe habitats in the Mediterranean region, such as vegetation conditions, biomass, droughts, and surface temperatures (Cerasoli et al., 2018; Fernández et al., 2010; von Keyserlingk et al., 2021). Co-occurrence textural indices (i.e., GLMC; Haralick et al., 1973) were also calculated to infer vegetation horizontal structure through the NDVI index (Fernández et al., 2010; Wood et al., 2012), whereas radiometric L-bands (SM1) from ALOS PALSAR satellites were used to infer vertical structure (Lucas et al., 2010). The latter information was retrieved annually, in concomitance with an included measure of human imperviousness (Table 4.1 of main text), available from the Copernicus program (European Union & Copernicus Land Monitoring Service, 2021) from which were also retrieved the Corine land cover classes as categorical predictor. The static predictors, however, referred to relatively stable landscape characteristics such as soil properties (pH, sand content, organic carbon and bulk density; Poggio et al., 2021), bioclimatic conditions (mean temperature, mean diurnal range, precipitation and precipitation of driest month; Fick & Hijmans, 2017), as well as topographic (altitude, slope, terrain roughness and wetness; Conrad et al., 2015; Crippen et al., 2016) and anthropogenic information (distance from major roads, distance from power lines; GeoFabrik, 2021) (Table 4.1 of main text).

Data sources: Web-references to data sources given in Table E.1 of Appendix E.

Spatial extent: Longitude 7.31° W – 4.43° W; Latitude 40.30° N – 37.53° N

Spatial resolution: Information is given in Table 4.1 of the main text.

Coordinate reference system: EPSG:4326

Temporal extent: 2009-2020

Temporal resolution: Information is given in Table 4.1 of the main text.

Data processing: All predictors with native resolution above 250m were downscaled to 250m and georegistered to one common origin. More Information is given in Table E.1 of Appendix E.

Errors and biases: Accuracy metrics were performed for classification analyses.

Dimension reduction: Predictor variables underwent variance inflation (VIF) and Pearson correlation analysis to reduce their number and avoid highly correlated variables.

Model

Variable pre-selection

Variable pre-selection: Models ran as probabilistic classifications by selecting Random Forests (Breiman, 2001), for which the variant algorithm 'Boruta' (R package v.6.0.0; Kursa & Rudnicki, 2010) was employed for a prior screening procedure to filter out irrelevant predictors, following the parametrization in (Valerio et al., 2020).

Multicollinearity

Multicollinearity: To overcome multicollinearity issues among the retained predictors, only those with a Pearson's correlation |r| <0.9 (Figure E.1 of Appendix E) and a VIF<5 (Table E.2 of Appendix E) were considered for further analysis (Christophe, 2011).

Model settings

Random Forest: number of trees = 2000

Model estimates

Coefficients: Associable to performed Random forests analyses described in the paper.

Parameter uncertainty: Associable to performed Random forests analyses described in the paper.

Variable importance: Associable to performed Random forests analyses described in the paper.

Threshold selection

Threshold selection: Calculated independently for each phenological phase as the average of four different threshold selection methods. The methods we use include: (1) minimizing the absolute difference between sensitivity and specificity (SeSpeql); (2) maximizing the sum of sensitivity and specificity (SeSpmax); (3) maintaining the original prevalence (PredPrev = Obs); and (4) taking the mean of the probabilities of occurrence of occupied locations for presence/absence data as the threshold (AvgProb) (see Liu et al. 2005, 2013; Nenzén and Araújo 2011, for detailed explanation).

Assessment

Performance statistics

Performance on training data: The performance of each multivariate model (SDM) with retained predictors was evaluated through four accuracy metrics produced by the confusion matrix (Swets, 1988): sensitivity (proportion of occurrences correctly classified), specificity (proportion of absences correctly classified) (Fielding and Bell 1997), and the area under the receiver operating characteristic (ROC) curve (AUC; Swets, 1988), where metrics values near 1 indicate a complete predictability by models (e.g. Araújo et al., 2005). Additionally, we also included the Boyce Index (Boyce et al., 2002) performed with the “modEvA“ R package (v.3.9; Barbosa et al., 2013), coupled with Matthews’ correlation coefficient (MCC; Baldi et al., 2000; Matthews, 1975) given its robustness from all the categories of the confusion matrix (true positives, true negatives, false positives, and false negatives) (Chicco & Jurman, 2020).

Plausibility check

Response shapes: Partial dependence plots

Expert judgement: We compared predictions on the basis of opinions between authors, who are considered experts on the species and its distribution.

Prediction

Prediction output

The continuous outputs of the final composite Random Forests models (one for each of the three phenological phases) were projected for the Extremadura region (Spain) for the period between 2005 and 2021, covering the period between the first Spanish national census and the present.

References

Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. Glob Chang Biol 11, 1504–1513. https://doi.org/10.1111/j.1365-2486.2005.01000.x

Baldi, P., Brunak, S., Chauvin, Y., Andersen, C.A.F., Nielsen, H., 2000. Assessing the accuracy of prediction algorithms for classification: An overview. Bioinformatics 16, 412–424. https://doi.org/10.1093/bioinformatics/16.5.412

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: How, where and how many? Methods Ecol Evol 3, 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Barbosa, A.M., Real, R., Muñoz, A.R., Brown, J.A., 2013. New measures for assessing model equilibrium and prediction mismatch in species distribution models. Divers Distrib 19, 1333–1338. https://doi.org/10.1111/ddi.12100

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecol Modell 157, 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Breiman, L., 2001. Random Forests. Mach Learn 45, 5–32. https://doi.org/10.1023/A:1010933404324

Cerasoli, S., Campagnolo, M., Faria, J., Nogueira, C., da Conceição Caldeira, M., 2018. On estimating the gross primary productivity of Mediterranean grasslands under different fertilization regimes using vegetation indices and hyperspectral reflectance. Biogeosciences 15, 5455–5471. https://doi.org/10.5194/bg-15-5455-2018

Chicco, D., Jurman, G., 2020. The advantages of the Matthews correlation coefficient (MCC) over F1 score and accuracy in binary classification evaluation. BMC Genomics 21, 1–13. https://doi.org/10.1186/s12864-019-6413-7

Christophe, E., 2011. Hyperspectral data compression tradeoff, in: Optical Remote Sensing. Springer, Berlin, Heidelberg, pp. 9–29. https://doi.org/10.1007/978-3-642-14212-3

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., Böhner, J., 2015. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. Geosci Model Dev 8, 1991–2007. https://doi.org/10.5194/gmd-8-1991-2015

Crippen, R., Buckley, S., Agram, P., Belz, E., Gurrola, E., Hensley, S., Kobrick, M., Lavalle, M., Martin, J., Neumann, M., Nguyen, Q., Rosen, P., Shimada, J., Simard, M., Tung, W., 2016. NASADEM global elevation model: Methods and progress. International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives 41, 125–128. https://doi.org/10.5194/isprsarchives-XLI-B4-125-2016

European Union, Copernicus Land Monitoring Service (2021). Available online: https://land.copernicus.eu/ (accessed on 20 October 2021).

Fernández, N., Paruelo, J.M., Delibes, M., 2010. Ecosystem functioning of protected and altered Mediterranean environments: A remote sensing classification in Doñana, Spain. Remote Sens Environ 114, 211–220. https://doi.org/10.1016/j.rse.2009.09.001

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37, 4302–4315. https://doi.org/10.1002/joc.5086

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24, 38–49. https://doi.org/10.1017/S0376892997000088

GeohjFabrik. GeoFabrik: Download Server for OpenStreetMap data. 2021. Web Based Download Application: Available online: http://download.geofabrik.de/ (accessed on 20 October 2021).

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sens Environ 202, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Gudka, M., Santos, C.D., Dolman, P.M., Abad-Gómez, J.M., Silva, J.P., 2019. Feeling the heat: Elevated temperature affects male display activity of a lekking grassland bird. PLoS One 14, e0221999. https://doi.org/10.1371/journal.pone.0221999

Haralick, R.M., Shanmugam, K., Dinstein, I., 1973. Textural Features for Image Classification. IEEE Trans Syst Man Cybern SMC-3, 610–621. https://doi.org/10.1109/TSMC.1973.4309314

Hijmans, A.R.J., Phillips, S., Leathwick, J., Elith, J., 2022. Dismo: Species Distribution Modeling.

Iturbide, M., Bedia, J., Herrera, S., del Hierro, O., Pinto, M., Gutiérrez, J.M., 2015. A framework for species distribution modelling with improved pseudo-absence generation. Ecol Modell 312, 166–174. https://doi.org/10.1016/j.ecolmodel.2015.05.018

Kursa, M.B., Rudnicki, W.R., 2010. Feature selection with the boruta package. J Stat Softw 36, 1–13. https://doi.org/10.18637/jss.v036.i11

Lucas, R., Bunting, P., Clewley, D., Armston, J., Fairfax, R., Fensham, R., Accad, A., Kelley, J., Laidlaw, M., Eyre, T., Bowen, M., Carreiras, J., Bray, S., Metcalfe, D., Dwyer, J., Shimada, M., 2010. An Evaluation of the ALOS PALSAR L-Band Backscatter—Above Ground Biomass Relationship Queensland, Australia: Impacts of Surface Moisture Condition and Vegetation Structure. IEEE J Sel Top Appl Earth Obs Remote Sens 3, 576–593. https://doi.org/10.1109/JSTARS.2010.2086436

Matthews, B.W., 1975. Comparison of the predicted and observed secondary structure of T4 phage lysozyme. BBA - Protein Structure 405, 442–451. https://doi.org/10.1016/0005-2795(75)90109-9

Poggio, L., de Sousa, L.M., Batjes, N.H., Heuvelink, G.B.M., Kempen, B., Ribeiro, E., Rossiter, D., 2021. SoilGrids 2.0: Producing soil information for the globe with quantified spatial uncertainty. Soil 7, 217–240. https://doi.org/10.5194/soil-7-217-2021

Silva, J.P., Palmeirim, J.M., Alcazar, R., Correia, R., Delgado, A., Moreira, F., 2014. A spatially explicit approach to assess the collision risk between birds and overhead power lines: A case study with the little bustard. Biol Conserv 170, 256–263. https://doi.org/10.1016/j.biocon.2013.12.026

Valerio, F., Ferreira, E., Godinho, S., Pita, R., Mira, A., Fernandes, N., Santos, S.M., 2020. Predicting Microhabitat Suitability for an Endangered Small Mammal Using Sentinel-2 Data. Remote Sens (Basel) 12, 562. https://doi.org/10.3390/rs12030562

VanDerWal, J., Shoo, L.P., Graham, C., Williams, S.E., 2009. Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? Ecol Modell 220, 589–594. https://doi.org/10.1016/j.ecolmodel.2008.11.010

von Keyserlingk, J., de Hoop, M., Mayor, A.G., Dekker, S.C., Rietkerk, M., Foerster, S., 2021. Resilience of vegetation to drought: Studying the effect of grazing in a Mediterranean rangeland using satellite time series. Remote Sens Environ 255, 112270. https://doi.org/10.1016/j.rse.2020.112270

Wood, E.M., Pidgeon, A.M., Radeloff, V.C., Keuler, N.S., 2012. Image texture as a remotely sensed measure of vegetation structure. Remote Sens Environ 121, 516–526. https://doi.org/10.1016/j.rse.2012.01.003

Supplementary Material for Chapter 5

Appendix G – TRACE Protocol

This is a TRACE document ("TRAnsparent and Comprehensive model Evaludation") which provides supporting evidence that our model presented in:

Spatially explicit individual-based models as tools to address pressing conservation decisions: A case study with the little bustard

was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows:

Schmolke A, Thorbek P, DeAngelis DL, Grimm V. 2010. Ecological modelling supporting environmental decision making: a strategy for the future. *Trends in Ecology and Evolution* 25: 479-486.

and uses the updated standard terminology and document structure in:

Grimm V, Augusiak J, Focks A, Frank B, Gabsi F, Johnston ASA, Kułakowska K, Liu C, Martin BT, Meli M, Radchuk V, Schmolke A, Thorbek P, Railsback SF. 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecological Modelling*

and

Augusiak J, Van den Brink PJ, Grimm V. 2014. Merging validation and evaluation of ecological models to 'evaludation': a review of terminology and a practical approach. *Ecological Modelling*.

Contents

1. Problem formulation

This TRACE element provides supporting information on: The decision-making context in which the model will be used; the types of model clients or stakeholders addressed; a precise specification of the question(s) that should be answered with the model, including a specification of necessary model outputs; and a statement of the domain of applicability of the model, including the extent of acceptable extrapolations.

Summary:

Scenarios of rapid species decline require the rapid and efficient exploration of cost-effective management options. This spatially explicit individual-based model was developed to assist managers in the Extremadura region, Spain, in optimizing management and conservation measures to reverse the decline of the little bustard in the area. However, due to the lack of spatially explicit representation of anthropogenic mortality and reliable future habitat suitability prediction models, the current approach does not yet provide endpoints that are immediately operational for decision-making and field application. Despite these limitations, the model's framework shows promise for future applications in the conservation of the little bustard both within and beyond the Extremadura region.

When addressing the urgent need to reverse a species' rapid decline, both time and financial resources are often constrained. Therefore, it becomes imperative to implement targeted, precise, and well-founded management strategies that maximize cost-effectiveness. In tackling this challenge, spatially explicit population models, incorporating population and ecological dynamics, emerge as invaluable tools. They facilitate the rapid exploration of management options, assessment of feasibility, and evaluation of potential conservation measures' success. Specifically tailored for the little bustard in the Extremadura region, Spain, this model addresses the species' pronounced decline in an area historically recognized as a crucial breeding habitat.

We synthesized and incorporated into the model all relevant knowledge available for the species' Western European distribution and particularly for the Extremadura region. The simulation approach we employ aims to connect spatio-temporal habitat suitability with the survival and habitat usage patterns of the little bustard, integrating key life-history traits of the species. This comprehensive framework encompasses behaviours such as migration and dispersion, as well as mortality events resulting from both natural and anthropogenic causes. Notably, it offers a realistic depiction of the landscape, accounting for inter- and intra-annual variability. This comprehensive approach offers new possibilities for simulating and assessing various conservation strategies, providing managers with the opportunity to simulate and evaluate different approaches before implementing them in real-world scenarios. This includes fine-tuning the extent and location of intervention areas to improve habitat suitability and integrating different levels of mitigation for anthropogenic mortality.

The model was developed to be used by both managers and scientists interested in the conservation of the little bustard and in exploring and understanding the relationships between ecological and demographic parameters with the landscape. In particular, the model aims to assist decision-making by managers in the Extremadura region regarding the implementation of conservation measures targeted at the little bustard in the area. The model was developed and calibrated to realistically mimic the little bustard population in the Extremadura region using empirical data collected between 2005 and 2022. For this period, the model utilizes habitat suitability maps projected for each phenological phase of each year, allowing for extrapolation of the species' occupancy areas during this period, how they varied over time, and the current distribution of the species in the region. However, while the model was developed to test the implementation of different conservation strategies in future scenarios, the current approach does not yet provide endpoints that are immediately operational for field application. At this stage, the future scenarios implemented are simply based on the suitability of the last 10 years in the region (median and 1st and 3rd quartiles), without considering interannual variation or information from climate models. Additionally, anthropogenic mortality is not yet implemented in a spatially explicit way, so the extrapolation of results regarding the selection of conservation strategies should be done with caution and taking these aspects into account.

The inclusion of specific habitat suitability maps for the Extremadura region and the adjustment of demographic parameters for this region means that the model, as it stands currently, may not be suitable for making inferences about other populations or sub-populations outside of Extremadura. However, the set of behavioural rules implemented is applicable across all Western European populations and subpopulations. Therefore, the model can be adapted and calibrated to make inferences about other populations.

2. Model description

This TRACE element provides supporting information on: The model. Provide a detailed written model description. For individual/agent-based and other simulation models, the ODD protocol is recommended as standard format. For complex submodels it should include concise explanations of the underlying rationale. Model users should learn what the model is, how it works, and what guided its design.

Summary:

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2010, 2006). The model was implemented in NetLogo 6.3.0 (Wilensky, 1999). We used R (R Core Team, 2021) for testing and analysing the model, taking advantage of the NLRX package (Salecker et al., 2019) that allows the integration of NetLogo in R.

2.1 Purpose and patterns

The overall purpose of this model is to support and guide conservation management initiatives for the little bustard in the Extremadura region, Spain. Despite the region being considered a stronghold for the species, the little bustard has experienced a substantial population decline in the Iberian Peninsula in recent decades. Recognizing the critical conservation significance of Extremadura within the Iberian context, it is imperative to implement a targeted and effective conservation strategy in this area.

The model was designed to simulate a real-world scenario for the little bustard in Extremadura, capturing the dynamics of a realistic population and the complex behaviours of the species throughout the yearly cycle. High-resolution suitability maps were included for each phenological phase, governing the spatial organization of individuals, their reproductive success and survival, as well as migration and dispersal movements within and beyond the study area.

We evaluate the performance of our model by assessing its ability to replicate various demographic patterns. This includes the population trajectory of the Little Bustard in Extremadura from 2005 to 2022, the average survival of adult males, their fidelity to breeding sites, specific well-documented reproductive parameters, and the average size of flocks during different phenological phases.

Given the limited empirical information regarding some parameters and the relationship between survival across various life stages of little bustards and the habitat suitability of their location, one of the model's purposes was to calibrate these parameters (see Section 6). This calibration aims to contribute to expanding knowledge about the species in the region and gaining a better understanding of the biological factors influencing its persistence.

The main purpose of the model is to identify the most cost-effective conservation strategies for stabilizing the little bustard population in Extremadura over a 50-year timeframe (2022 – 2072). This entails simulating various scenarios with diverse management approaches, including adjusting the extent and location of intervention areas to enhance habitat suitability, and incorporating varying levels of mitigation for anthropogenic mortality.

2.2 Entities, state variables, and scales

The model encompasses various entities, including habitat cells (250x250m), male little bustards, female little bustards, nests, flocks (Collectives), and the global environment (referred to as "Observer" in NetLogo). The state variables characterizing these entities are detailed in Table G.2.1. Male and female little bustards were incorporated into the model to represent each individual along with their spatial location in an individual and explicit manner. They were modelled as distinct entities due to variations in behaviour during the breeding phase and differences in survival rates. The inclusion of nests aimed to provide a more accurate representation of nest failure, while flocks were utilized to depict groups of individuals during the gregarious phenological phases of the species (post-breeding and winter).

One time step in the model corresponds to one week, and the species' yearly cycle is represented through the recreation of different phenological phases, each characterized by distinct behavioural rules: breeding (1 April – 21 May); post-breeding (15 July – 15 September); and winter (15 December – 1 March), with migration periods between these phases. The weekly time scale is considered suitable for accurately capturing the individual behaviours of the species, particularly during the breeding phase and migration periods.

Table G.2.1 List of entities intervening in the model, whit 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 (0 - 1)
occupants	Current number of occupants of the cell	Numeric (-)
intervened	Indicates whether a habitat cell had a habitat improvement intervention	Boolean (True; False)
Male little bustards		
ID	Unique identification code	Numeric (-)
location	Location in the local patch	Numeric (spatial coordinates)
age	Age	Numeric (weeks)
migration_pattern	Migration pattern	Categoric (See Section 3.1)
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 (-)
location	Location in the local patch	Numeric (spatial coordinates)
age	Age	Numeric (weeks)
migration_pattern	Migration pattern	Categoric (See Section 3.1)
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 (-)
Nests		
female	Female’s ID	Numeric (-)
Flocks		
size	Number of individuals within the flock	Numeric (-)
Global environment		
date	Date in current time-step	Date (day/month/year)
phenological_phase	Current phenological phase	Categoric (“breeding”; "migration_post-breeding"; “post-breeding”; "migration_winter"; “winter”; "migration_breeding")
nesting_prob	Current nesting probability	Numeric (0 – 1)
migration_prob	Current migration probability	Numeric (0 – 1)

The time horizon of the model is distinct for the implementation phase (calibration, sensitivity analysis, and validation) and the main experiment. The implementation phase has a time horizon of 17 years (from 01-04-2005 to 01-04-2022), resulting in 887 ticks. This temporal extent is deemed appropriate for this phase since it encompasses a period in the past for which empirical data is available, allowing for model calibration and validation. On the other hand, the time horizon of the main experiment is 50 years (from 01-04-2022 to 01-04-2072), resulting in 2663 ticks. This temporal extent aligns with the main purpose of the model, which is to identify the most cost-effective management strategies for stabilizing the little bustard population in Extremadura over a 50-year timeframe.

The two-dimensional model provides a realistic representation of the little bustard population in the Extremadura region, Spain, with a resolution of 250 m (1004 x 1128 cells). This spatial resolution was selected to accurately depict the species' distribution with high detail, operating on a scale that holds biological significance for the species and proves valuable for stakeholders, decision-makers, and policy developers.

Each habitat cell is assigned a habitat suitability value ranging from 0 to 1. This value represents the average suitability of surrounding cells within a buffer zone, which changes between phenological phases according to the average home range size of an individual during that specific phase. This approach eliminates the need to account for small-scale movements of individuals within their home range during a phenological phase, as the cell where the individual is located acts as the centroid of its home range and contains information about its average suitability. The suitability maps for each phenological phase were based on the predictions from the species distribution models (SDMs) developed in Crispim-Mendes et al. (2024) for the period between 2005 and 2022.

2.3 Process overview and scheduling

The model was designed to capture the yearly cycle of the little bustard population in Extremadura, encompassing all aspects of the species' life cycle deemed relevant for an adequate and realistic response to the model's purpose. A flow diagram illustrating the processes within the yearly cycle is provided in Figure G.2.1. The model is structured into eight processes or submodels: one related to the update of variables (global environment updating), six concerning little bustards (ageing, nesting, hatching, migration, dispersion, and survival), and one focusing on data collection (outputs collection).

These different processes are scheduled and executed at specific moments depending on the phenological phase in which the simulation finds itself, as described below. The submodels representing these processes are detailed in Section 2.7.

1. Global environment updating – Each time-step (one week) begins with the update of the simulation date, and if applicable, the phenological phase and the habitat suitability values of the habitat cells are also updated (see *Submodel Update Suitability* below). During migration phases, the migration probability (*migration_prob*) is updated on a weekly basis (see *Submodels Migration* and *Dispersion* below for more details). The same applies to the mating probability (*nesting_prob*) during the breeding phase (see *Submodel Reproduction* below for more details). At the beginning of the breeding phase, the reproductive states of females and survival groups are also updated (see *Submodels Reproduction* and *Survival* below for more details).

2. Ageing – At the beginning of the breeding phase, each individual adds one year to its age.

3. Nesting – At each time-step during the breeding phase, sexually active females without a nest or chicks have the chance to nest based on the nesting probability (*nesting_prob*), adding a new *nest* to the model (see *Submodel Nesting* below).

4. Hatching – Three weeks after nesting, the chicks hatch (see *Submodel Hatching* below).

5. Migration – At each time-step during the migration phases, males and females without an active *nest* or chicks under seven weeks have the chance to migrate, based on the migration probability (*migration_prob*), to the local area where they will spend the next phenological phase (the same location as the previous year) (see *Submodel Migration* below).

6. Dispersion – At each time-step during the migration to breeding location phase, males and females have the opportunity to disperse (instead of performing the normal migration movement), based on a dispersion probability, to a new breeding local. After the dispersion movement, the individual updates its post-breeding and winter locations according to its migration strategy. (see *Submodel Dispersion* below).

7. Survival – Each time-step concludes with a survival trial for every individual and every *nest* (nest failure) (see *Submodel Survival* below).

8. Outputs collection – At specific moments, depending on the implementation phase (calibration, sensitivity analysis, and validation) or the main experiment, data on the population is collected from the model (see *Submodel Outputs collection* below).

The model uses "asynchronous updating", in which the agents update the state variables one at a time as they execute a submodel that uses the variable. There is no hierarchy among agents of the same type (i.e. the order in which agents conduct each process is random and varies each time step), to avoid artefacts of execution order.

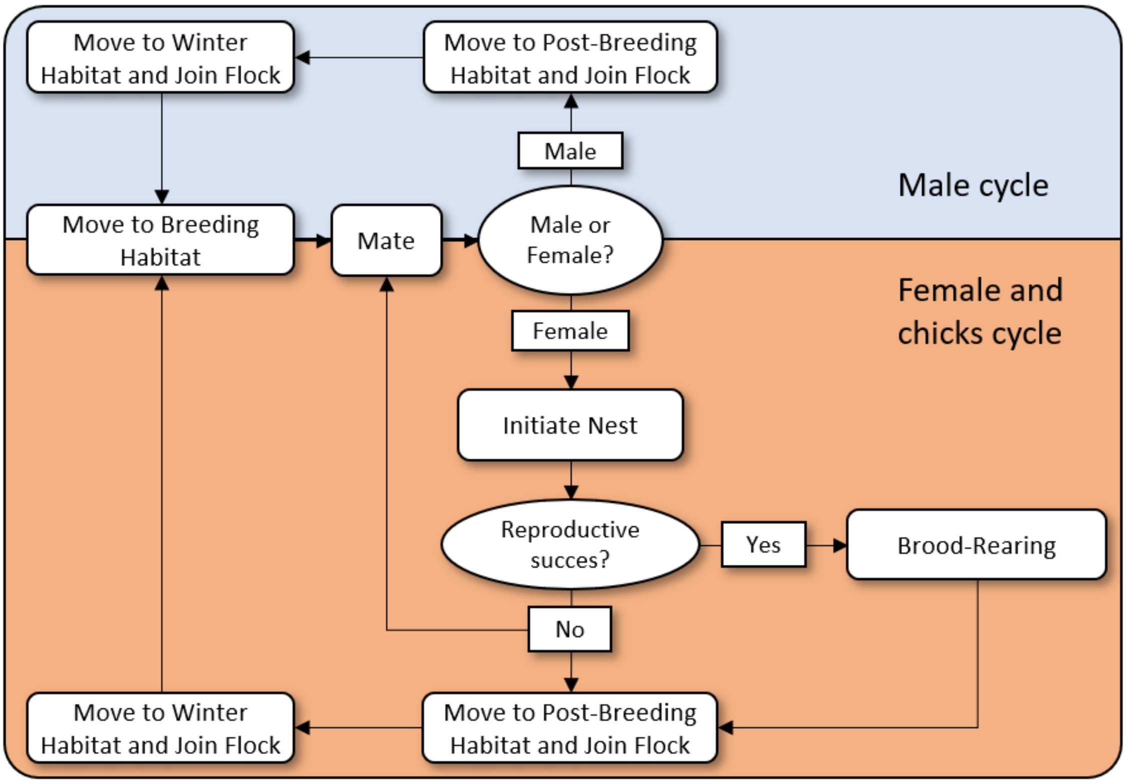


Figure G.2.1 Flow diagram of the yearly-cycle processes included in the model.

2.4 Design concepts

The design concepts *Learning* and *Prediction* do not apply to this model.

2.4.1 Basic principles

The model is built upon several fundamental principles that serve as the foundation for its structure and assumptions. These principles are crucial for comprehending the model's functioning and its connection to real-world observations.

Firstly, the model assumes that the annual cycle of the little bustard is divided into three distinct phenological phases: breeding, post-breeding, and winter (Silva et al., 2015, 2014). These phases are interspersed with periods of migration, reflecting the species' ecological behaviour and movement patterns (García de la Morena et al., 2015). The segmentation of the annual cycle serves as a fundamental framework in the model, allowing for the accurate simulation of the timing and movement of little bustards. In this sense, the model acknowledges various migration patterns, each occurring in different proportions (Silva et al., 2024), enhancing ecological realism.

Furthermore, the model incorporates the concept of philopatry, adding a temporal aspect to the simulation. Philopatry implies that in each phenological phase, individuals return to the locations where they spent the previous year, capturing the species' site fidelity (Alonso et al., 2019; García de la Morena et al., 2015). However, the model also considers the possibility of dispersal to new breeding areas (see *Submodels migration* and *dispersion* below).

The model also considers connectivity with populations outside of the Extremadura region. Although individuals are present in the Extremadura region during the breeding phase, their presence in the region in the post-breeding and/or winter phases is contingent upon their migration patterns (Silva et al., 2024). However, individuals that spent the breeding phase outside Extremadura are assumed not to enter the region during the post-breeding or winter phases. This rule is based on the fact that the impact of the entry of individuals into Extremadura during the winter phase can be considered negligible (Serrano-Davies et al., 2023). This feature helps account for the complex dynamics of the little bustard population within and beyond the study area.

Regarding spatial organization and considering the spatial scale of the model (250 m), it is assumed that female habitat preferences are similar to those of males (Crispim-Mendes et al., 2024). During the breeding phase, the model stipulates that each habitat cell (250 m) can only be occupied by a single individual, representing territorial behaviour in this phase, in contrast to the gregarious behaviour observed in other phenological phases, where the species forms flocks. There is no movement considered within each phenological phase, and the individual's location is assumed as the centroid of its home range. In this regard, the suitability value for each habitat cell is the average of all patches within a buffer with an area equivalent to the average home range, calculated for each phenological phase. Although individuals form flocks during gregarious phenological phases, the members of the same flock may have different destinations in the subsequent phenological phase, with each individual migrating independently.

To establish the relationship between individuals and space, the model assumes a fundamental connection between little bustard occupancy and habitat suitability, with a higher preference for areas with higher suitability values (see *Submodels migration* and *dispersion* below). This relationship is also considered at the level of individual survival probability, which is correlated with the suitability of the location where the individual is situated (see *Submodel Survival* below). The correlation between survival probability and suitability follows examples from other studies demonstrating this relationship for various species (e.g. Hollenbeck et al., 2011; Monnet et al., 2015; Moore et al., 2023). In our case, this correlation is well-founded due to the nature of the predictor variables used in developing suitability maps (Crispim-Mendes et al., 2024), many of which can directly relate to the survival probability of individuals.

Regarding the mating system, the model assumes an “exploded-lek” system where males do not provide parental care during chick development (Jiguet et al., 2000). During the breeding phase, it is assumed that females are attracted by males, forming their territories in the vicinity of male territories (leks). The model also considers the percentage of females reproducing in a given year, with the non-breeding share being filled by one-year-old females. While one-year-old females can reproduce, they, on average, produce one fewer offspring than older females (Bretagnolle and Inchausti, 2005). The model also accounts for the possibility of re-nesting, up to 2 times, in case of nest or chick loss during the breeding phase (see *Submodel Mating* below).

These principles collectively form the foundation of the model, providing a robust scientific basis for understanding little bustard behaviour and population dynamics in the Extremadura region.

2.4.2 Emergence

The model's key outcomes, such as population growth rate, the number of males in Badajoz and Cáceres provinces, adult population sex ratio, and breeding success, arise from the initial number, location, migration patterns, and sex ratio of individuals at the beginning of the simulation. Additionally, these outcomes result from the interactions between individuals and their interactions with habitat suitability during mating, migration, dispersion, and survival behaviours, which occur during the simulation.

The secondary outcomes used to test the model, including nest failure, chick survival, male survival, male site fidelity, and flock sizes, are believed to be driven by the same mechanisms that produce the primary results. Therefore, these patterns must also be emergent, making them useful for testing the model’s suitability for its primary purpose.

2.4.3 Adaptation

Individuals (males and females) possess adaptive traits regarding the selection of the location for each phenological phase in response to changes in habitat suitability and the presence of other individuals. During the breeding phase, individuals return to the same habitat cell where they established themselves in the previous year. They then move within the core area to the location with the highest habitat suitability value that is not already occupied by another individual. This strategy increases the probability of survival and, for breeding females, the reproductive success. If there is no suitable cell (with a suitability value higher than the defined minimum for the phenological phase) in the core area, the individual moves to the nearest suitable cell, and then to the cell with the highest habitat suitability value that is not occupied by another individual within a buffer equivalent to the home range (see *Submodel Migration* below).

In the case of breeding females, the choice of the breeding location also depends on the presence of males within a certain radius, ensuring that reproduction can occur. If there are no males in Extremadura or available habitat cells that meet the requirements, females migrate to another region (outside of Extremadura). During the breeding phase, individuals also have the option to disperse to a new location, which occurs in 16.6% of cases (see *Submodel Dispersion* below).

During the gregarious phenological phases, post-breeding and winter, individuals attempt to join existing flocks within a specified buffer around the location where they spent that phase in the previous year. If there is no flock or the existing flock has reached the maximum number of individuals, the individual forms a new flock (see *Submodels Migration* and *Dispersion* below).

2.4.4 Objectives

The selection of the location for each phenological phase by each individual seeks to increase the fitness of individuals. Choosing habitat cells with higher suitability values increases the probability of individual survival, reduces nest failure, and increases chick survival (for more details about the suitability vs. survival correlation, see *Submodel Survival* below). The rationale for this objective is based on the fact that populations in degraded habitats exhibit lower survival and reproductive success compared to populations in optimal habitats (Serrano-Davies et al., 2023).

The choice of breeding locations near males by females aims to ensure the possibility of reproduction. The rationale for this objective is that most breeding females tend to nest in close proximity to flocks (Faria et al., 2012; Morales et al., 2013; Silva et al., 2014), which not only ensures access to males for reproduction but also guarantees high-quality habitat, as males tend to choose lek habitats of high quality.

2.4.5 Sensing

Individuals are assumed to be able to sense the passage of time, phenological phases, and migration periods. They are also assumed to sense habitat suitability and select habitat from among cells within a radius, depending on the phenological phase and their current situation (see *Submodels Migration* and *Dispersion* below). It is also assumed that they can perceive if a habitat cell is occupied by another individual or flock.

Breeding females are capable of sensing when they have a nest or chicks during the breeding phase, preventing new mating and possibly causing a delay in migration to post-breeding local.

2.4.6 Interaction

The model considers the interaction between habitat cells, where the suitability value of each cell is directly affected by the suitability of the patches around it. The radius of this interaction varies between phenological phases and represents the average size of the little bustard's home range in the study area, Extremadura (data derived from GPS tracking, Silva et al., 2024). The suitability value of a cell is calculated as the average suitability of the cells within this radius. This interaction allows the cell where an individual establishes itself during a phenological phase (centroid of its home range) to contain information about the average suitability of its entire home range.

The model also considers different types of interactions among individuals. One such interaction occurs during the selection of a location to spend a phenological phase (centre of the home range). In the breeding phase, where the species exhibits territorial behaviour, only one individual is allowed per habitat cell, resulting in a mediated interaction among individuals to avoid choosing an already occupied location. During the breeding phase, there is also a mediated interaction between breeding females and adult males, where females can only nest within a certain radius of one or more males. During the phenological phases when the species exhibits gregarious behaviour (post-breeding and winter), there is a direct interaction among individuals, leading to the formation of flocks.

The model also considers a direct interaction between breeding females and their nests and chicks. In this case, if the female dies, the nest fails, or dependent chicks die. Additionally, females with dependent chicks may experience a delay in migration until the chicks are old enough to migrate. The interaction between the female and chicks persists during the first year of the chicks' lives, accompanying the female in migration movements.

Finally, the model considers direct interactions between individuals (nests, males and females) and habitat cells, where the survival of individuals is correlated with the suitability of the cell they occupy.

2.4.7 Stochasticity

Stochasticity is integrated into the model through various processes. First, the model is stochastically initialized, meaning that the total number of individuals (males and females), their locations, migration patterns, and ages are all subject to stochastic variation (see *Initialization* below). This allows for different possibilities of initial population distribution.

Additionally, the allocation of migration and dispersion destinations is stochastically assigned, taking into account the range of distances predicted by the respective migration pattern, with the direction of dispersal determined randomly.

Bernoulli trials are employed to determine the occurrence of different processes, such as whether a first-year female will breed, the week of mating for breeding females, clutch size, and the sex of chicks. This method is also used to determine which individuals will migrate or disperse, the week each individual will undertake migration or dispersion movements, and their weekly survival. This approach ensures that each behaviour is performed with a frequency consistent with observed real-world data.

In the main experiment, the selection of intervention sites, when the percentage of intervened leks is less than 100%, is also carried out randomly (see Section "Initialization").

2.4.8 Collectives

The model considers groups of individuals during the gregarious phenological phases (post-breeding and winter) as collectives, represented in the model as a specific kind of entity (flocks) with their own state variables. These collectives are included in the model to represent the aggregation of individuals sharing the same resources, keeping track of their location and the number and sex-ratio of their integrants.

2.4.9 Observation

The model was designed to collect data on the population depending on the depending on the implementation phase (calibration, sensitivity analysis, and validation) or the main experiment, as presented in Table G.2.4.

2.5 Initialization

Model initialization occurs differently for the implementation phase (calibration, sensitivity analysis, and validation) and the main experiment. While the implementation phase spans from 2005 to 2022, the main experiment occurs between 2022 and 2072.

2.5.1 Initialization of implementation phase

The model's initialization during the implementation phase aims to mimic the little bustard population in Extremadura during the breeding phase of 2005. This is based on the results of the national censuses of male little bustards conducted in that year (García de la Morena et al., 2006) and predictive habitat suitability maps for the species developed for each phenological phase in Extremadura (Crispim-Mendes et al., 2024).

2.5.1.1 Simulation scheduling

During initialization, the 'time' extension of NetLogo is used to set the simulation's initial date and the schedule for all submodels throughout the simulation.

2.5.1.2 Loading habitat suitability maps and geographical boundaries

In one of the initial steps of the initialization, the model loads the habitat suitability map corresponding to the breeding phase of 2005. Each habitat cell is assigned its respective suitability value.

At this stage, the geographical boundaries of the Extremadura region and the provinces of Cáceres and Badajoz within it are also loaded. Additionally, the geographical limits of the Special Protection Areas (SPAs) designated for steppe birds in Extremadura are included.

These steps are crucial for defining the spatial context of the model, considering habitat preferences and geographical constraints in the study area.

2.5.1.3 Individuals' allocation

For the initialization process of the IBM during the implementation phase, a relationship between little bustard occupancy and habitat suitability was established. To achieve this, a logarithmic regression was independently calculated for each province of the Extremadura region (Cáceres and Badajoz), using the male population estimates from the 2005 censuses (corrected values presented in the 2016 census report) and the modified suitability maps generated for the 2005 breeding season (see Section 3.3).

In the initialization process, a raster is imported into the model, where the value of each cell is the expected average density of males based on the regression. The number of males assigned to each cell is defined through a Poisson distribution with the mean at the estimated density value for that habitat cell. The *breed_local* variable of each individual is updated to the habitat cell where they have been allocated. The number of females in each habitat cell is assigned in the same way, but by multiplying the density value of each cell by the sex-ratio considered at the beginning of the simulation. The sex-ratio considered is 0.716 females for each male, the same value used for estimating the population size in the 2005 census report (García de la Morena et al., 2006).

After being allocated to the model, males and females run the *Migration* submodel to the breeding location, which applies the same rules of spatial organization as those applied during migration throughout the simulation (see *Submodel Migration* below).

2.5.1.4 Individuals' age

To obtain a realistic age structure, the age of each individual was assigned with a probability according to a stable age distribution calculated for the Extremadura population (see Section 3.4 and Figure G.3.6).

Considering that the model assumes a biased sex ratio and does not account for differential survival probability between males and females during the first year of life, the number of males and females at the age of 1 at the beginning of the model is equal. The percentage of females for each age over one year is recalculated (see Section 3.4).

2.5.1.5 Individuals' migration strategy

The migration pattern is assigned to each individual based on the occurrence percentages recorded in Extremadura for each pattern (Table G.3.2). The post-breeding and winter locations are then defined according to the individual's migration pattern. Only individuals with patterns of Long-Distance (Summer strategy A, Summer strategy B, and Summer-Winter) have their post-breeding location (and winter location in the case of the Summer-Winter pattern) outside of Extremadura, all others spend the entire annual cycle in the Extremadura region.

The model uses the habitat suitability map for the post-breeding phase of 2005 to define the post-breeding location. It selects a patch above the minimum threshold value within the specified search radius. The winter location destination is determined based on the migration pattern, either matching the location of the breeding or post-breeding phase. If individuals migrate outside the Extremadura region, cell 00 is designated as their destination, as the model does not consider the suitability of locations outside Extremadura.

2.5.2 Initialization of main experience

2.5.2.1 Simulation scheduling

Similar to the initialization of the implementation phase, the 'time' extension of NetLogo is used to set the simulation's initial date and the schedule for all submodels throughout the simulation.

2.5.2.2 Loading habitat suitability maps and geographical boundaries

During initialization, the model loads the habitat suitability map corresponding to the breeding phase of 2022, which is the same phenological phase in the same year when the simulations of the implementation phase end. Each habitat cell is assigned its respective suitability value.

Similarly to what happens in the initialization of the implementation phase, the geographical boundaries of the Extremadura region and the provinces of Cáceres and Badajoz, as well as the Special Protection Areas (SPAs), are loaded into the model.

2.5.2.3 Individuals’ allocation

The allocation of individuals utilizes a database generated during the model validation procedure. This database includes the location and state variables of each individual collected at the end of each replication of the validation (100 replications), at the beginning of the breeding phase of 2022.

At the beginning of the simulation, one of the replicates from the database is randomly chosen. Individuals are then generated in the same locations and with the same values of state variables as at the end of the validation simulation. In practice, the starting point of each simulation in the main experiment is the endpoint of one of the replications of the validation.

2.5.2.4 Implementation of the management approach

The main experiment aims to test various management approaches, including reducing anthropogenic mortality and enhancing suitability in the breeding locations of males (leks) (Table G.2.2). Suitability improvement can occur across the entire study area or specifically within SPAs, and it may be implemented on all leks or only a fraction of them, with variations in the radius around leks and different intensities of suitability improvement. The management parameters are defined during initialization, but the effects of the management approach only begin to manifest at the start of the second year of the simulation, specifically during the breeding phase of 2023.

Table G.2.2 Main experience settings

Variable	Possible values
Survival_Anthropogenic (weekly survival)	0.9989; 0.9993; 0.9996; 1
Scenario	Median; Q1; Q2
Intervention_type	All; SPAs
Intervention_fraction	0.25, 0.5, 0.75, 1
Intervention_radius	1, 3, 5
Intervention_HS	0.1, 0.2, 0.3

To apply the suitability improvement, the model first loads the suitability map of the breeding phase of the scenario to be tested (median, quantile 1, or quantile 3 of suitability between 2012 and 2022). This suitability map is calculated using the original suitability values of each habitat cell, without averaging with the suitability of neighbouring cells, allowing the suitability increase from the management approach to be applied only to the specific patches defined in the approach. Only after the respective increase in suitability in the selected cells for intervention, the average suitability of cells within a buffer with the same size defined for the home range of an individual during the breeding phase (radius of 3 habitat cells) is calculated for each habitat cell.

This suitability map with the increased suitability regarding the management approach is stored as a variable in the model and is used in all breeding phases during the simulation. During initialization, the suitability maps for the post-breeding and winter phases of the scenario to be tested are also loaded into the model and stored as variables. The suitability of these phases is not altered by the management strategy, as the suitability requirements differ between phenological phases.

2.6 Input data

Two input data files from external sources are used in the model: 1) Habitat suitability maps 2005 - 2022; and 2) Future habitat suitability scenarios.

2.6.1 Habitat suitability maps (2005 – 2022)

During the simulations of the implementation phase (calibration, sensitivity analysis, and validation), a raster with predictive information on habitat suitability for the respective year is loaded into the model at each phenological phase. This information is based on predictions of the Species Distribution Models developed by Crispim-Mendes et al. (2024) for the Extremadura region. However, the raster's loaded into the model have been modified so that the suitability value for each habitat cell is the average of the suitability of the surrounding cells, with a buffer that varies between phenological phases. This buffer variation was calculated based on the average home range size of individuals during that phenological phase in Extremadura. The data used for calculating the average home range size in each phenological phase was obtained through GPS tracking (see section 3.1 and Table G.3.1).

For each phenological phase, a minimum suitability threshold was defined for a habitat cell to be considered usable by the little bustard. This threshold was calculated based on the average suitability value (within the buffer defined for each phenological phase) predicted for the specific year of individual tracking, at the centroids of the core areas of individuals tracked by GPS in Extremadura. The selected threshold value for each phenological phase is the 0.05% probability quantile of the average suitability of all core areas in that phenological phase.

The calculation of average suitability based on the average size of the individuals' home ranges and the use of the minimum threshold based on the average suitability at the centroid of their core area is due to the fact that the model does not consider movements during each phenological phase. The location of each individual is a representation of the centroid of its core area. Therefore, the habitat cell where each individual is located contains information about the average suitability of its entire home range in that phenological phase.

2.6.2 Future habitat suitability scenarios (2023 – 2072)

During the simulations of the Main Experience, a raster with predictive information on habitat suitability for each phenological phase is loaded into the model. This information is based on three scenarios for future habitat suitability: median, quantile 1, or quantile 3 of suitability between 2012 and 2022. These three suitability predictions for the future represent different scenarios, one more negative, which assumes an increase in the occurrence of years with lower suitability, one more positive, which assumes an increase in the occurrence of years with higher suitability, and another assuming the continuity of suitability from the last 10 years in the study area.

The scenarios for the post-breeding and winter phases are calculated based on the maps of average suitability for each habitat cell (see 2.6.1 Habitat Suitability Maps 2005 – 2022). In turn, the scenarios for the breeding phase were calculated based on the original suitability maps without the average value for each habitat cell. This allows for the application of the suitability increase in the focal habitat cells of the management approach at the beginning of the simulation (see *Initialization* above).

2.7 Submodels

The model includes 8 submodels or processes, and their description follows the fixed scheduling presented in Section 2.3 (Process overview and scheduling). Model parameters used in the submodels are listed in Table G.2.3.

2.7.1 Global environment updating

Each time-step (one week) begins with the update of the simulation date, and if applicable, the phenological phase and the habitat suitability values of the habitat cells are also updated (see *Submodel Update Suitability* below). During migration phases, the migration probability (*migration_prob*) is updated on a weekly basis (see *Submodels Migration* and *Dispersion* below for more details). The same applies to the mating probability (*nesting_prob*) during the breeding phase (see *Submodel Reproduction* below for more details). At the beginning of the breeding phase, the reproductive states of females and survival groups are also updated (see *Submodels Reproduction* and *Survival* below for more details).

Table G.2.3 Summary of parameters used in the IBM.

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

2.7.2 Ageing

Every year, at the beginning of the breeding phase, one year is added to the age state variable of all individuals in the model. By tracking the age of individuals in this way, it is possible to apply the rules defined in the *Mating* submodel, where the age of individuals at the beginning of the breeding phase is relevant.

2.7.3 Nesting

At the beginning of each breeding phase, the breeding females for that annual cycle are determined. The percentage of breeding females is set by the variable "percentage of non-breeders," calibrated during the model's implementation phase. It is assumed that all females over one year old are breeders (they will attempt to nest), and the non-breeders' portion is filled by one-year-old females, selected stochastically.

Within the breeding phase, at each time-step, breeding females without an active nest or dependent chicks have the opportunity to mate. The mating probability is 0.5 in the first week and 1 in the second week. This strategy assumes that half of the females visit males in leks in the first week, and the other half visit in the second week of the breeding phase. Since the identity of the males with which females mate is not relevant for the model's purpose, it is assumed that the territory of all females in the reproductive phase is established near a lek (see *submodels migration and dispersion* below). Therefore, the females' visits to leks are implicitly modelled

Nesting occurs 2 weeks after mating (Cuscó et al., 2021), at which point a new *Nest* is added to the model, located at the same habitat cell as the female. The *Nest* contains information about the female's identity, as well as her migration pattern and destinations. Each nest has a weekly probability of failure (see *submodel survival* below) during the 3 weeks until the hatching of the chicks (see *submodel hatching* below).

If a female loses her nest or if all the chicks die during the breeding phase, she has the potential to mate and nest again, up to a maximum of 3 times. After the first attempt, the probability of nesting again is 67%, and after the second attempt, it decreases to 57% (Cuscó et al., 2021). The new lek visit occurs in the week immediately following the loss of chicks or the nest. This reproductive pattern is adapted from the observed behaviour of little bustards, considering a time frame of 5.0 - 18.8 days to replace a failed nest, as reported by Cuscó et al. (2021). If the female dies, the nest will fail.

2.7.4 Hatching

The chicks are scheduled to hatch three weeks after nesting. The number of chicks (brood size) is determined based on a normal distribution with a mean of 2.11 and a standard deviation of 0.85, as reported by Bretagnolle et al. (2018). One-year-old females, on average, have one less chick than older females, a value obtained by subtracting 1 from the result of the normal distribution.

The sex ratio at birth is assumed to be 1:1, and chicks are characterized by an age of 0 until the beginning of the next breeding phase. The chicks are born in the same patch as the mother, where they will remain during the first seven weeks of life. Afterward, they migrate to the post-breeding location along with the mother, inheriting the same migration pattern and destinations from her. They are considered dependent on the mother for their first seven weeks, and if the mother dies during this period, the chicks also die. During this period of dependence, their survival probability also follows a specific correlation with Habitat Suitability of the habitat cell where they were born (see *submodel Survival* below).

2.7.5 Migration

The migration submodel occurs slightly differently for each phenological phase, taking into account the specific behaviours of the little bustard throughout the annual cycle.

2.7.5.1 Migration to breeding location

At the beginning of the migration phase to the breeding location (March 1st), it is stochastically determined which individuals will undergo normal migration, moving to the same location where they spent the phase in the previous year, and which will undergo a dispersal movement, which occurs with a probability of 0.1666 (see *submodel Dispersion* below).

To make the migration to the breeding location as realistic as possible considering the model's objectives, males migrate in one of the first three weeks of March, with movements scheduled to occur on March 1st, 8th, and 15th. The migration probabilities are updated weekly so that the number of individuals migrating is similar in all weeks (1st week = 0.333; 2nd week = 0.5; and 3rd week = 1).

On the other hand, females undergo the migration movement in one of the last two weeks of March, with movements scheduled for March 15th and 22nd. Weekly migration probabilities are adjusted to ensure a similar number of individuals migrating on both weeks (1st week = 0.5; 2nd week = 1).

Males migrate to the suitable habitat cell (not occupied by another individual that has already migrated and with a suitability value above the minimum threshold for the breeding phase; see input data above) with the highest habitat suitability value within the home range area of the previous year. If there is no suitable habitat cell within the core area, they search for the nearest suitable habitat cell, and then move to the suitable habitat cell with the highest suitability value within a radius equivalent to a home range (3 habitat cells), establishing their new breeding location (centroid of the home range). This migration strategy ensures that males prioritize unoccupied, high-suitability habitat cells within their known areas, adapting their breeding locations based on the environmental conditions of the current year.

In the case of females, an additional requirement is imposed for a habitat cell to be considered suitable: it must be within a maximum distance of 4 habitat cells (1000 meters) from a male (Faria et al., 2012; Morales et al., 2013; Silva et al., 2014). Other than this, females follow the same behaviour for selecting their breeding location as exhibited by males. In the event that no suitable habitat cell is found within the Extremadura region, the female migrates outside the region, represented by habitat cell 00. This migration strategy ensures that females prioritize suitable habitat cells close to males.

2.7.5.2 Migration to post-breeding and winter locations

Migration to post-breeding and winter locations follows similar rules, with individuals joining an existing flock or establishing a new one. Unlike the breeding phase, both males and females migrate simultaneously throughout the migration period (post-breeding from 15 July to 15 September; and winter from 15 December to 1 March). An exception occurs during the migration to post-breeding locations for breeding females that, at the start of the migration period, have a nest or chicks aged 7 weeks or less. In this case, females only migrate, accompanied by the chicks, after they reach 7 weeks of age, which may happen later than the normal migration period for the rest of the individuals (after July 15). If the nest fails or all the chicks die, the female migrates the following week.

During the migration phase, the migration probability is updated weekly to ensure a similar number of individuals migrate each week. Migrating individuals check for existing flocks that have not already reached the maximum allowed number of individuals (100 in post-breeding and 300 in winter; guesstimated based on Morales et al. (2022) and Silva et al. (2024)) within a buffer with a radius that differs between post-breeding and winter (calibrated values: 1500 m in post-breeding and 2750 m in winter) around the habitat cell where they spent the previous year's phase. If one or more flocks meet the requirements, individuals join the closest one to the previous year's location. If no flock is found in the search area, they move to the suitable habitat cell (with a suitability value above the minimum threshold for the respective phase; see input data above) with the highest habitat suitability value within the home range area of the previous year, establishing a new flock (of which they are the only member until the arrival of other individuals). Overlapping home ranges between different flocks are not allowed. If there is no suitable habitat cell within the core area, the individuals search for the nearest suitable habitat cell and then move to the suitable habitat cell with the highest suitability value within a radius equivalent to a home range (5 habitat cells in post-breeding and 7 in winter). There, they check for existing flocks within a buffer equivalent to the home range; if any, they join the closest one, and if not, they establish a new one.

2.7.6 Dispersion

At the beginning of the migration phase to the breeding location (March 1st), it is stochastically determined which individuals will undergo normal migration, moving to the same location where they spent the phase in the previous year, and which will undergo a dispersal movement (see *submodel Migration* above).

Dispersion movements represent individuals that, instead of spending the breeding phase in the same location as the previous year, disperse to a new breeding location. The probability of an individual dispersing each year is 0.1666, and the average dispersal distance is 51.67 km +/- 19.41, values calculated based on GPS tracking data of individuals in Extremadura (Silva et al., 2024).

Each week during the migration phase to the breeding location, after the migration movements have been made (see *submodel Migration* above), dispersion movements are performed by the selected individuals. The fact that the dispersion process occurs after the migration process is based on empirical data, where individuals that disperse typically return to the breeding location of the previous year first and only then perform the dispersal movement. However, in the model, individuals performing the dispersion movement do not undergo the migration process first, for efficiency reasons.

The probability of an individual selected for dispersal to perform the movement in a given week is equal to the migration probability for that same week, with males performing the movements in the first three weeks of March and females in the last two weeks (see *submodel Migration* above).

The dispersing individual begins by searching for suitable habitat cells (not occupied by another individual that has already migrated or dispersed and with a suitability value above the minimum threshold for the breeding phase; see input data above) in a search range between 32.26 km and 71.07 km (129 – 284 habitat cells). Then, it randomly chooses one of the habitat cells and moves there, making it its new breeding location. Once established, the individual also defines its new post-breeding and winter locations, taking into account its migration pattern (see Section 5.1.1. Individuals' Migration Strategy above).

If there is no suitable habitat cell in the search area, the individual undergoes the normal migration process to the location of the previous year (see *submodel Migration* above).

2.7.7 Survival

For the survival process, five different groups of individuals/agents are considered, each with different survival probabilities:

1) Nests;

2) Chicks (males and females under 8 weeks old);

3) Adults (males over 7 weeks old and less than 10 years old; non-breeding females over 7 weeks old; breeding females outside the breeding season and less than 10 years old);

4) Breeding females (breeding females with less than 10 years old during the breeding season); and

5) Old individuals (males and females 10 years old or older).

For each of the groups, except "old individuals," a correlation between weekly survival probability and the suitability of the habitat cell where they are located was calibrated using a logistic regression (equation x), where different values of A and B were tested for each group.

(Eq. 1)

$$\text{Probability of Survival} = \mathrm{A} + \mathrm{B} \ln x$$

Where:

- x equals the suitability value of the habitat cell where the individual is located.

The calibration was conducted during the model implementation phase, considering the period between 2005 and 2022. The calibration process was carried out using the ABC-rejection method (Beaumont et al., 2002; van der Vaart et al., 2015), employing various population parameters as target values (see Section 6).

In addition to "natural mortality", correlated with habitat suitability, "adults" and "breeding females" are also affected by anthropogenic mortality factors. The weekly probability of survival to anthropogenic factors is defined uniformly across the entire study area, representing a continuous probability over time and space. This probability was defined based on empirical data from individuals tracked by GPS in Extremadura (Silva et al., 2024).

The survival trials for each group are the last action to occur each week in the model.

2.7.7.1 Nests

The weekly nest´s survival probability is applied to each nest during the three weeks between laying and hatching of the chicks, and is defined by the equation 1

If the female that laid the nest dies, the nest fails in the same week.

2.7.7.2 Chicks

The weekly chick's survival probability is applied to each chick during their first seven weeks of life, where they are dependent on their mother, and is defined by the equation 1.

If the mother of the chicks dies, the chicks also perish in the same week.

2.7.7.3 Adults

The weekly adult´s survival probability is applied to each adult individual throughout their lifespan, except for breeding females between the start of the breeding phase and until they migrate or disperse to the post-breeding location. It is defined by the equation 1.

Where: x equals the suitability value of the habitat cell where the individual is located. This value is updated to the suitability of the following phase when the migration or dispersal movement is carried out. For individuals outside of Extremadura (habitat cell 00; see submodel migration above), the suitability value used is the average suitability of the habitat cells of all individuals within Extremadura (value updated weekly during migration phases).

2.7.7.4 Breeding females

The weekly breeding female´s survival probability is applied to each breeding female between the start of the breeding phase and until they migrate or disperse to the post-breeding location. It is defined by the equation 1.

This distinct survival probability for breeding females during this phase of the annual cycle represents the lower survival probability expected for this group during this period. This is due to the significant energy costs associated with reproduction, which are anticipated to increase even more in situations where the suitability of the location is low, reflecting resource scarcity. This justifies the existence of unbalanced sex ratios in areas with more degraded habitats.

2.7.7.5 Old individuals

For males and females aged 10 years or older, their weekly survival probability is lower than that of other adults, based on the assumption that the majority of individuals in nature do not surpass 10 years of age (Inchausti and Bretagnolle, 2005). This reduced survival probability is set at a fixed value to ensure that these individuals do not survive beyond the age of 11, with a probability of 0.0001 of surviving until they reach 11 years. The weekly survival probability for this group was calculated using the equation (2):

(Eq. 2)

$$\text{Probability of Survival} = \left(\text{probability\_reach\_11\_years}^{\left(1/_{\text{N of weeks}}\right)}\right)$$

Where:

probability_reach_11_years equals 0.0001 (the probability of surviving until 11 years);

N of weeks equals 52 (the number of weeks in a year).

Resulting in a weekly survival probability of approximately 0.837678 for this group.

2.7.8 Outputs collection

At specific moments, depending on the implementation phase (calibration, sensitivity analysis, and validation) or the main experiment, data on the population is collected from the model.

Table G.2.4 List of the outputs collected from the model, their collection timing, and the implementation phases during which they are collected (C - Calibration; SA - Sensitivity Analysis; V - Validation; ME - Main Experiment).

Variable	Description	Collection timing	C	SA	V	ME
N_males_C_2005	Count all males at Caceres at the beginning of the 2005 breeding season	Tick 0 Beginning of breeding of 2005	X		X	
N_males_B_2005	Count all males at Badajoz at the beginning of the 2005 breeding season	Tick 0 Beginning of breeding of 2005	X		X	
N_males_C_2016	Count all males at Caceres at the beginning of the 2016 breeding season	Tick 575 Beginning of breeding of 2016	X		X	
N_males_B_2016	Count all males at Badajoz at the beginning of the 2016 breeding season	Tick 575 Beginning of breeding of 2016	X		X	
N_males_C_2022	Count all males at Caceres at the beginning of the 2022 breeding season	Tick 888 Beginning of breeding of 2022	X		X	
N_males_B_2022	Count all males at Badajoz at the beginning of the 2022 breeding season	Tick 888 Beginning of breeding of 2022	X		X	
median_CA_fidelity	Percentage of males that remained in the core area from the previous year	Data collected every year at the beginning of the breeding season; Median calculated at Tick 888 (Beginning of breeding of 2022)			X	
median_HR_fidelity	Percentage of males that remained in the home-range from the previous year	Data collected every year at the beginning of the breeding season; Median calculated at Tick 888 (Beginning of breeding of 2022)			X	
median_nest_failure	Median of the percentage of nests that failed each year	Data collected every year at 08-19 (first week after the end of reproduction procedures);			X	

Variable	Description	Collection timing	C	SA	V	ME
		Median calculated at Tick 888 (Beginning of breeding of 2022)				
median_chicks_survival	Median of the percentage of chick's survival until the 7th week (49 days) in each year	Data collected every year at 08-19 (first week after the end of reproduction procedures); Median calculated at Tick 888 (Beginning of breeding of 2022)			X	
median_breeding_success (Fledging rate (FR))	Median of the breeding success (the probability that a female with a brood manages to fledge at least one young)	Data collected every year at 08-19 (first week after the end of reproduction procedures); Median calculated at Tick 888 (Beginning of breeding of 2022)		X	X	
median_juv/fem (fecundity (f))	Median of the mean number of juveniles per female each year	Data collected every year at 08-19 (first week after the end of reproduction procedures); Median calculated at Tick 888 (Beginning of breeding of 2022)		X	X	
median_juv/b_fem (Number of chicks at fledging (FS): the average number of chicks per successful brood.)	Median of the mean number of juveniles per breeding female each year	Data collected every year at 08-19 (first week after the end of reproduction procedures); Median calculated at Tick 888 (Beginning of breeding of 2022)		X	X	
growth_rate	Annual population growth rate (λ), estimated as: $\lambda = \left(\frac{present}{past}\right)^{\frac{1}{n}}$ Were: "past" is the number of individuals at the beginning of the simulation, "present" is the number of individuals at the end of the simulation and "n" the number of years of	Calculated at Tick 888 (Beginning of breeding of 2022)		X		X

Variable	Description	Collection timing	C	SA	V	ME
	simulation. Values <1 indicate a population decline, while values >1 indicate a population growth.					
sex_ratio_PB_2021	Sex-ratio of adults (>0 years) at the post-breeding	Tick 860 End of post-breeding of 2021	X	X	X	X
sex_ratio_W_2021	Sex-ratio of adults (>0 years) at the winter	Tick 881 End of winter of 2021		X	X	X
flock_W_med_2021	Mean size of flocks in winter of 2021	Tick 881 End of winter of 2021	X		X	
flock_W_sd_2021	Standar deviation of the size of flocks in winter of 2021	Tick 881 End of winter of 2021	X		X	
flock_PB_med_2021	Mean size of flocks in post-breeding of 2021	Tick 860 End of post-breeding of 2021	X		X	
flock_PB_sd_2021	Standar deviation of the size of flocks in post-breeding of 2021	Tick 860 End of post-breeding of 2021	X		X	

3. Data evaluation

This TRACE element provides supporting information on: The quality and sources of numerical and qualitative data used to parameterize the model, both directly and inversely via calibration, and of the observed patterns that were used to design the overall model structure. This critical evaluation will allow model users to assess the scope and the uncertainty of the data and knowledge on which the model is based.

Summary:

Here we provide the source of all the data incorporated in the model.

The model was parameterized using empirical data specific to the little bustard in Extremadura. When regional empirical data were lacking, information from the species' Western European distribution was used. For parameters where no empirical data were available, reverse parameterization was conducted through calibration.

In the following sections, we present the sources of the data used and how they were employed in the parameterization of the model.

3.1 Movement and spatial organization data

The information used to define the spatial organization and movements of individuals in the IBM comes from GPS telemetry data from little bustards in Extremadura, data presented in Silva et al. (2004).

These data yield the following information used in the model:

Home ranges and core areas

The average size of an individual's core area and home range in each phenological phase (Table G.3.1) was calculated based on the core areas and home ranges of several individuals tracked in Extremadura. The average home range value was used to recalculate the habitat suitability maps, taking into account the area of influence (home range) in each phenological phase (see Section 2.6). The average core area value was used to define, for each phenological phase, a minimum suitability threshold for a habitat cell to be considered usable by the little bustard (see Section 2.6).

Individual tracking data was also used to calculate the fidelity of breeding males to the core area and home range of the previous year. In this case, a 43% probability of overlap with the previous year's home range and a 93% probability of overlap with the previous year's home range were calculated. These values were used in the model validation process (see Section 8)

Table G.3.1 Size of core areas and home ranges recorded in Extremadura for each phenological phase, and the calculated radius and number of habitat cells considered in the IBM. [Adapted from Silva et. al. (2004)]

	Breeding	**Post-breeding**	**Winter**
Number of individuals	35	45	23
Core area (km^2)	0.105 ± 0.162 (0.008 – 0.764)	0,686 ± 0,523 (0,116 - 2,149)	1,157 ± 1,068 (0,069 - 3,949)
Home range (km^2)	1.742 ± 2.548 (0.053 - 13.144)	5.629 ± 4.573 (0.665 - 20.145)	9.356 ± 7.449 (3.232 - 31.896)
Radius (km)	0.745	1.339	1.726
(n habitat cells 250m)	(3 habitat cells)	(5 habitat cells)	(7 habitat cells)

Migration and dispersion patterns

The analysis of tracking data for individuals in Extremadura identified six migration patterns, which vary in the distances travelled by individuals between each phenological phase (Table G.3.2).

Table G.3.2 Characteristics of each of the six migration patterns identified in Extremadura, including the distances travelled over the year cycle and distances between the breeding (B) location and the post-breeding (PB) and winter (W) locations. *Proportion of individuals in the observed population (%). [Adapted from Silva et. al. (2004)]

	Number of individuals (*%)	**Distance travelled (km)**		**Distance to PB and W (km)**	
		Average	**Maximum**	**Range**	
SD - Short-Distance	17 (47.2)	11.77 ± 5.6	77.4	B - PB B – W	6.17 – 17.37 W = PB
MDS - Medium-Distance Summer	8 (22.2)	21.8 ± 6.9	129.5	B - PB B – W	14.9 – 28.7 W = B
MDSW - Medium-Distance Summer-Winter	7 (19.4)	45.55 ± 13.77	119.4	B - PB B – W	31.78 - 59.52 W = PB
LDSA - Long-Distance Summer strategy A	2 (5.6)	69.44 ± 14.5	160.3	B - PB B – W	Outside Extremadura W = B
LDSB - Long-Distance Summer strategy B	1 (2.8)	112.77	351.88	B - PB B – W	Outside Extremadura W = B
LDSW - Long-Distance Summer-Winter	1 (2.8)	162.33	229.99	B - PB B – W	Outside Extremadura Outside Extremadura

These patterns are characterized by the following types of migratory behaviour:

SD – short-distance movements around their breeding grounds during the summer, autumn, and/or winter periods.

MDS - left their breeding grounds during the summer (mainly in June), moving mostly to nearby agricultural areas and pastures. On average, these birds returned to their breeding grounds in November.

MDSW - left their breeding grounds during the summer (mainly in July) and only returned in March after winter.

LDSA - left their breeding grounds during the summer and autumn periods, covering distances of around 150 km.

LDSB - left their breeding grounds in July to spend the summer and autumn in cooler regions near the city of León. This bustard began returning in October, with a maximum distance travelled of 351.8 km.

LDSW - left their breeding grounds in June to spend the summer and autumn-winter in cooler regions near the city of Toledo, covering a maximum distance of 229.9 km. This bustard returned in March, but soon after dispersed to areas up to 50 km away.

Dispersion distances

The tracking data for individuals in Extremadura also served to identify the probabilities and distances of dispersal movements (Table G.3.3).

Given the lack of representativeness of some migration patterns, a uniform dispersal probability of 16.7% annually was considered for all individuals in the parameterization of the IBM, with movements ranging from 32.25 to 71.0 km (equivalent to 129 to 284 habitat cells of 250 m).

Table G.3.3 Probabilities and distances of dispersal movements by migration pattern. [Adapted from Silva et. al. (2004)]

	Number of individuals (*%)	**Number of dispersers (*%)**	**Distance travelled (km)**
SD - Short-Distance	17 (47.2)	2 (33.3)	20; 60
MDS - Medium-Distance Summer	8 (22.2)	1 (16.7)	50
MDSW - Medium-Distance Summer-Winter	7 (19.4)	2 (33.3)	50; 80
LDSA - Long-Distance Summer strategy A	2 (5.6)	-	-
LDSB - Long-Distance Summer strategy B	1 (2.8)	-	-
LDSW - Long-Distance Summer-Winter	1 (2.8)	1 (16.7)	50

3.2 Suitability maps

The habitat suitability maps used in the IBM are derived from the projections of the SDMs presented in Crispim-Mendes et al. (2024) for each phenological phase of the little bustard in Extremadura. For the implementation phase (calibration, sensitivity analysis, and validation) of the IBM (2005 to 2022), the suitability projection maps for each year were modified so that the value of each cell (250m) is the average of the suitability of the surrounding cells, with a buffer that varies between phenological phases, based on the average home range (see Section 2.6). For the main experiment (2022 – 2072), three scenarios for future habitat suitability were calculated: median, quantile 1, and quantile 3 of suitability between 2012 and 2022 (see Section 2.6).

For each phenological phase, a minimum suitability threshold was defined for a habitat cell to be considered usable by the little bustard (Table G.3.4). Modified habitat suitability maps and GPS tracking data of individuals in Extremadura were used for this purpose. The thresholds were calculated based on the suitability value predicted for the specific year of individual tracking, at the centroids of the core areas of tracked individuals. The selected threshold value for each phenological phase is the 0.05% probability quantile of the average suitability of all core areas in that phenological phase.

Table G.3.4 Minimum suitability threshold for each phenological phase.

Phenological Phase	Minimum suitability threshold
Breeding	0.330
Post-Breeding	0.291
Winter	0.284

3.3 Census data

The IBM leverages the national census conducted in 2005 (García de la Morena et al., 2006) and 2016 (García de la Morena et al., 2018), and the regional census of 2022 (SEO, in prep) (Table G.3.5) for the initialization, calibration and validation processes.

Table G.3.5 Estimates of the number of males for Extremadura and each of its regions (Badajoz and Cáceres), obtained through the 2005 and 2016 national censuses and the 2022 regional censuses. The values presented for 2005 are corrected values presented in the 2016 census report.

Year	Province	Mean	Minimum	Maximum
2005	Badajoz	7.194	5.181	10.270
	Cáceres	1.715	1.085	2.538
	Total	8.909	6.266	12.808
2016	Badajoz	3.216	2.114	4.612
	Cáceres	656	273	1.145
	Total	3.872	2.387	5.757
2022	Badajoz	1.041	707	1.405
	Cáceres	229	120	362
	Total	1.270	827	1.767

For the initialization process of the IBM during the implementation phase, a relationship between little bustard occupancy and habitat suitability was established. To achieve this, a logarithmic regression was independently calculated for each province of the Extremadura region (Cáceres and Badajoz), using the male population estimates from the 2005 censuses (corrected values presented in the 2016 census report) and the modified suitability maps generated for the 2005 breeding season. The process involved the following steps:

1) Extract the habitat suitability value for each census listening point by overlaying the listening points with the suitability map;
2) Calculate the density per hectare for each listening point;
3) Calculate the expected number of individuals per 250 m grid cell for each listening point;
4) Perform a logistic regression between the expected number of individuals per 250 m grid cell for each listening point and the corresponding habitat suitability value.

The results of the logistic regressions are presented in Figures X and Y.

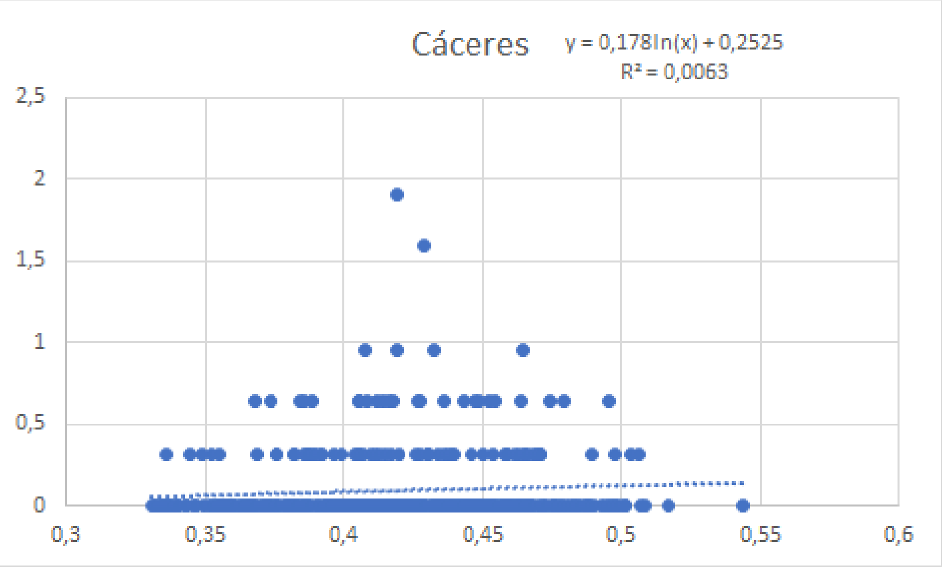


Figure G.3.1 Relationship between Little Bustard Occupancy and Habitat Suitability for Cáceres.

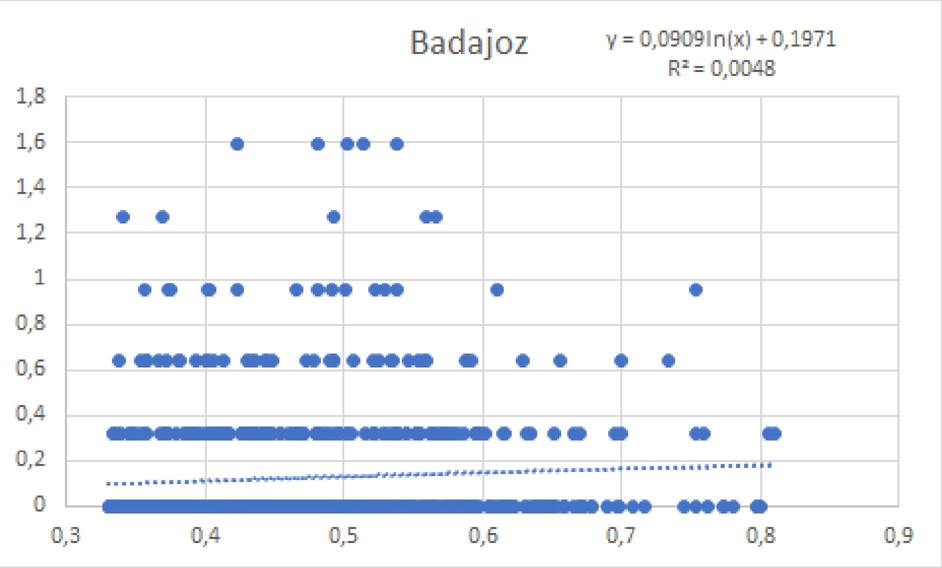


Figure G.3.2 Relationship between Little Bustard Occupancy and Habitat Suitability for Badajoz.

3.4 Stable age distribution

To obtain a realistic age structure, the age of each individual was assigned with a probability according to a stable age distribution calculated for the Extremadura population (Table G.3.6. For this calculation, an annual fertility value of 0.47 and an annual survival rate of 0.689 were used, estimated for the Extremadura population (Silva et al., 2024). The fertility value for one-year-old individuals (0.28) was taken from (Bretagnolle and Inchausti, 2005).

Table G.3.6 Stable age distribution for the little bustard male population in Extremadura in 2005.

Age	Relative %	Cumulative %
1	36.87	36.87
2	23.42	60.29
3	14.88	75.17
4	09.45	84.62
5	06.00	90.63
6	03.81	94.44
7	02.42	96.86
8	01.54	98.40
9	00.98	99.38
10	00.62	100.00

Considering that the IBM assumes a biased sex ratio and does not account for differential survival probability between males and females during the first year of life, the number of males and females at the age of 1 at the beginning of the model is equal. The percentage of females for each age over one year is recalculated according to the following formula:

$$\%Fx = \left(\frac{\%Cx - \%R1}{\left(\frac{\%C > 1}{1 - \% F1} \right)} \right) + \%F1$$

Where:

- %Fx: Percentage of females of age x
- %Cx: Cumulative percentage of males of age x

- %R1: Relative percentage of males of age 1
- %C>1: Cumulative percentage of males of age over 1
- %F1: Percentage of females of age 1

3.5 Flocks and sex ratio

For the model calibration and validation process, data on flock counts and sex ratios in Extremadura collected between 2020 and 2022 were used (Table G.3.7), data originally presented in Silva et. al. (2004). Regarding flock size, it should be noted that empirical counts can be quite variable depending on the time of day they are conducted, considering the species' behaviour, with greater aggregation at night and more dispersion during the day.

Table G.3.7 Summary of the records of little bustard flocks collected during the post-reproductive period (from mid-July to late September, when females and juveniles are easily distinguishable) and during the winter (considering all female and female-like individuals, including juveniles, between February 13 and March 9). Information on the average flock size and the average sex ratio is presented for both seasons. [Adapted from Silva et. al. (2004)]

	Post-breeding flocks		**Winter flocks**	
	Flock size	**Sex ratio**	**Flock size**	**Sex ratio**
Mean ± SD	13.4 ± 16.2	0.51 ± 0.57	28.5 ± 34.1	0.43 ± 0.38
Maximum	84	2	130	1.31
Minimum	3	0	4	0
Number of flocks	26		12	

4. Conceptual model evaluation

This TRACE element provides supporting information on: The simplifying assumptions underlying a model’s design, both with regard to empirical knowledge and general, basic principles. This critical evaluation allows model users to understand that model design was not ad hoc but based on carefully scrutinized considerations.

Summary:

The conceptual model is represented in Figure 1. The design concepts underlying model design are presented in section 2, Model description. Further information regarding simplifying assumptions is presented in section 3, Data evaluation.

5. Implementation verification

This TRACE element provides supporting information on: (1) whether the computer code implementing the model has been thoroughly tested for programming errors, (2) whether the implemented model performs as indicated by the model description, and (3) how the software has been designed and documented to provide necessary usability tools (interfaces, automation of experiments, etc.) and to facilitate future installation, modification, and maintenance.

Summary:

To the best of our ability, we have ensured the model operates as described in this TRACE document, having employed various strategies of model checking. The model as described, along with associated files, are available to interested parties.

Model verification

The tests executed to verify the implementation of the model ranged from very simple checks using the tools provided by the software platform NetLogo, to more in-depth analyses. Tests included:

- Syntax checking of the code.
- Visual testing through NetLogo interface.
- Spot tests with “agent monitors”, i.e. opening a few NetLogo “agent monitors” and manually recording the value of the variables, calculating by hand how they should change, and then stepping the model through one iteration of its schedule and seeing if the change reported by the agent monitor matches the expectation.

- Stress tests with extreme parameters values to expose errors that may be hidden under normal conditions.
- Test procedures, i.e. adding new procedures to the code just to produce intermediate output, used only for testing.

How to install and use the model

The model is implemented in NetLogo 6.3.0, a programmable environment particularly suited to modelling complex, individual-based systems evolving over time (Wilensky, 1999). NetLogo is free to download and runs on all major operating systems. Version 6.3.0 can be downloaded here: https://ccl.northwestern.edu/netlogo/6.3.0/. The model and associated files are available at:

https://github.com/TCrispimMendes/IBM_Decision-Support_Tool_for_Little_Bustard_in_Extremadura

6. Model output verification

This TRACE element provides supporting information on: (1) how well model output matches observations and (2) how much calibration and effects of environmental drivers were involved in obtaining good fits of model output and data.

Summary:

This section details the number and types of parameters that were inversely determined through calibration. For the calibration process, we employed the rejection Approximate Bayesian Computation (ABC) algorithm. ABC is a valuable method for estimating parameters by comparing model-simulated data to empirically derived summary statistics, making it particularly useful for complex models like IBMs. Rejection Approximate Bayesian Computation (r-ABC), a specific application of ABC, rejects parameter sets that fail to recreate adequate summary statistics based on a predefined cutoff.

Among the parameters integrated into the model (Table G.2.3), three were considered uncertain due to limited or absent empirical data, necessitating calibration. These parameters encompassed the proportion of non-breeding females and the conspecific attraction radius during the post-breeding and winter phases. Furthermore, no prior correlation had been established between the survival rates of the agents and individual groups considered in the model and the suitability of their habitat locations. To address this, the correlation was attained for each group through the calibration of parameters A and B in the logarithmic regression formula: survival ~ A + B ln (habitat suitability)

For the calibration process we utilized the rejection Approximate Bayesian Computation (ABC) algorithm (Beaumont et al., 2002; van der Vaart et al., 2015), implemented through the 'abc' package (Csilléry et al., 2012).

ABC represents a set of computational techniques grounded in Bayesian statistics that can be used to estimate posterior distributions of model parameters. These approaches proves particularly useful for intricate models such as Individual-Based Models (IBMs), as it compares model-generated data with empirically derived summary statistics (Beaumont, 2010). Despite the existence of various ABC algorithms, they all entail four essential steps: (1) drawing parameters from proposed distributions, (2) simulating data using the selected parameters, (3) generating summary statistics, and (4) accepting or rejecting parameters based on the comparison of dissimilarity statistics, i.e., disparities between summary statistics from observed and simulated data, against a predefined acceptance threshold (Chen et al., 2017).

In rejection-ABC, the simplest ABC algorithm, the core idea involves running numerous simulations with the IBM, employing various sets of parameter values drawn from the prior distribution, and computing summary statistics from the model's outputs. The rejection-ABC algorithm then estimates posterior distributions for each input parameter, retaining only those model parameterizations that closely match the empirical target (as determined by the Euclidean distances between the simulated and empirically derived summary statistics). The posterior density of the parameters is then constructed based on the accepted parameterizations (Hartig et al., 2011; van der Vaart et al., 2015).

6.1 Calibration process

The calibration process involved two main phases: defining the priors training region and determining the acceptance rate for the posterior estimates. Initially, prior distributions for the eleven parameters were established based on a literature review or ecological considerations, particularly for the A and B parameters of logarithmic regressions for survival/suitability correlations (seeTable G.6.1, initial priors). Subsequently, a pilot rejection ABC analysis was conducted to refine the priors and identify the training region. This involved generating 25,000 different sets of parameter values randomly drawn from the prior distribution using a Latin Hypercube Sample method. Simulations were run in parallel using the R package *NLRX* (Salecker et al., 2019). The priors were then refined based on the credible intervals of the posterior estimates, with a tolerance rate of 0.005 (see Table G.6.1, Refined priors). Summary statistics included the number of males in Cáceres and Badajoz in 2016 and 2022, the adult sex-ratio in the post-breeding phase in 2020 and 2021, the fecundity value in 2021, and the mean size and standard deviation of flocks in post-breeding and winter phases.

Table G.6.1 Initial and refined prior for calibration

Variables	Initial priors		Refined priors	
	min	max	min	max
Percent_Non_Breeders	0.14	0.23	0.14	0.23
R_PB	5	30	7	30
R_W	10	35	11	35
A_NS	0.75	1	0.7652	0.9980
B_NS	0	0.3	0.0142	0.2697
A_CS	0.9	1	0.9099	0.9985
B_CS	0	0.3	0.0030	0.2111
A_FS	0.98	1	0.9818	0.9996
B_FS	0	0.05	0.0007	0.0434
A_AS	0.99	1	0.9947	0.9999
B_AS	0	0.05	0.0001	0.0065

After refining the priors, we conducted another rejection ABC analysis with 25,000 different parameter samples randomly drawn from the refined prior distribution using the Latin Hypercube Sample method. This time, we used a tolerance value of 0.0005, leading to the acceptance of 13 parameter samples. The summary statistics utilized were the same as those used in the refining phase. Posterior distributions were then derived from the accepted runs (see Table G.6.2).

Since the calibration aimed to determine a single value for each parameter, we selected the mean of the posterior distribution as a point estimate of each parameter. Additionally, we utilized the 95% Bayesian credible interval (BCI), representing the central 95% range of the posterior, to indicate the precision of this estimate (see Table G.6.2).

Table G.6.2 Parameters estimates by approximate Bayesian computation.
*BCI - Bayesian credible interval.

Variable	Mean (95% BCI*)
Percent_Non_Breeders	18.46 (15.00 – 22.70)
R_PB	20.3077 (8.6000 - 27.0000)
R_W	32.6154 (30.3000 - 34.0000)
A_NS	0.9582 (0.8596 - 0.9937)
B_NS	0.1546 (0.0358 - 0.2574)
A_CS	0.9745 (0.9420 - 0.9958)
B_CS	0.0765 (0.0300 - 0.1815)
A_FS	0.9965 (0.9932 - 0.9988)
B_FS	0.0212 (0.0016 - 0.0367)
A_AS	0.9984 (0.9963 - 0.9998)
B_AS	0.0024 (0.0003 - 0.0054)

Calibrated survival curves of the various life stages of the little bustard relative to habitat suitability are presented in Figure G.6.1.

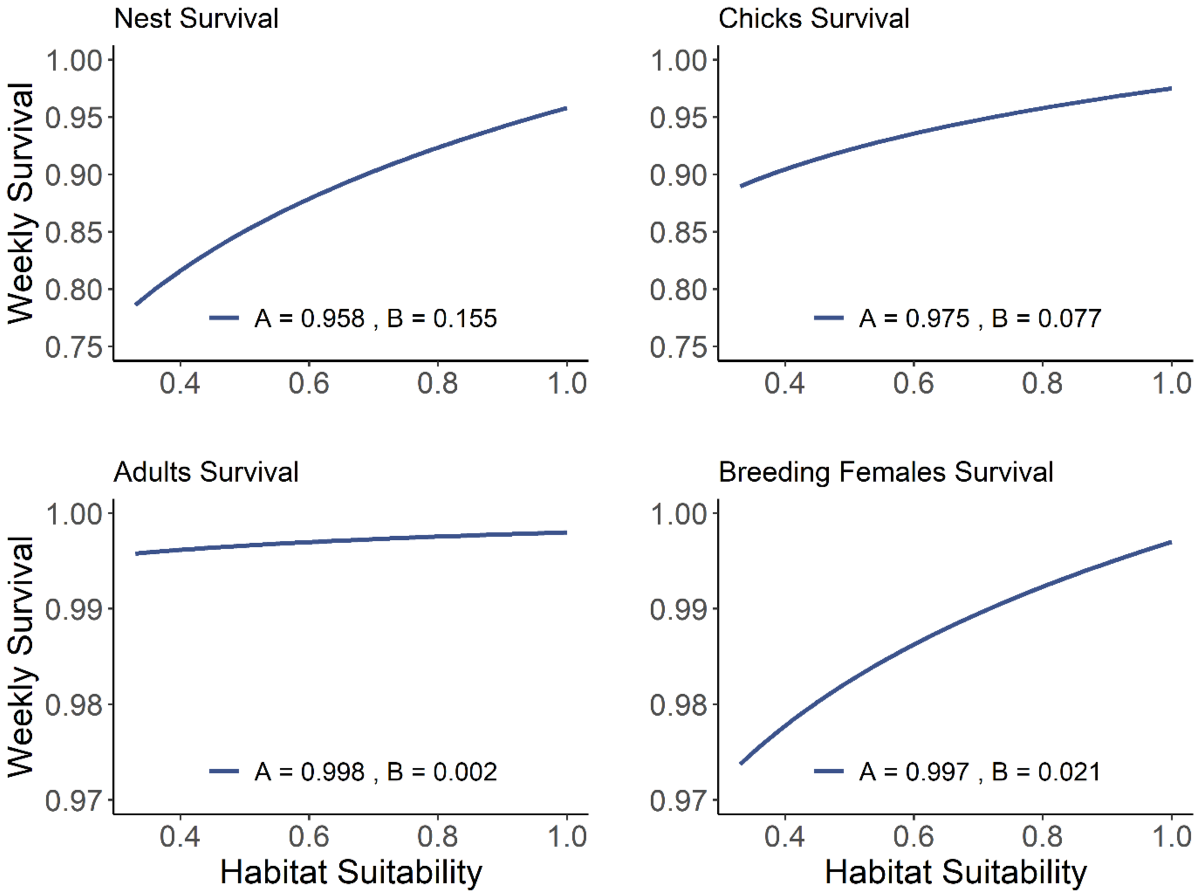


Figure G.6.1 Calibrated survival curves of the various life stages of the little bustard relative to habitat suitability, obtained from logarithmic regression. The A and B values of each curve represent the mean of the posterior distributions after the rejection-ABC calibration process.

7. Model analysis

This TRACE element provides supporting information on: (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

Summary:

A sensitivity analysis was conducted using the Morris screening method to examine the model's response to variations in both literature-derived and calibrated parameters. This analysis utilized three key model outputs: annual growth rate, final sex ratio, and time to extinction.

A Local Sensitivity Analysis was conducted using the Morris screening method, which employs randomized one-factor-at-a-time designs to evaluate the impact of parameter value changes on model outputs (Morris, 1991). This method does not require assumptions about the model, such as the signs of effects. The Morris method provides two measures for each input factor: μ (mean), which estimates the overall influence of the parameter on the model output, and σ (standard deviation), which estimates higher-order effects, including non-linear and interaction effects. A modified version of the Morris method that reduces Type-II error was employed (Campolongo et al., 2007). This version estimates μ* (mean*), representing absolute differences to prevent the cancellation of negative and positive effects at different parameter values.

The modified Morris screening was implemented using the *NLRX* package for R (Salecker et al., 2019), examining the model's response to variations in both literature-derived (5 parameters) and calibrated parameters (11 parameters), which were varied by 10% above and below their default values. The number of tested settings is determined by the formula r × (K + 1), where r represents the number of elementary effects or trajectories computed per parameter (K). With our selection of 100 trajectories, this resulted in 100 × (16 + 1) = 1,700 runs. Literature-derived parameters included brood size, the sex-ratio at the beginning of the simulation (year 2005), the probability of anthropogenic mortality, and the probability of re-nesting once and twice. The default values for these parameters are presented in Table G.2.3. All calibrated parameters were also considered, with their default values presented in Table G.6.2. Results are presented in Figures G.7.1, G.7.2 and G.7.3.

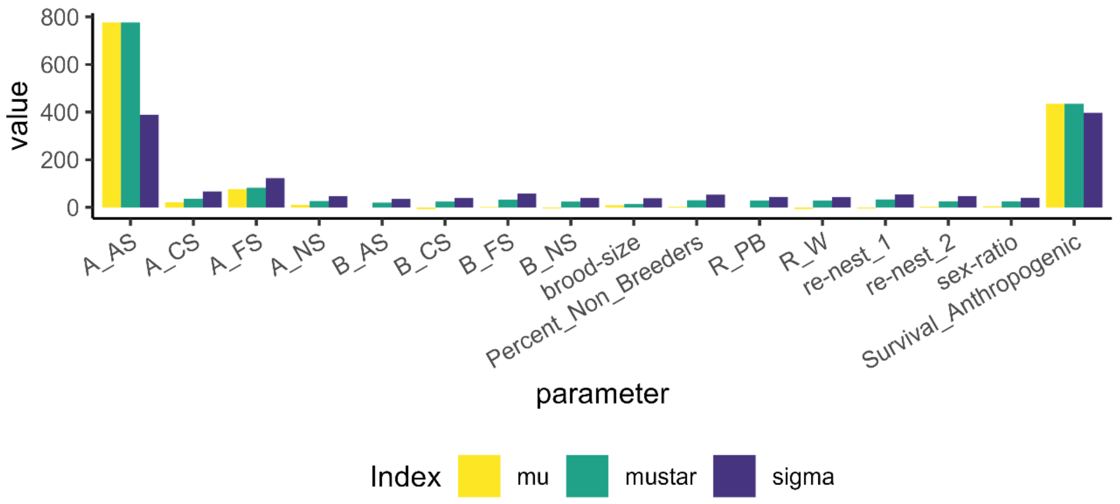


Figure G.7.1 Results of the sensitivity analysis for the annual growth rate.

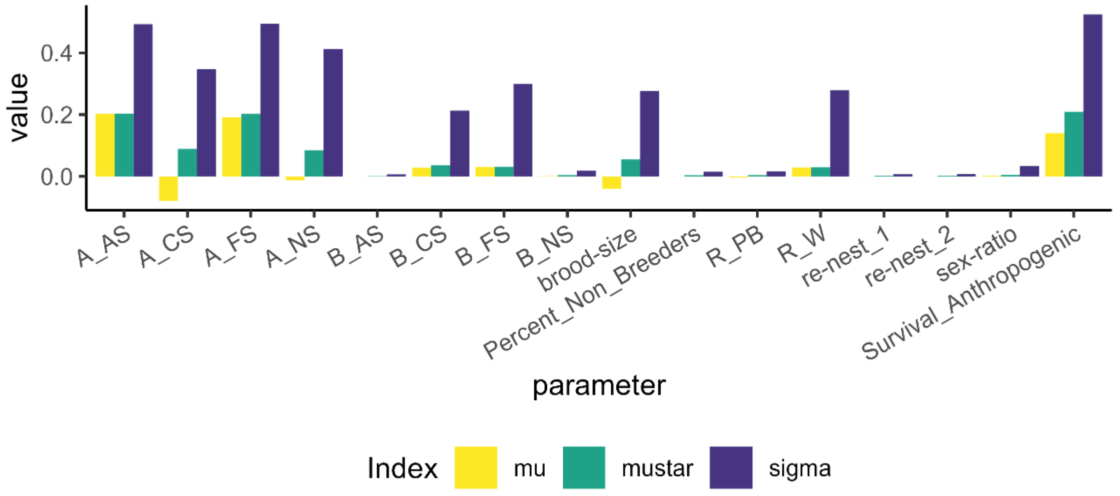


Figure G.7.2 Results of the sensitivity analysis for the sex ratio.

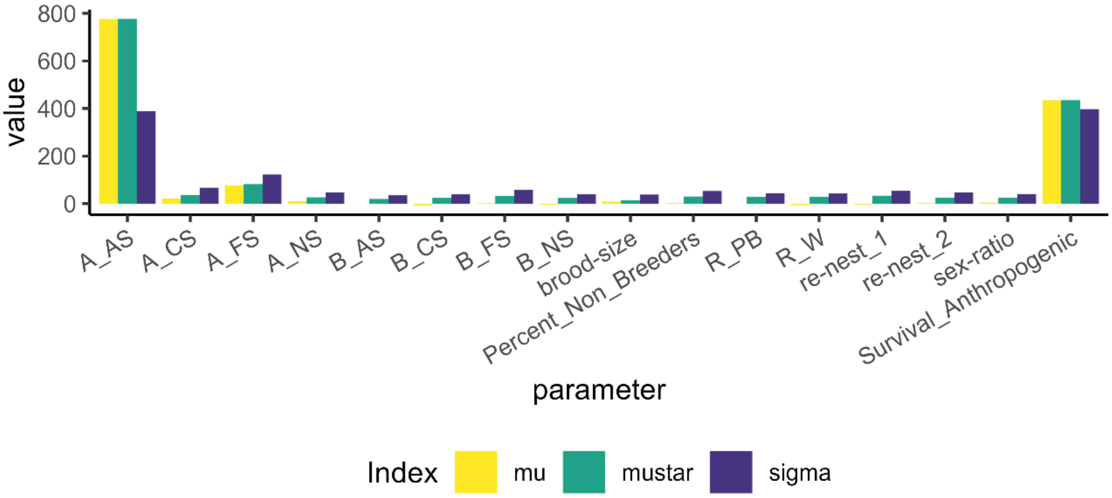


Figure G.7.3 Results of the sensitivity analysis for the time to extinction.

8. Model output corroboration

This TRACE element provides supporting information on: How model predictions compare to independent data and patterns that were not used, and preferably not even known, while the model was developed, parameterized, and verified. By documenting model output corroboration, model users learn about evidence which, in addition to model output verification, indicates that the model is structurally realistic so that its predictions can be trusted to some degree.

Summary:

Here we present how model predictions compare to independent data

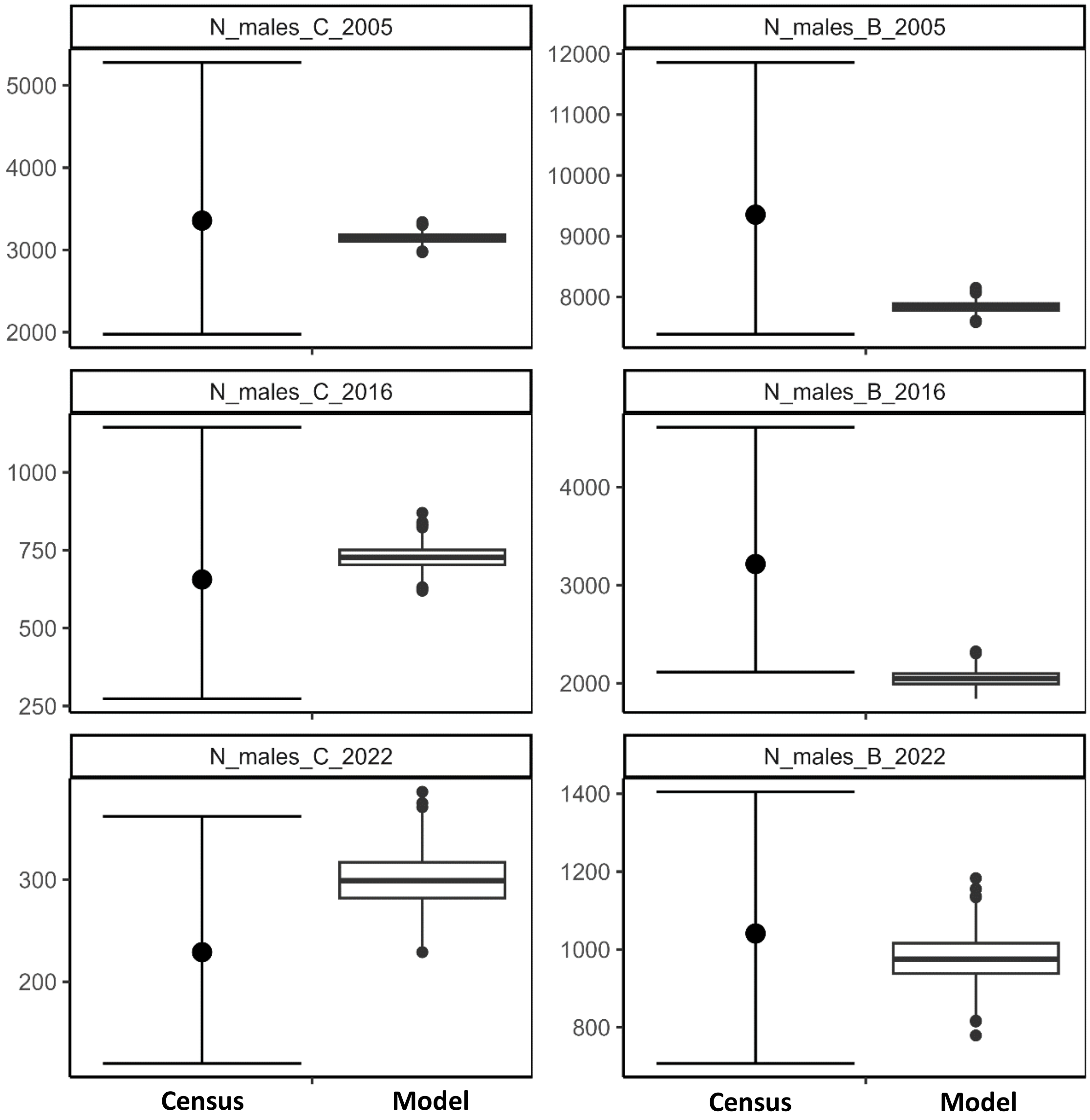


Figure G.8.1 Estimated number of males in Caceres and Badajoz in 2005, 2016, 2022, comparing the estimates from the census with those from the IBM.

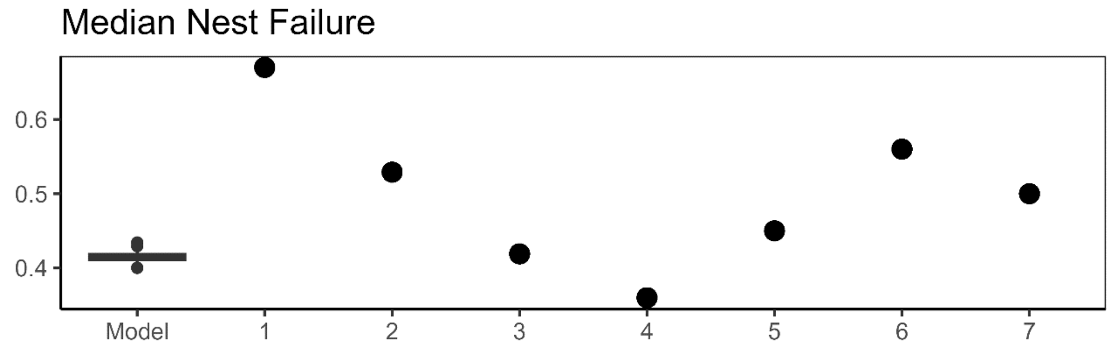


Figure G.8.2 Median nest failure, comparing the estimates from the IBM with those from bibliography. 1- Cuscó et al. (2021); 2- Lapiedra et al. (2011); 3- Bretagnolle et al. (2018); 4- Bretagnolle et al. (2011); 5- Wolff et al. (2002); 6- Boutin and Metais (1995); 7- Berthet et al. (2012).

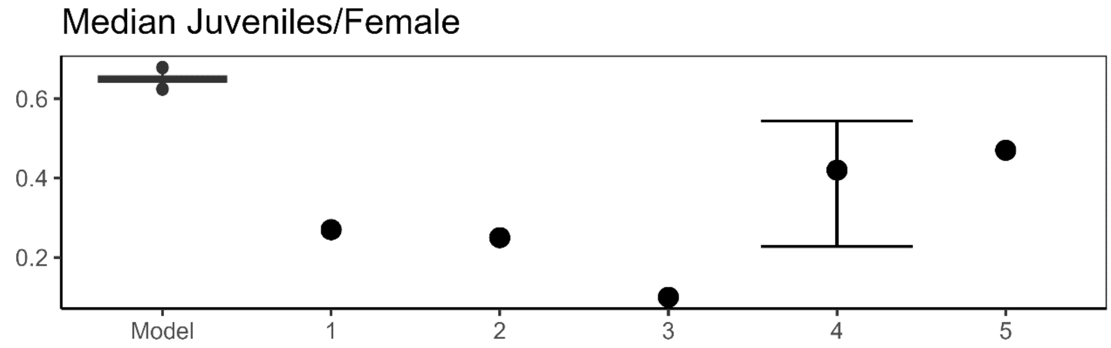


Figure G.8.3 Median Juveniles per female, comparing the estimates from the IBM with those from bibliography. 1- Lapiedra et al. (2011); 2- Cuscó et al. (2021); 3- Bretagnolle et al. (2011); 4- Inchausti and Bretagnolle (2005); 5- Silva et al. (2024).

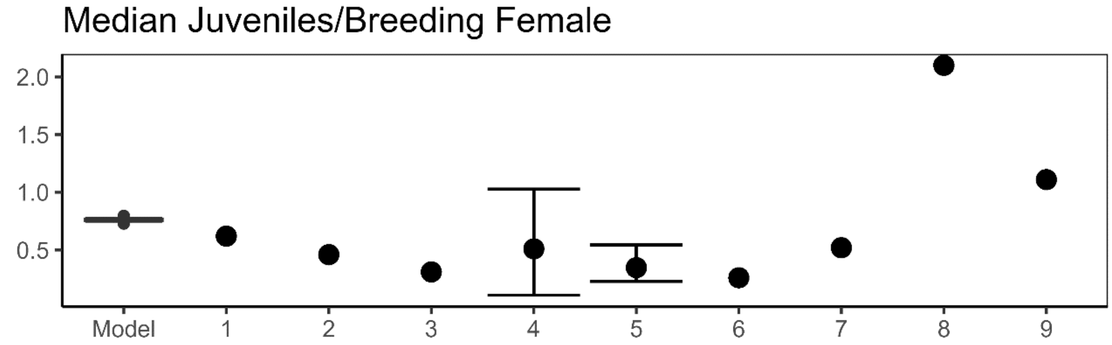


Figure G.8.4 Median Juveniles per breeding female, comparing the estimates from the IBM with those from bibliography. 1- Bretagnolle et al. (2018); 2 - Lapiedra et al. (2011); 3- Cuscó et al. (2021); 4- Morales et al. (2005); 5- Bretagnolle and Inchausti (2005); 6- Bretagnolle et al.; 1997-2003 (2011; 1997-2003); 7- Bretagnolle et al.; 2004-2008 (2011; 2004-2008); 9- (Tarjuelo et al., 2013).

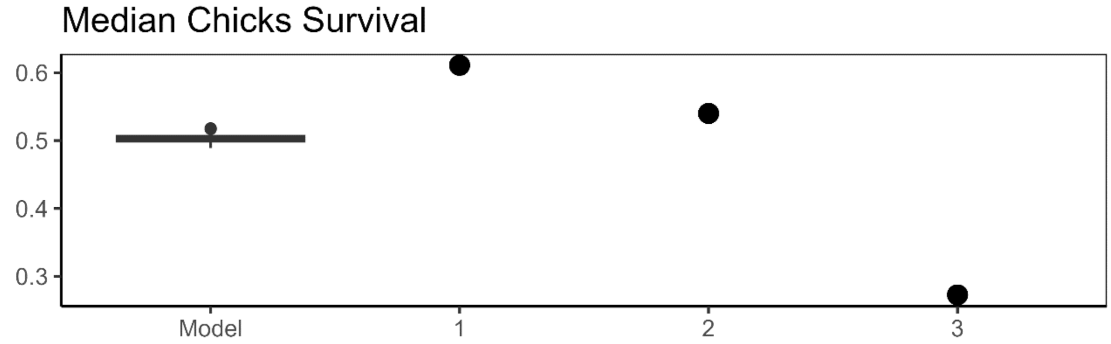


Figure G.8.5 Median chicks survival, comparing the estimates from the IBM with those from bibliography. 1- Bretagnolle et al. (2018); 2- Schulz (1987); 3- Bretagnolle et al. (2011).

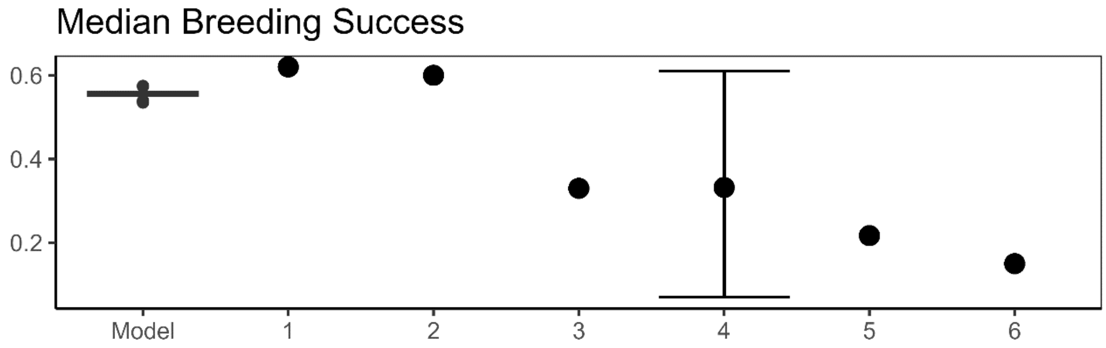


Figure G.8.6 Median breeding success, comparing the estimates from the IBM with those from bibliography. 1- Lapiedra et al. (2011); 2- Berthet et al. (2012); 3- Cuscó et al. (2021); 5- Morales et al. (2005); 6- Lapiedra et al. (2011); Cuscó et al. (2021).

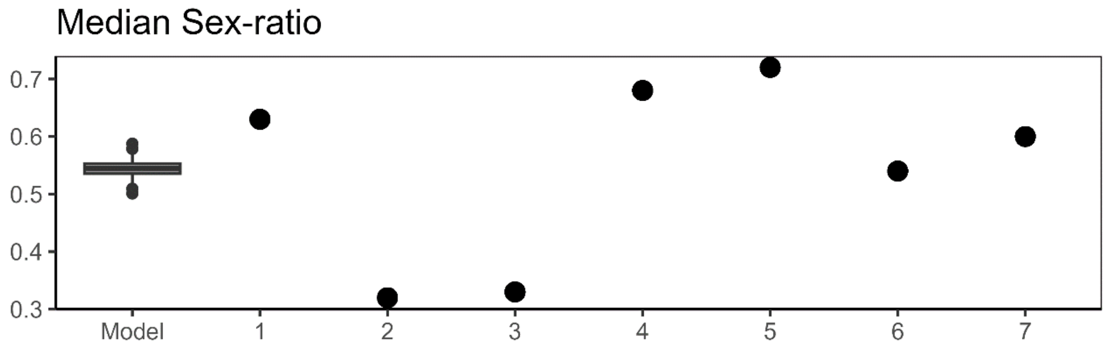


Figure G.8.7 Median sex ratio, comparing the estimates from the IBM with those from bibliography. 1- Faria and Morales (2018); 2- Boutin and Metais (1995); 3- Cheylan (1985); 4- Jiguet and Bretagnolle (2014); 5- Morales et al.; Valdetorres (2008b; Valdetorres); 6- Morales et al.; Campo Real (2008b; Campo Real); 7- Morales et al. (2008a).

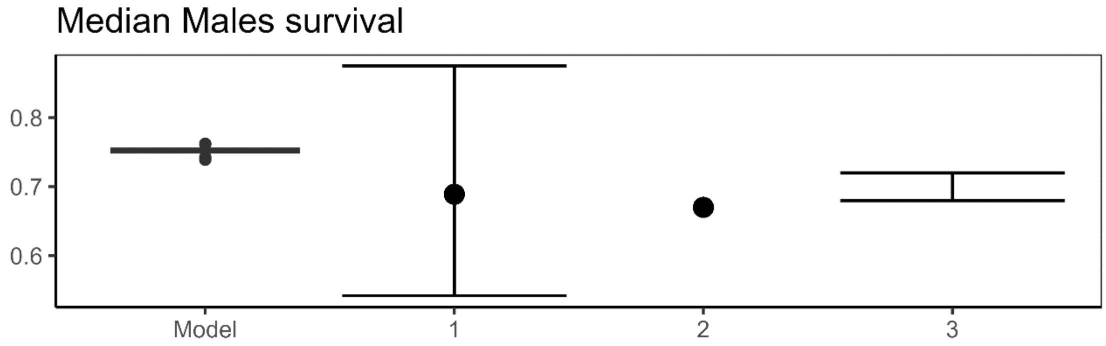


Figure G.8.8 Median males survival, comparing the estimates from the IBM with those from bibliography. 1- Silva et al. (2024); 2- Marcelino et al. (2017); Inchausti and Bretagnolle (2005).

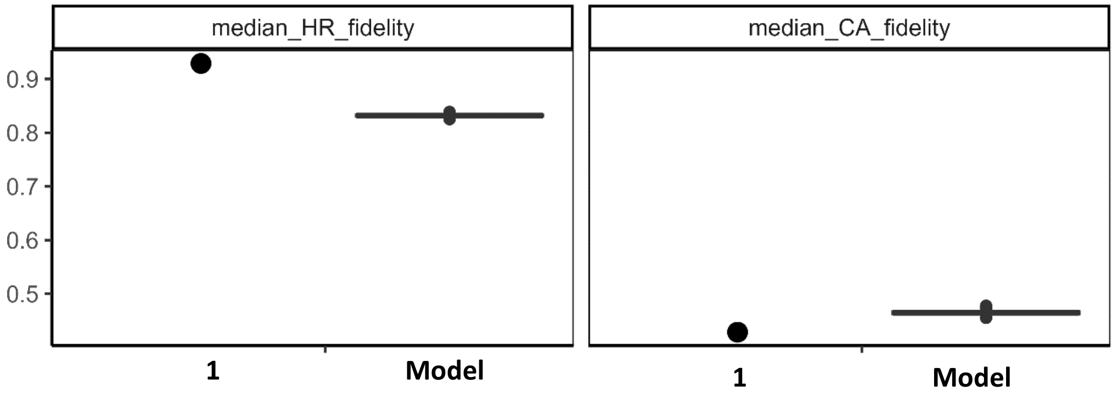


Figure G.8.9 Median home range fidelity and median core area fidelity, comparing the estimates from the IBM with those from bibliography. 1- Silva et al. (2024).

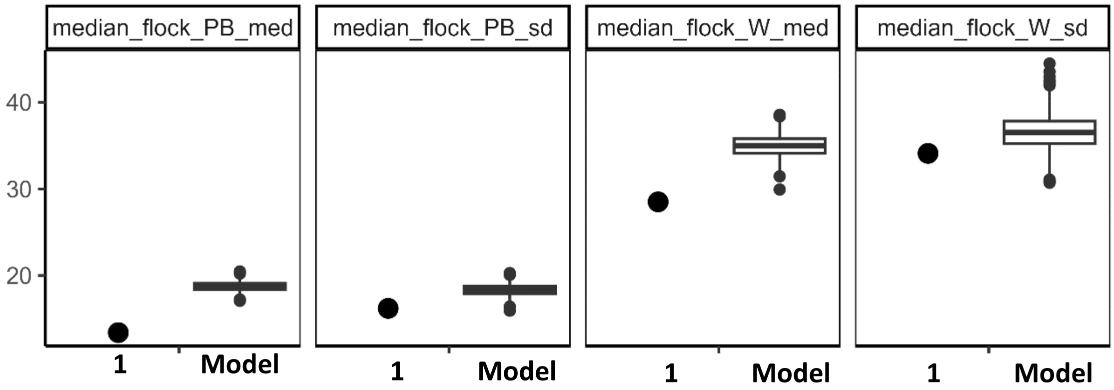


Figure G.8.10 Median and Standard Deviation (SD) of flock size in Post-Breeding and Winter, comparing the estimates from the IBM with those from bibliography. 1- Silva et al. (2024).

9. Supplementary results

Summary:

Here we present some supplementary results of the main experience.

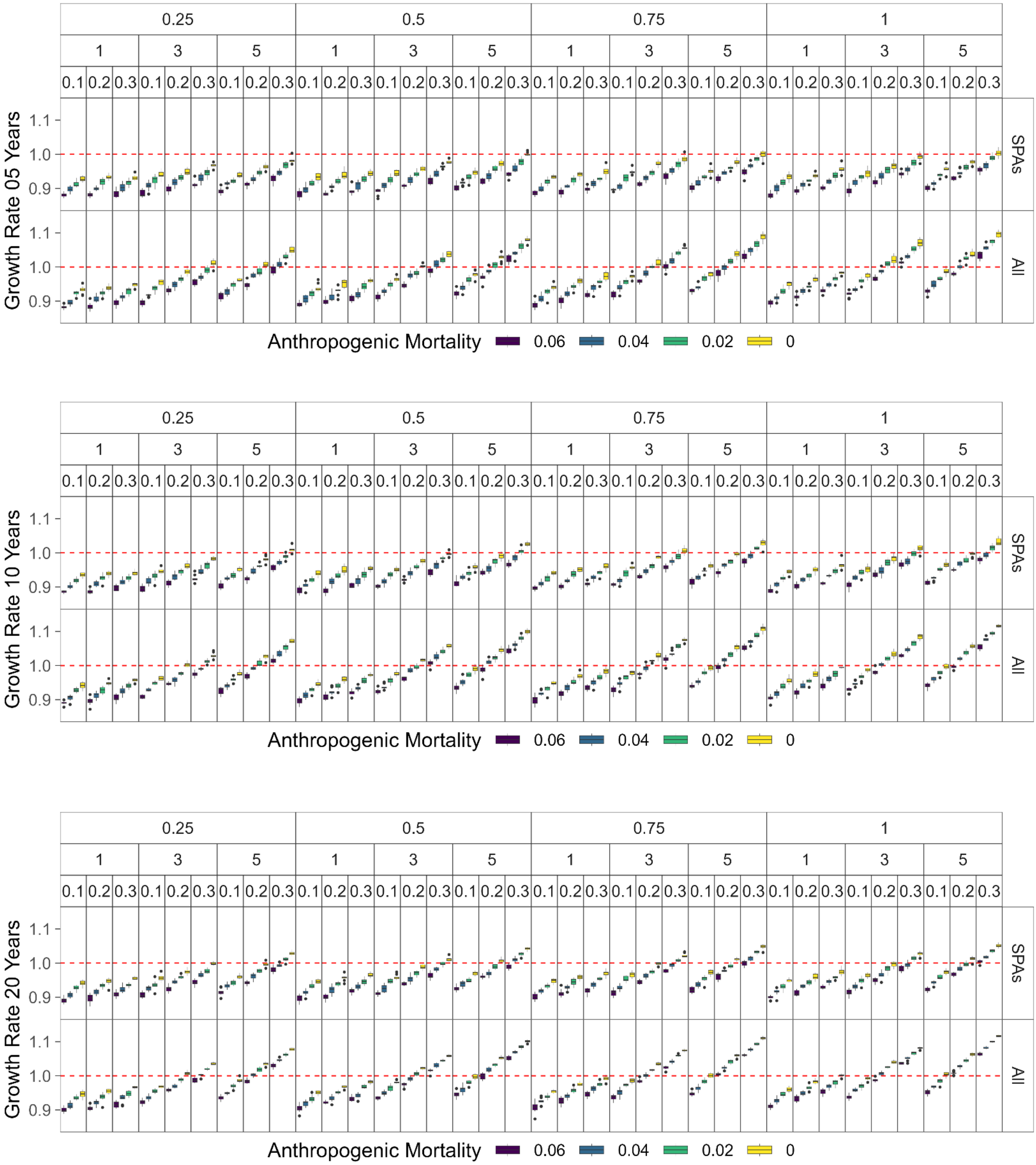


Figure G.9.1 Model estimates of growth rate for the different management strategies simulated over time. The red line indicates the point at which the population remains stable (Y=1).

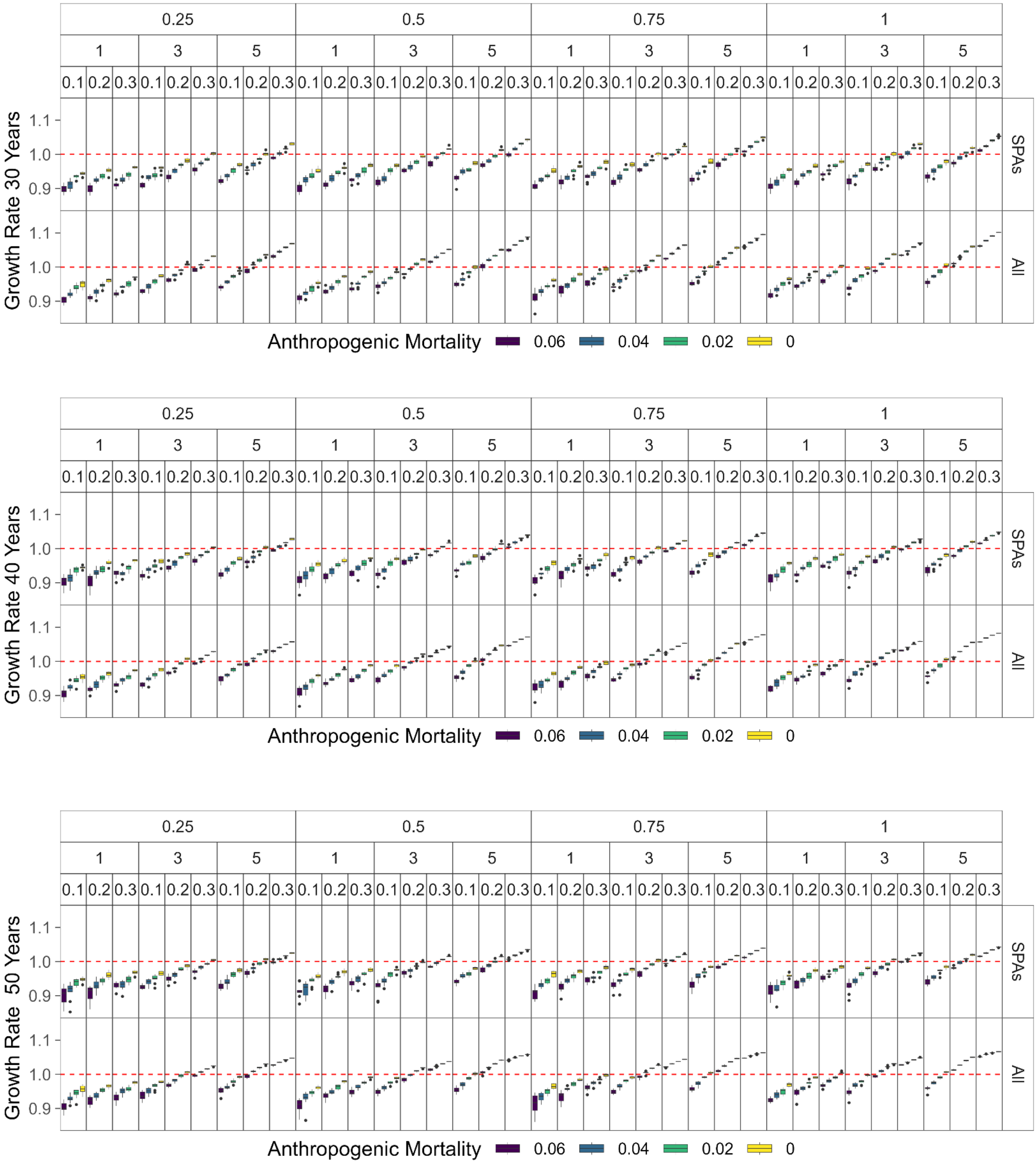


Figure G.9.1 (Continuation)

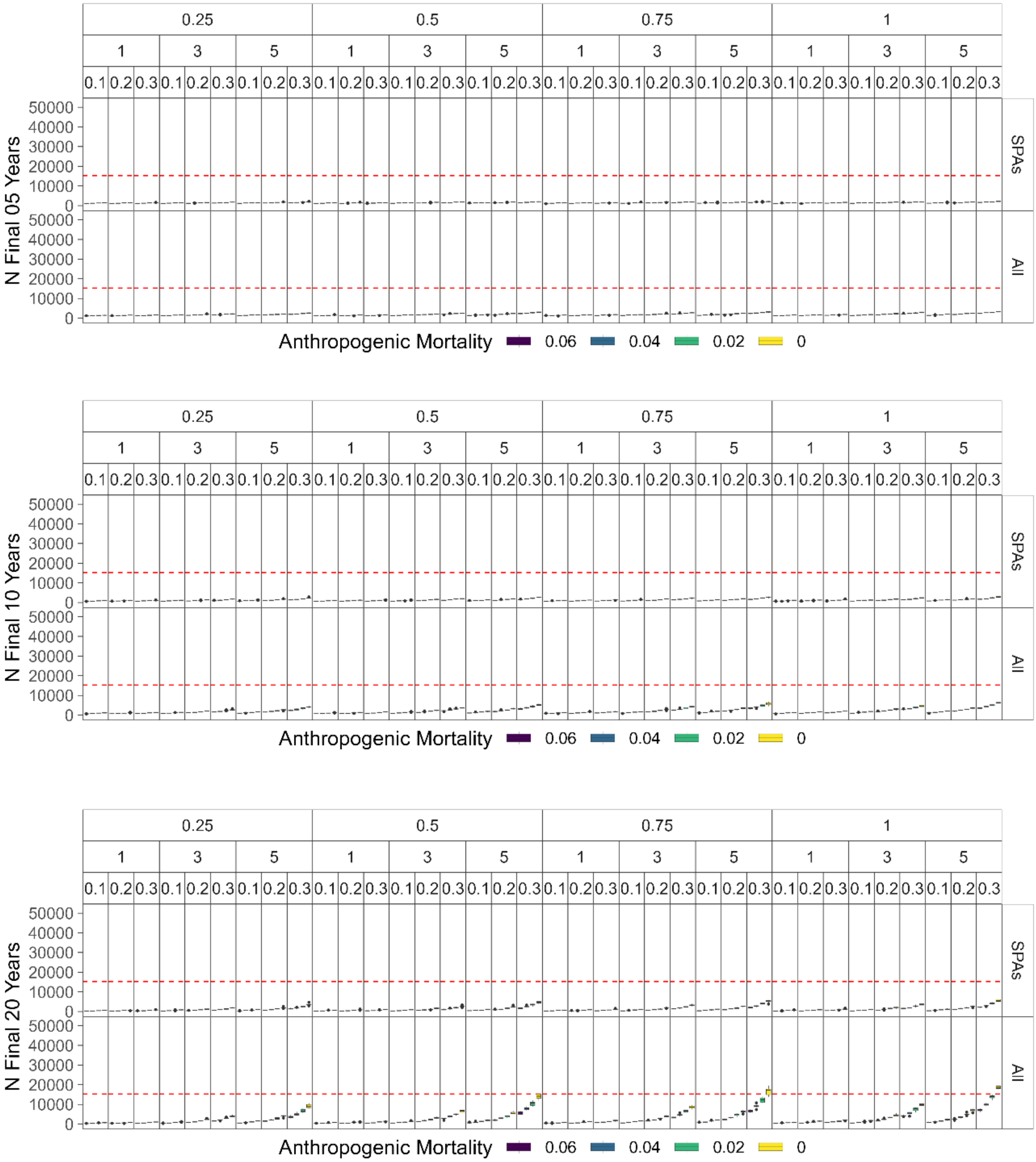


Figure G.9.2 Model estimates of population size for the different management strategies simulated over time. The red line indicates the estimated numbers for 2005.

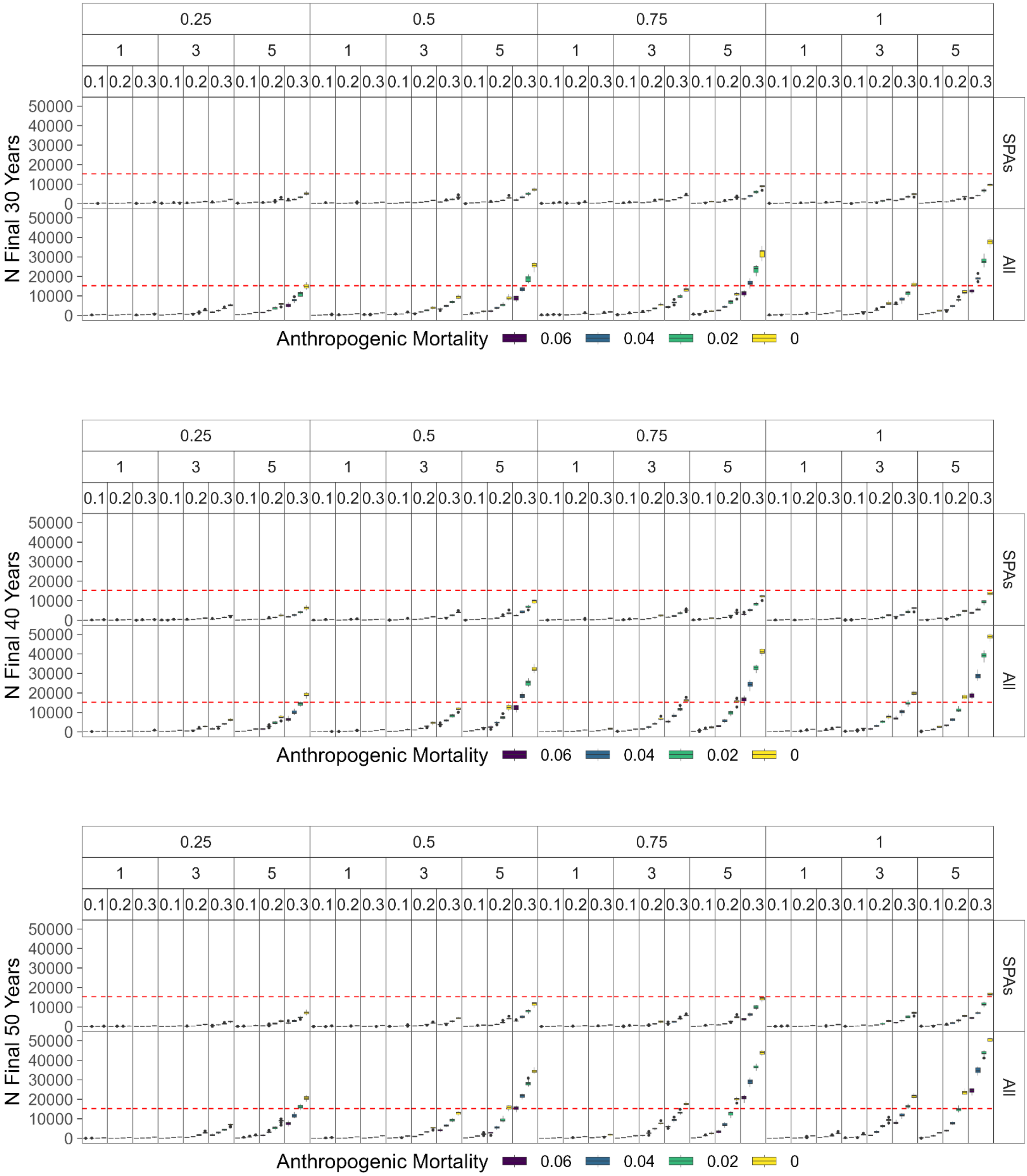


Figure G.9.2 (Continuation)

10. 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

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. Journal of Sustainable Agriculture 36, 319–336. https://doi.org/10.1080/10440046.2011.627988

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. Environmental Modelling & Software 22, 1509–1518. https://doi.org/10.1016/J.ENVSOFT.2006.10.004

Chen, C.C.M., Drovandi, C.C., Keith, J.M., Anthony, K., Caley, M.J., Mengersen, K.L., 2017. Bayesian semi-individual based model with approximate Bayesian computation for parameters calibration: Modelling Crown-of-Thorns populations on the Great Barrier Reef. Ecol Modell 364, 113–123. https://doi.org/10.1016/j.ecolmodel.2017.09.006

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

Csilléry, K., François, O., Blum, M.G.B., 2012. Abc: An R package for approximate Bayesian computation (ABC). Methods Ecol Evol 3, 475–479. https://doi.org/10.1111/j.2041-210X.2011.00179.x

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

Faria, N., Morales, M.B., 2018. Population productivity and late breeding habitat selection by the threatened Little Bustard: the importance of grassland management. Bird Conserv Int 28, 521–533. https://doi.org/10.1017/S0959270917000387

Faria, N., Rabaça, J.E., Morales, M.B., 2012. The importance of grazing regime in the provision of breeding habitat for grassland birds: The case of the endangered little bustard (*Tetrax tetrax*). J Nat Conserv 20, 211–218. https://doi.org/10.1016/j.jnc.2012.03.003

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

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, 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

Hartig, F., Calabrese, J.M., Reineking, B., Wiegand, T., Huth, A., 2011. Statistical inference for stochastic simulation models - theory and application. Ecol Lett. https://doi.org/10.1111/j.1461-0248.2011.01640.x

Hollenbeck, J.P., Saab, V.A., Frenzel, R.W., 2011. Habitat suitability and nest survival of white-headed woodpeckers in unburned forests of Oregon. Journal of Wildlife Management 75, 1061–1071. https://doi.org/10.1002/jwmg.146

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*. Behavioural Processes 51, 63–82. 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. Behavioural Processes 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

Marcelino, J., Moreira, F., Mañosa, S., Cuscó, F., Morales, M.B., García de la Morena, E., Bota, G., Palmeirim, J.M., Silva, J.P., 2017. 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

Monnet, A.C., Hardouin, L.A., Robert, A., Hingrat, Y., Jiguet, F., 2015. Evidence of a link between demographic rates and species habitat suitability from post release movements in a reinforced bird population. Oikos 124, 1089–1097. https://doi.org/10.1111/oik.01834

Moore, H.A., Dunlop, J.A., Nimmo, D.G., 2023. Habitat suitability correlates with mean population fitness of a threatened marsupial predator. Wildlife Research. https://doi.org/10.1071/WR23023

Morales, M.B., Bretagnolle, V., Arroyo, B., 2005. 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., García de la Morena, E., Delgado, M.P., Traba, J., 2008a. Tendencia reciente y viabilidad futura de las poblaciones de sisón común (*Tetrax tetrax*) en la Comunidad de Madrid. Anuario Ornitológico de Madrid 2006 11, 40–55.

Morales, M.B., Mañosa, S., Villers, A., Morena, E.L.G. de la, 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., Traba, J., Carriles, E., Delgado, M.P., de la Morena, E.L.G., 2008b. Sexual differences in microhabitat selection of breeding little bustards *Tetrax tetrax*: Ecological segregation based on vegetation structure. Acta Oecologica 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

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/.

Salecker, J., Sciaini, M., Meyer, K.M., Wiegand, K., 2019. The NLRX r package: A next-generation framework for reproducible NetLogo model analyses. Methods Ecol Evol 10, 1854–1863. https://doi.org/10.1111/2041-210X.13286

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., Catry, I., Palmeirim, J.M., Moreira, F., 2015. Freezing heat: Thermally imposed constraints on the daily activity patterns of a free-ranging grassland bird. Ecosphere 6. https://doi.org/10.1890/ES14-00454.1

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., 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.

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

van der Vaart, E., Beaumont, M.A., Johnston, A.S.A., Sibly, 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

Wilensky, U., 1999. NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling. Northwestern University, Evanston, Illinois, U.S.

Wolff, A., Dieuleveut, T., Martin, J.L., Bretagnolle, V., 2002. Landscape context and little bustard abundance in a fragmented steppe: Implications for reserve management in mosaic landscapes. Biol Conserv 107, 211–220. https://doi.org/10.1016/S0006-3207(02)00087-3