Animal Conservation

ZSL LET'S WORK FOR WILDLIFE

Animal Conservation. Print ISSN 1367-9430

What to expect from alternative management strategies to conserve seabirds? Hints from a dynamic modelling framework applied to an endangered population

A. De la Cruz[1], R. Bastos[2], E. Silva[3], J. A. Cabral[2] & M. Santos[2,4]

1 Marine Research University Institute (INMAR), Campus of International Excellence of the Sea (CEIMAR), University of Cádiz, Cádiz, Spain
2 Laboratory of Applied Ecology, CITAB – Centre for the Research and Technology of Agro-Environment and Biological Services, Institute for Innovation, Capacity Building and Sustainability of Agri-food Production (Inov4Agro), University of Trás-os-Montes e Alto Douro, Vila Real, Portugal
3 Portuguese Society for the Study of Birds (SPEA), Lisboa, Portugal
4 Laboratory of Ecology and Conservation, Federal Institute of Education, Science and Technology of Maranhão, R. Dep. Gastão Vieira, Buriticupu, MA, Brazil

Keywords
population dynamics; ecological indicators; umbrella species; environmental management; marine protected areas; *Gulosus aristotelis*; seabirds; dynamic modelling frameworks.

Correspondence
Andrés De la Cruz, Marine Research University Institute (INMAR), Campus of International Excellence of the Sea (CEIMAR), University of Cádiz, Puerto Real, 11510 Cádiz, Spain.
Email: andres.delacruz@uca.es

Editor: Rahel Sollmann
Associate Editor: Sven Kerwath

Received 13 October 2020; accepted 23 September 2021

doi:10.1111/acv.12751

Abstract

The worldwide decline of seabird populations due to the combined effects of global and regional changes is creating immense challenges for managers and conservationists. Predicting population responses to proposed management strategies could provide the most effective tools to prevent, halt and reverse ongoing declines. System dynamic modelling frameworks are considered particularly relevant to interrelate biological, ecological and environmental characteristics and to predict population trends. A system dynamics model was designed, compiling diverse information concerning a relict population of the European Shag located in western Iberia, to outline the most effective management options for its conservation. The simulations demonstrate that mortality caused by invasive animals and bycatch mortality were the main reasons for the current population decline. Without management interventions, a decrease of 8% was projected for the next decade, which could be mitigated by specific conservation actions. The results show the usefulness of dynamic modelling frameworks to understand local cause-effect relationships and species responses to ecosystem management under changing environmental conditions. We highlight that the framework proposed, after specific parameterization, could be easily adaptable to other species within similar socio-ecological systems.

Introduction

Seabirds face complex and multiscale conservation challenges, such as breeding habitat loss, rapid decline of their prey populations, overfishing and water pollution (Croxall *et al*., 2012; Dias *et al*., 2019). Furthermore, low reproduction rates and late sexual maturity contribute to the imperilled conservation status of many species, threatening the keystone roles played by these predators in marine ecosystems (Hall, Alverson & Metuzals, 2000; Tam *et al*., 2017). Moreover, seabirds are highly mobile, cover large areas and depend on diverse resources triggered by ecosystem dynamics (Lambert *et al*., 2017). Therefore, species have been relatively well-monitored and used for evaluating the ecological status of marine environments, namely for detecting changes in fish stocks and the impacts of oceanographic events (Furness & Camphuysen, 1997; Paleczny *et al*., 2015; Provencher *et al*., 2019).

The conservation and management of threatened species is dependent on realistic demographic parameters, essential to foresee changes in populations when management actions are applied (Lambert *et al*., 2018). Besides, understanding the effects of anthropogenic pressures requires knowledge of life history and how parameters change with environmental stochasticity (Lande, Engen & Saether, 2003). To address this challenge and predict population trajectories under different management scenarios, different techniques have been used, such as the biologically-inspired Population Dynamic P-system models (Colomer, Margalida & Pérez-Jiménez, 2013) together with the surface response model Box-Behnken design (Margalida *et al*., 2015) and Population Viability Analysis (PVA) (Genovart *et al*., 2016; Genovart *et al.*, 2017*a*). Among the mentioned methods, PVA has been extensively used, particularly to predict the extinction risk of threatened species (Hamilton & Moller, 1995; Morris & Doak, 2002; Oro *et al.*, 2004; Genovart *et al.*, 2017*a*), namely by projecting population estimates into the future to help managers in decision-making (Sutherland, 2006; Naveda-Rodríguez *et al.*, 2016; Tucker *et al.*, 2020). However, PVAs face challenges when it comes to calibrating parameters, particularly when estimating their sensitivity to changing socio-ecological conditions (Genovart *et al.*, 2016). This is especially relevant whenever using generic PVA software and when detailed information on the spatial distribution of species or habitat requirements is not available (Chaudhary & Oli, 2020). In this instance, some authors recommend developing tailor-made applications for the particular purpose and data available (Bennett *et al.*, 2019; Lucas, 2020). Dynamic modelling frameworks underpinned by bio-ecological information are especially promising (Anderson *et al.*, 2018; Miller *et al.*, 2019). In fact, dynamic modelling is currently considered a fundamental tool in ecology to predict the future consequences of alternative management scenarios and, therefore, could be used as a complementary method to PVAs (Warwick-Evans *et al.*, 2016; Weller *et al.*, 2016; Crookes & Blignaut, 2019; Drechsler, 2020). Several types of dynamic models have been used to evaluate and predict the outcome of contrasting scenarios in the scope of conservation ecology (Banos-González *et al.*, 2016; Morinha *et al.*, 2017; Li *et al.*, 2020), ranging from the classical Lotka-Volterra model in the 1920s and population dynamics in the 1950s, to the current highly complex and integrative socio-ecological and environmental ones (Jørgensen & Fath, 2011; Buchadas *et al.*, 2017; Moon *et al.*, 2019; Steger *et al.*, 2021).

In this context, mechanistic modelling approaches, such as System Dynamics (SD), have proven to be particularly useful, by their straightforward design, enhanced software, end-user acceptance, but mainly by optimizing management strategies and measures assisting local decision-making (Santos, Bastos & Cabral, 2013; Gillson *et al.*, 2019). Moreover, SD allows mimicking the structure and functioning of local systems, incorporating nonlinearity of complex systems using feedback loops, stocks and flows to represent key entities and process-based dynamics (Trappey *et al.*, 2012; Bastos *et al.*, 2016; Buchadas *et al.*, 2017; Petrescu Bakış *et al.*, 2021). When SD models are properly designed, parameterized and calibrated, the resulting outcomes can effectively simulate conditions and processes that might be difficult to understand otherwise (Jørgensen & Fath, 2011; Santos *et al.*, 2018). Furthermore, SD models allow expert opinion to be easily integrated, to project long-term population patterns in response to ecological constrains and environmental scenarios (Bastos *et al.*, 2012; Arosa *et al.*, 2017; Weller *et al.*, 2016).

The Iberian-Atlantic populations of Shag (*Gulosus aristotelis* subsp. *aristotelis*) have approximately 1400 breeding pairs, mainly inhabiting rocky islands and islets of Galicia (Cíes Islands, NW, Spain), Asturias and west Portugal (del Moral & Oliveira, 2019). Significant declines were detected for this population (del Moral & Oliveira, 2019), namely in Galicia (the most important Iberian population) with a reduction of 500 pairs in the last two decades (26% overall reduction) (Munilla & Barros, 2019). Unlike Galicia, on the Portuguese west coast there are few rocky shores, islets or islands with good conditions for Shag nesting (Ramírez *et al.*, 2008; Meirinho *et al.*, 2014). In fact, most of the Portuguese relict population of approximately 100 breeding pairs inhabits the Berlengas islands and their surrounding waters (del Moral & Oliveira, 2019; Oliveira, 2019). This population also declined in the last decades. Despite the increase in protection associated with the establishment of the Berlengas' Special Protection Area (BSPA) in 1988 (Rodrigues *et al.*, 2011; Oliveira *et al.*, 2016; Oro, Álvarez & Velando, 2018): for the period 2002–2019, an average reduction of 22% in the breeding population was noticed (Alonso *et al.*, 2019).

Anthropogenic and environmental factors seem to be correlated with this population trend, such as invasion by exotic species, bycatch in different fishing gear, oil spill catastrophes, tourism disturbance and climate and oceanographic change (Velando, Ortega-Ruano & Freire, 1999). Hence, Shag might be considered, apart from a species conservation perspective, an indicator of the ecological status of coastal rocky environments whose futures are interconnected (Ramírez *et al.*, 2008).

Considering the multiple coexisting threats, deciding the best options for conservation may require discussing the feasibility of their implementation. Decision analysis tools, such as SD modelling frameworks, can help rank specific management actions from the forecasted results (Santos *et al.*, 2013; Arosa *et al.*, 2017). Therefore, the main objective of this study was to develop a SD model to predict possible trends for the Berlengas' Shag population, considering current biological and ecological constrains, environmental conditions and their interplay with management actions. Our specific objectives were: (1) to integrate scattered information from different studies in a SD framework, aimed at recreating realistic population dynamics; (2) to predict the outcome of competing BSPA management scenarios and to determine the most effective ones; (3) to discuss the use of Shag population dynamics as a surrogate of the conservation status of the BSPA.

Materials and methods

Study area

The Berlengas Natura 2000 Special Protected Area (BSPA) (PTZPE0009, EU Birds Directive) (39° 27' 5.7" N; 9° 31' 2.2" W) comprises 102 662 ha of protected waters surrounding the Berlengas archipelago, located approximately 10 km from the Portuguese west coast (Fig. 1). The area is influenced by two geomorphological structures, the Carvoeiro Cape and the Nazaré Canyon, which intensify coastal upwelling and concomitant primary production (Fiúza, 1983). The archipelago (composed by three groups of islands: Berlenga Grande, Estelas and Farilhões) is also an important insular ecosystem due to the occurrence of several endemic species of plants and reptiles, but also seabirds, marine invertebrates, fish and marine mammals (Mendes *et al.*, 2018). In particular for seabirds, BSPA holds important breeding populations of Cory's shearwater *Calonectris borealis*, Band-rumped

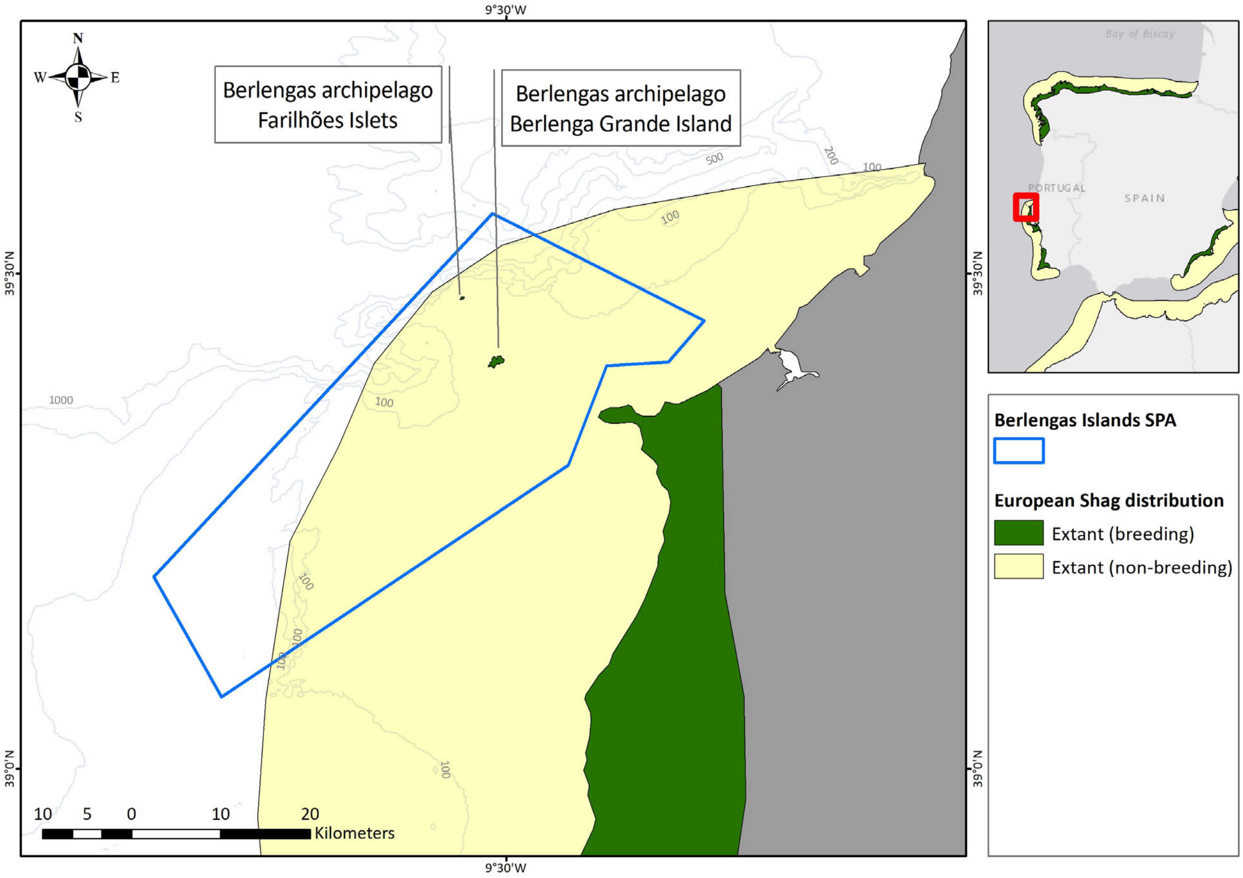

Figure 1 Map of the Berlengas Islands Special Protected Area, Portugal, and the distribution of the European Shag (BirdLife International, 2018).

storm-petrel *Oceanodroma castro*, Yellow-legged gull *Larus michahellis*, Lesser Black-backed gull *Larus fuscus* and European Shag *Gulosus aristotelis* (Lecoq, 2003). The area is also important to migratory species such as the Northern Gannet *Morus bassanus* and the critically endangered Balearic shearwater *Puffinus mauretanicus* (Meirinho *et al.*, 2014).

Conceptualization and parameterization of the model

The model integrates relevant information concerning Shag biology and ecology but also environmental and anthropogenic drivers (Fig. 2) (Snow, 1960; Velando & Freire, 2002). Whenever possible, specific BSPA data were used to parametrize the model but in the absence of that, we used reference information, namely from the closest Shag colony located in the Cíes Islands (Neto, 1997; Velando *et al.*, 1999; Velando & Munilla, 2008; Silva, 2015) (Table 1). Taking into account the isolated location of the Berlengas population in relation to other noteworthy colonies (Velando & Freire, 1999; Meirinho *et al.*, 2014), small-scale migration rates and philopatry behaviour displayed by the species (Potts, 1969; Barlow *et al.*, 2013), we did not consider immigration and emigration as relevant factors influencing short-term population dynamics (Aebischer, 1986; Barlow *et al.*, 2011). Even though occasional long-distance movements of juveniles from their natal colony and prior to recruitment have been detected for the closest population located in the Cíes islands, the dispersal movements are a way below the 300 km separating both islands, besides the fact that the patterns are still mostly unknown (Galbraith, Russell & Furness, 1981; Martínez-Abraín, Oro & Jiménez, 2001; Barros, Álvarez & Velando, 2013; Orta *et al.*, 2020).

Day was selected as the appropriate time unit for simulating stochastic events (e.g. anthropogenic disturbance) and environmental, biological and ecological processes affecting individuals' survival (Gonzalez *et al.*, 2015). Considering the multitude and variability of processes (biological, ecological and environmental) involved, one hundred independent simulations were ran by scenario, for a period of 10 years, to gauge possible effects of management actions in the population trends (White, 2019). The initial number of adults for all simulations (adult population at t0, 1st day of January) was set as 164 (82 males and 82 females), according to the estimates from the censuses compiled in the last decade

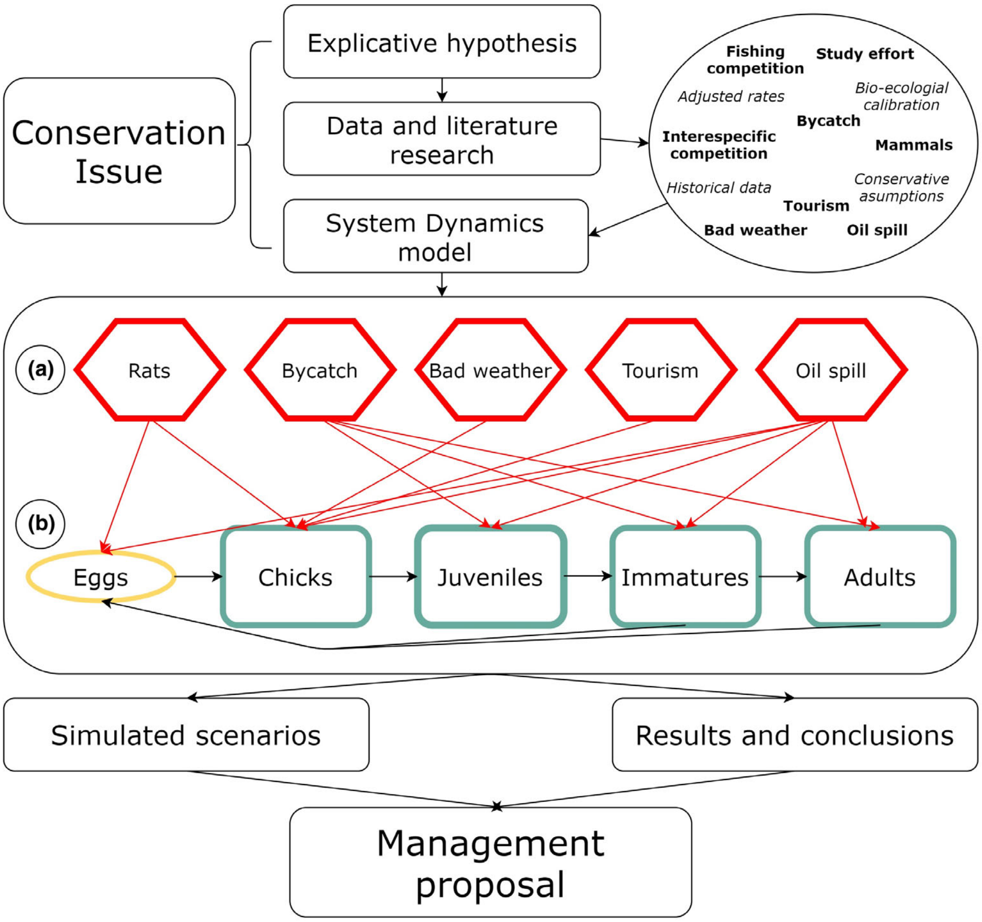

Figure 2 System dynamics model conceptual diagram to predict Shag population trends in the Berlengas archipelago, Portugal. (a) Main key factors affecting the Shag population in Berlengas archipelago; (b) Shag population dynamics and age classes considered. Bold words in the upper-right circle are factors explicitly included in the model. Non-bold words in the upper-right circle are core ideas, not explicitly included in the model. The explanation of the connections, different age classes and key factors can be found in Supporting Information Appendix S1–S3.

(Pereira & Oliveira, 2019) (Supporting Information Appendix S3, 1.1 Adults). Additionally, 19 immatures (immature-plumage first-year inexperience breeders) (Aebischer, 1985; Harris & Wanless, 1996) and 64 juveniles were estimated also for t0, based on average productivity and mortality rates (taking into account the previous adult population) (Velando & Freire, 2002; Velando & Munilla, 2011; Silva, 2015) (Supporting Information Appendix S3, 1.2 Immatures and 1.3 Juveniles). Apart from the previous information, a proportion of immature individuals was simulated to breed (47% of juvenile females) in their second year of life, accordingly with Velando & Freire (2002).

Shag population dynamics and demographic parameters

Population dynamics emerge from the balance between new individuals being born and natural and anthropogenic mortality influencing the different age classes asymmetrically. In this way, the SD model is structured on five age classes (each one associated with a state variable): *egg*, flightless *chick*, complete flying *juvenile*, *immature* (immature-plumage second year birds), and *adult* (birds aged 3 or more years old) (Fig. 2) (Supporting Information Appendix S1, Population dynamics sub-models).

A summary of the most important parameters is shown in Table 1. For all parameters included in the model, a range of values was applied, using the variability displayed by minimum and maximum and/or average rates with standard deviations, taken from reference bibliography (details concerning the parameterization of the model are depicted in Supporting Information Appendix S4).

Key factors influencing BSPA population dynamics were divided into ‘Ecological’, i.e. unmanageable natural abiotic and biotic factors, and ‘Anthropogenic’, for which specific management actions were defined. We assumed anthropogenic mortality as an additive factor to base/natural mortality (Table 1).

Table 1 Specification of the main variables included in the system dynamic model to predict Shag population trends in the Berlengas archipelago, Portugal, respective description, units and references

European Shag population dynamics in Berlengas

Variable	Description	Unit	Source
Adults			
Initial breeding adult pairs	Max. number of breeding adult pairs male in the last decade 82	Individuals	Pereira & Oliveira (2019)
Productivity	Proportion of flying juveniles per nest 1.32	Rate	Silva, Luís & Oliveira (2017)
Adult natural mortality rate	Proportion of dead adults per year Min 0.18 Max 0.32	Rate	Velando & Freire (2002)
Non-juvenile bycatch mortality rate	Proportion of dead adults from bycatch per year 0.03	Rate	Velando & Freire (2002)
Non-juvenile male mortality rate after spill oil catastrophe	Proportion of adult male mortality rate after spill oil catastrophe 0.0025	Rate	Velando *et al*. (2005) and Martínez-Abraín *et al*. (2006)
Non-juvenile female mortality rate after spill oil catastrophe	Proportion of adult female mortality rate after spill oil catastrophe 0.014	Rate	Velando *et al*. (2005) and Martínez-Abraín *et al*. (2006)
Immatures			
Initial immature population	Assumed number calculated of immature individuals 9.57	Individuals	Velando & Freire (2002) and Silva *et al*. (2017)
Immatures recruitment rate	Proportion of breeding in their 2 year 0.47	Rate	Velando & Freire (2002)
Immature mortality	Proportion of dead immature per year 0.30	Rate	Velando & Munilla (2008)
Productivity	Proportion of flying juveniles per nest Min 0.36 Max 0.77	Rate	Velando & Freire (2002) and Velando & Munilla (2008)
Non-juvenile bycatch mortality rate	Proportion of died immatures from bycatch per year 0.03	Rate	Velando & Freire (2002)
Non-juvenile male mortality rate after spill oil catastrophe	Proportion of immatures male mortality rate after spill oil catastrophe 0.0025	Rate	Velando *et al*. (2005) and Martínez-Abraín *et al*. (2006)
Non-juvenile female mortality rate after spill oil catastrophe	Proportion of immatures female mortality rate after spill oil catastrophe 0.014	Rate	Velando *et al*. (2005) and Martínez-Abraín *et al*. (2006)
Juveniles			
Initial juvenile population	Assumed number calculated of juvenile individuals 31.93	Individuals	Velando & Munilla (2011) and Silva *et al*. (2017)
Juvenile mortality	Proportion of dead juveniles per year 0.59	Rate	Velando & Munilla (2011)
Juvenile bycatch mortality rate	Proportion of dead juvenile from bycatch per year 0.10	Rate	Genovart *et al*. (2017*b*)
Juvenile male mortality rate after spill oil catastrophe	Proportion of juvenile male mortality rate after spill oil catastrophe 0.005	Rate	Velando *et al*. (2005) and Martínez-Abraín *et al*. (2006)
Juvenile female mortality rate after spill oil catastrophe	Proportion of juvenile female mortality rate after spill oil catastrophe 0.028	Rate	Velando *et al*. (2005) and Martínez-Abraín *et al*. (2006)

Table 1 Continued.

European Shag population dynamics in Berlengas

Variable	Description	Unit	Source
Chicks			
Chicks natural mortality rate (from adults)	Proportion of dead chicks per year 0.20	Rate	Velando *et al*. (1999)
Chicks natural mortality rate (from immatures)	Calculated proportion of dead chicks per year 0.25	Rate	Velando & Freire (2002) and Velando & Munilla (2008)
Bad weather chicks mortality rate	Calculated proportion of dead chicks due to bad weather per year 0.034	Rate	Velando *et al*. (1999)
Chicks mortality rate by rats	Proportion of dead chicks by rats per year 0.39	Rate	Silva (2015)
Chicks mortality rate by tourism disturbance	Proportion of dead chicks due to tourism disturbance per year 0.034	Rate	Velando *et al*. (1999)
Chick mortality rate after spill oil catastrophe	Assumed to be the same as adult female mortality rate after spill oil catastrophe 0.014	Rate	Velando *et al*. (2005) and Martínez-Abraín *et al*. (2006)
Eggs			
Eggs number laid	Averaged number of eggs laid per year 2.14	Eggs	Silva *et al*. (2017)
Egg natural failure rate (adults)	Proportion of eggs failure per year Min 0.24 Max 0.38	Rate	Neto (1997) and Silva *et al*. (2017)
Egg natural failure rate (immatures)	Calculated proportion of eggs failure per year Min 0.48 Max 0.60	Rate	Velando & Freire (2002), Velando & Munilla (2008), and Silva *et al*. (2017)
Eggs predation rate by rats	Proportion of eggs predation rate by rats 0.64	Rate	Silva (2015)
Eggs mortality rate after spill oil catastrophe	Assumed to be the same as adult female mortality rate after spill oil catastrophe 0.014	Rate	Velando *et al*. (2005) and Martínez-Abraín *et al*. (2006)

Daily rates applied in the model are depicted in Supporting Information Appendix S2 and S3. Additional references consulted are shown in Table S1 of Supporting Information Appendix S4.

Ecological factors

The model was conceptualized and parametrized by taking into consideration relevant information referenced in Table 1. The information concerns natural sources influencing natality and mortality of individuals from all age classes. Some of the factors involving mortality are highlighted below including their interannual variation, limited knowledge on their likely occurrence in the region and the influence this has on the outcome (Monteiro, 2017; Hénin *et al*., 2021).

Prey availability, environmental conditions and chick mortality

The Shag’s diet includes a diversity of fish species, captured in shallow and clear waters with good visibility (Velando & Freire, 1999). The fluctuation of fish stocks, particularly sandeels (family *Ammodytidae*), impacts the species’ breeding success (Furness & Tasker, 2000; Lilliendahl & Solmundsson, 2006). Actually, since the diet of chicks and juveniles is almost exclusively based on sandeels – adults can feed on a much wider spectrum of fish – daily mortality rates due to sandeel abundance were applied exclusively to the chicks and juveniles age classes (Howells *et al*., 2018). To increase realism, the model was designed to recreate three scenarios of sandeel abundance (low, medium and high), assuming annual variation in the corresponding mortality rate of chicks and juveniles (Cook & Reeves, 1993; Frederiksen *et al*., 2005), according to Cury *et al*. (2011) (see Supporting Information Appendix S3 for more details). Complementary simulations were made to illustrate the effects of fixed sandeel abundance (low, medium and high) on the population outcomes (Table S8, Supporting Information Appendix S7).

Also, adverse weather events during May have been pointed out to be responsible for an increase in chick mortality (Croxall *et al*., 2012; Newell *et al*., 2015). According to Velando *et al*. (1999), wind gusts stronger than 29 km h^{-1} and daytime rainfall over 10 mm reduce visibility underwater, ultimately limiting the amount of food that chicks receive from their parents. Therefore, the model simulated daily variation in weather conditions (in terms of rain and wind) and, given the impossibility of accurately predicting extreme weather events, historical trends were considered for simulating probabilities of extreme events (https://www.windguru.cz/1528, http://snirh.apambiente.pt). Whenever simulated meteorological conditions surpassed the threshold defined by Velando *et al.* (1999), mortality of chicks due to adverse weather was activated (Croxall *et al.*, 2012; Newell *et al.*, 2015) (Table 1 and Supporting Information Appendix S3, 2.3 Adverse weather and chick mortality).

Anthropogenic factors

The most important man-induced disturbance factors, with possible escalating effects on the mortality rates of the Berlengas population, were considered in the following paragraphs. In our conceptualization, these are the only factors that might be reduced or even removed using local management actions, which are explained in more detail in the scenarios section (Velando & Freire, 2002; Genovart, Oro & Tavecchia, 2017*b*; Andrade *et al.*, 2019).

Bycatch mortality

Incidental capture by different fishing gear is one of the top threats to seabirds worldwide (Arcos, Louzao & Oro, 2008; Dias *et al.*, 2019). Shags, particularly less experienced juveniles, are captured by gillnets and longlines as shown in a short-term study in the BSPA, evidencing high bycatch rates (Genovart *et al.*, 2017*b*; Oliveira *et al.*, 2018, 2020). Considering previous, cited studies and complementary information, we have assumed in the model different mortality rates for non-juveniles (immature and adults) and juvenile birds associated with bycatch (Velando & Freire, 2002; García-Barcelona *et al.*, 2010; Genovart *et al.*, 2017*a*) (Table 1 and Supporting Information Appendix S3, 2.1 Bycatch mortality).

Mortality due to rats

One of the most dramatic effects on the viability of seabird populations is that of predation by invasive mammals such as rats and cats (Jones *et al.*, 2008). The historic presence of rats in the BSPA was associated with declines of smaller seabirds and could have driven some species to extinction (Bell, Bell & Merton, 2016). Photo-trapping studies in the BSPA disclosed nest failure due to rat predation and disturbance of at least 30% of Shag nests (Silva, 2015). Thus, when rats were present, the model assumed an average reduction of egg and chick viability according to Igual *et al.* (2006) and Silva (2015) (Table 1 and Supporting Information Appendix S3, 2.2 Mortality due to rats).

Tourism disturbance-associated mortality

Coastal tourism is growing in marine protected areas, often in core breeding and feeding grounds for seabirds, with possible effects on chick survival (Martínez-Abraín *et al.*, 2008; Martín *et al.*, 2015; Gössling, Hall & Scott, 2018; Dehnhard *et al.*, 2020). During spring and summer, the shallow waters surrounding the archipelago are heavily used by recreational boats, particularly during weekends and holidays (Fernandes, 2016). Aggravation in chick mortality was simulated in the model during May weekends, when an overlap between recreational boat use and the presence of chicks in the nests occurred (Newell *et al.*, 2015; Fernandes, 2016) (Table 1 and Supporting Information Appendix S3, 2.4 Tourism disturbance-associated mortality).

Oil spill mortality

Oil spills have lethal effects on seabirds, by eliminating the waterproofing of their plumage and leading to loss of insulation and buoyancy, but also through several physiological effects, such as pulmonary oedema and endocrine disruption (Troisi, Barton & Bexton, 2016). Oil spills are recurrent along the NW Iberian coast – a recent one killed 5% of the Shag population, affecting particularly females and juveniles (Velando, Munilla & Leyenda, 2005; Martínez-Abraín *et al.*, 2006). For the model, we applied the corresponding oil spill mortality rate associated with specific mortality by sex and age (Martínez-Abraín *et al.*, 2006). Based on the historical data, a random probability of a catastrophic oil spill every 9 (±7.5) years was simulated, associated with sex and age-specific mortalities (ITOPF, 2007). These mortality rates were applied during one year after an oil spill occurrence, in compliance with Martínez-Abraín *et al.* (2006) (Table 1 and Supporting Information Appendix S3, 2.5 Oil spill mortality).

Sensitivity analyses

In order to provide a measure of the robustness of the model, Sensitivity Analyses (SA) were performed, testing the sensitivity of the obtained results to changes in the parameters, forcing functions and/or sub-models (Lee *et al.*, 2015). SA was done using the one-parameter-at-a-time technique (OAT), changing the population parameters of the model by ±10% and ±50% variation of the respective values and observing changes in the response of the most important state variables, *adults*, *immatures*, *juveniles*, *chicks* and *eggs* (Ligmann-Zielinska, 2013). To complement OAT, a Global SA, measuring the effect of combined parameters of a model in terms of sensitivity, was performed by estimating standardized model coefficients (SMC) of a Generalized Linear Model (GLzM) (Lee *et al.*, 2015). The outcomes of the GLzM were associated with the matrix of combinations of the parameters and included the variability of the respective values considered during simulations (Lee *et al.*, 2015; Santos *et al.*, 2016). SMC express the magnitude and significance of the effect of combined parameters measured using different units, as well as the explained variance, evaluating the main effects of the input parameters (Glantz & Slinker, 2001).

Scenarios

To predict future trends for the BSPA population and to identify the most effective conservation strategies, our model incorporated the key factors specified previously with comprehensive management actions. ‘Anthropogenic’ and ‘Ecological’ factors were included jointly in the projected scenarios: the management actions associated with each scenario reduce or remove one or more of the 'Anthropogenic factors' while maintaining all 'Ecological factors'. The number of adult females (the most critical sex-age class for sustaining a population in a monogamous species such as Shag) was defined as the core variable for gauging population dynamics and, subsequently, comparing the management actions (and scenarios) (Spelt & Pichegru, 2017). Eight scenarios were projected, considering sundry likelihoods and resources available for conservation (Table 2).

In scenario 1, our baseline scenario, no management actions were implemented and, in this way, all factors were considered in the simulation. The results were expected to reflect the population trend in recent years and were used to assess the effectiveness of the actions implemented in the other scenarios.

Scenario 2 simulated the removal of bycatch-associated mortality by implementing an exclusion of fisheries in the BSPA waters. Although, for socioeconomic reasons, this is most unlikely, the outcomes could provide pertinent information to outline regulations for specific areas and/or periods.

Scenario 3 simulated the elimination of rats in the archipelago, which was carried out in the BSPA in 2016 (Oliveira *et al*., 2019). Predictions from this scenario are especially interesting to be compared, apart from the baseline scenario, with real post-eradication data associated with the monitoring programs and future reports.

In scenario 4, disturbance from tourism was removed, namely during May weekends, when boats displace adults from the most productive feeding areas and chicks are still highly dependent. If effective in terms of conservation, this scenario could be possibly implemented by restricting access to the shallow waters of the BSPA.

Scenarios 5–6–7 combined the previous ones, namely 2 and 3 (scenario 5), 3 and 4 (scenario 6) and 2 and 4 (scenario 7). This was considered important to discuss, regarding logistics and budget, effort-effectiveness of integrating several management actions.

Finally, scenario 8 contemplated the unlikely situation in which all 'Anthropogenic factors" have been removed (apart from oil spills, considered impossible to prevent and to solve using local management actions), mostly improbable but fundamental to gauge the overall anthropogenic stress when comparing with the other scenarios (especially scenario 1) (Table 2).

We used STELLA software (version 9.0.3; Isee Systems, Inc.) to conceptualize the dynamic model. This software is a popular system dynamic modelling platform, integrating conceptual diagrams with mathematical equations (Naimi & Voinov, 2012). All processes explanation, flow diagrams and equations are depicted in Supporting Information Appendix S1–S3. More detailed information and supplementary bibliography consulted are depicted in Supporting Information Appendix S4.

Table 2 Scenarios simulated in a system dynamic model for the Berlengas Shag population (Portugal) over 10 years

Scenario	Key variables	Pressures
1	Baseline scenario	Anthropogenic factors (bycatch + rats + disturbances + oil spill*) + ecological factors
2	No bycatch	Anthropogenic factors (rats + disturbances + oil spill*) + ecological factors
3	No rats *(scenario after 2016)*	Anthropogenic factors (bycatch + disturbances + oil spill*) + ecological factors
4	No disturbance	Anthropogenic factors (bycatch + rats + oil spill*) + ecological factors
5	No rats No bycatch	Anthropogenic factors (disturbances + oil spill*) + ecological factors
6	No rats No disturbance	Anthropogenic factors (bycatch + oil spill*) + ecological factors
7	No bycatch No disturbance	Anthropogenic factors (rats + oil spill*) + ecological factors
8	No rats No bycatch No disturbance	Anthropogenic factors (oil spill*) + ecological factors

Scenarios varied according to anthropogenic factors included: bycatch mortality (bycatch), rat-caused mortality (rats), tourism disturbance-associated mortality (disturbances) and oil spill-associated mortality (oil spill). All scenarios included as ecological factors: temporal variation in prey availability (prey availability) and adverse weather events (bad weather).

* Although the oil spill is an anthropogenic factor, it was not considered manageable through local actions, but mostly a stochastic factor.

Statistical analysis

Cohen's effect size was computed to reveal the magnitude of the differences in the projected population of adult females (after 10 years) between scenarios (Cohen, 1988; Santos *et al*., 2016). Cohen's d estimate can be interpreted as negligible ($d < 0.2$), small ($d = 0.2$–0.49), medium ($d = 0.5$–0.79) or large ($d > 0.8$) (Lakens, 2013). To complement effect sizes, a Generalized Linear Model (GLzM) using adult females as response variable and scenario as predictor variable was applied (Donald, 2007). The model was fitted with a Quasi-Poisson distribution, in order to accommodate over-dispersion of data (mean 86.29; variance 365.94) (Crawley, 1993). Finally, to analyse the differences between paired scenarios, the Steel-Dwass post-hoc test, especially useful for discriminating all-pairs comparisons (Morley, 1982), was applied (also for juvenile females, considering that half are breeders, see please Supporting Information Appendix S4). All statistical analyses were carried out using 'PMCMRplus' (Pohlert, 2020), 'Steel.Dwass.test' (Douglas Steel, Shigenobu & Mei, 2017), 'effsize' (Torchiano, 2020) and 'stats' package in the statistical programming language 'R' (R Development Core Team, 2020).

Results

Sensitivity analysis

The results from the OAT sensitivity analysis highlights the state variables *adults*, *immatures*, *juveniles* (females and males), *chicks from adults* and *chicks from immatures*, as the most sensitive to manipulation of parameters (Table S6 in Supporting Information Appendix S5). Specifically, small changes in the parameters *number of laid eggs*, *bad weather chick mortality* and *non-juvenile bycatch mortality rate* had critical influence on the outcomes of model runs, namely by affecting the results of most of the state variables (Table S6 in Supporting Information Appendix S5). Conversely, the global sensitivity analysis highlighted the parameters *adult mortality*, *immature mortality* and *juvenile mortality*, along with the *number of eggs laid* as particularly impactful on the population trends obtained (Table S7 in Supporting Information Appendix S5).

Scenario outcomes for the next decade

Our baseline scenario (scenario 1) resulted in a predicted reduction of 7.90% in the adult females (hereon population) (min: −13.60%; max: −2.13%) (Fig. 3, 3.1), most likely compromising its med/long-term viability, while a population increase of 13.52% (min: 5.02%; max: 22.12%) was estimated if fishing were forbidden in the BSPA, by eliminating bycatch (scenario 2) (Fig. 3, 3.2).

On the other hand, the eradication of rats (scenario 3), increased the population by 48.50% (min: 34.61%; max: 62.49%) (Fig. 3, 3.3), whereas only prohibiting recreational boats during the weekends of May (scenario 4) was associated with an average population decrease of 5.27%, similar to the baseline scenario (min: −13.89%; max: 3.50%) (Fig. 3, 3.4).

When rat eradication was combined with no fishing (scenario 5), the results depicted an increase of 83.61% (min: 67.32%; max: 100.07%) (Fig. 3, 3.5). Conversely, rat eradication combined with no tourism (scenario 6) was predicted to produce an increase in the population of 50.39% (min: 37.10%; max: 63.81%) (Fig. 3, 3.6) while no fishing and no tourism (scenario 7) could yield a population increase of 13.04% (min: 5.23%; max: 20.93%) (Fig. 3, 3.7).

Finally, for scenario 8, where all ‘Anthropogenic factors’ were simulated to be removed (apart from oil spills), increases in the population of approximately of 86.21% were forecasted (min: 67.69%; max: 104.94%) (Fig. 3, 3.8).

Large changes in the population were predicted when comparing the baseline scenario with all others, except for scenario 4 (no tourism disturbance), which only showed a small difference (Cohen’s effect size, Table 3). Especially large differences were expected for scenarios 5 and 8 (no rats and no bycatch; no rats, no bycatch and no disturbance) (Table 3). As expected from the previous results, the most significant differences (associated with higher t-values) were simulated for scenarios 5 and 8 (Table S4 in Supporting Information Appendix S5). Additionally, the pairwise

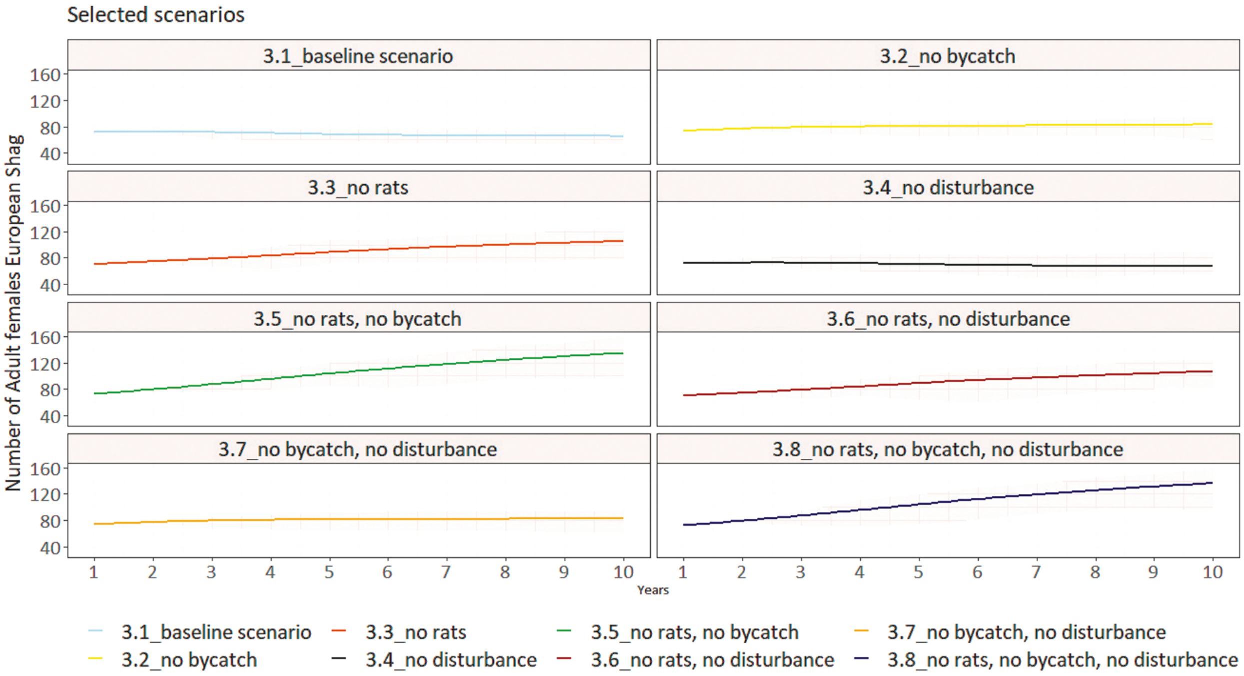

Figure 3 Average trend in adult female Shag numbers in the Berlengas archipelago, Portugal, by simulated scenario considering diverse ecological and anthropogenic factors for a period of 10 years and using 100 independent simulations per scenario. Grey shade shows maximum and minimum simulated values reached by considered scenario. Baseline scenario does not consider management actions so contains fisheries bycatch, impact of rats and tourism disturbance on Shag demographic parameters, in addition to effects of prey availability, bad weather and oil spills; scenarios 2–8 remove one or several of these anthropogenic factors. ‘No disturbance’’ refers to tourist disturbance.

Table 3 Results comparison, based on Cohen's effect size, between the baseline scenario (scenario 1) and all other scenarios used in a system dynamic model for the Berlengas Shag population (Portugal) over 10 years

Pairwise comparisons	Cohen's *d* estimate	Lower 95% CI	Upper 95% CI	Interpretation
1:2	3.631	4.085	3.177	Large
1:3	5.541	6.155	4.928	Large
1:4	0.422	0.704	0.140	Small
1:5	8.156	9.007	7.305	Large
1:6	6.029	6.685	5.372	Large
1:7	3.753	4.216	3.289	Large
1:8	7.489	8.279	6.700	Large

Cohen's d estimate = effect sizes using Cohen estimator (with lower and upper 95% CI); Interpretation = magnitude of Shag population differences between scenarios 1: baseline scenario (scenario 1, including mortality due to fisheries bycatch, rats, tourism disturbance and oil spills [anthropogenic factors]); scenario 2: no bycatch mortality; scenario 3: no rats; scenario 4: no tourist disturbances; scenario 5: no rats, no bycatch; scenario 6: no rats, no tourist disturbances; scenario 7: no bycatch, no tourist disturbances and scenario 8: no rats, no accidental capture, no tourist disturbance (all scenarios contain variation in prey availability and weather conditions [ecological factors]). Complementary comparisons are depicted in Table S3, Supporting Information Appendix S5.

comparisons between all scenarios for adult and juvenile females were found to be statistically different (Adult female, chi-squared = 4636.8, d.f. = 7, *P*-value < 0.001; Juvenile female, chi-squared = 5041.3, d.f. = 7, *P*-value < 0.001), except between scenarios 2–7, 3–6 and 5–8 (Table S5 in Supporting Information Appendix S5 and Fig. 4).

Discussion

Simulated population trends and effectiveness of management actions

Our baseline scenario estimated a decrease of 8% for the adult females, in line with the trends detected for the BSPA population in recent years (Oliveira, 2019; Pereira & Oliveira, 2019). A large inter-annual variation in the number of breeding pairs characterizes this population (e.g. ~35 pairs in 1978, ~90 pairs in 1995, ~15 pairs 1998, ~80 pairs in 2002, ~32 pairs 2008, ~82 pairs in 2012, ~38 pairs 2014 and 62 pairs in 2019). This variation might be associated with different census methods and difficulties in monitoring inaccessible nest locations but is probably due to the number of females that do not reproduce yearly (Neto, 1997; Oliveira, 2019; Pereira & Oliveira, 2019). In fact, intermittent nonbreeding or sabbatical years is a common behaviour in long-lived seabirds such as Shag (Aebischer & Wanless, 1992; Cairns, 1992; Giudici *et al*., 2010). This might be triggered by physiological constrains and/or fewer feeding resources associated with specific periods (Chastel, Weimerskirch & Jouventin, 1995; Labocha & Hayes, 2012).

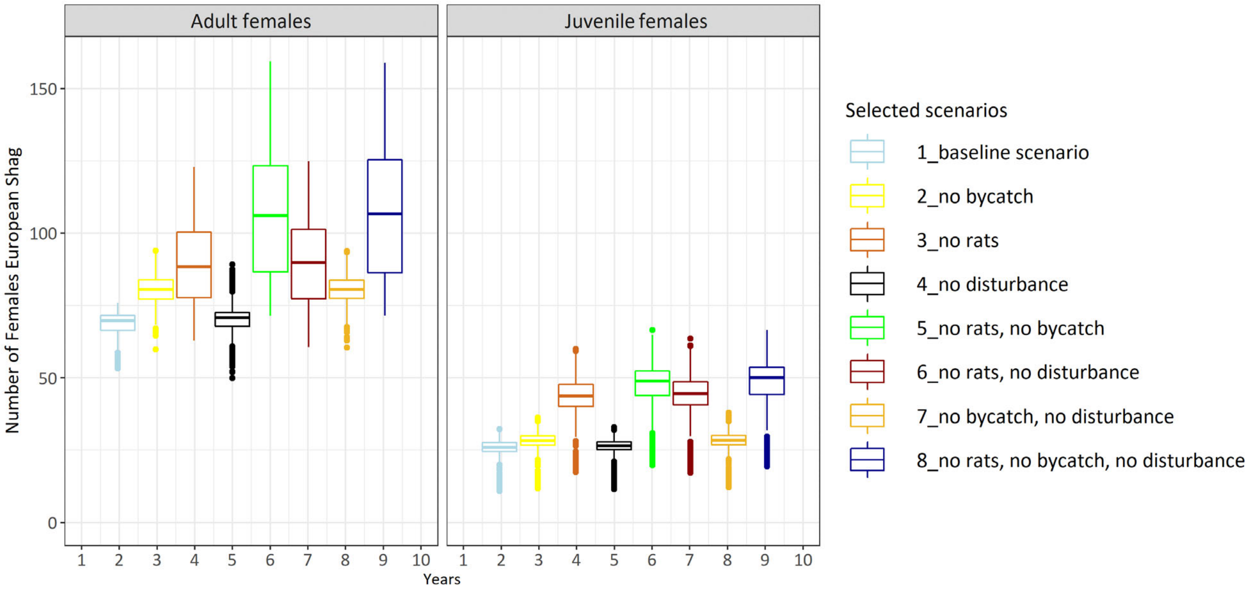

Figure 4 Boxplots comparing average trends of adult and juvenile female Shag populations in the Berlengas archipelago, Portugal, for all scenarios, considering a period of 10 years and 100 independent simulations by scenario. Baseline scenario does not consider management actions so contains fisheries bycatch, impact of rats and tourism disturbance on Shag demographic parameters, in addition to effects of prey availability, bad weather and oil spills; scenarios 2–8 remove one or several of these anthropogenic factors. 'No disturbance' refers to tourist disturbance. The lower and upper limits of each box represent the first and third quartiles, respectively, and the line inside each box represents the median. The bottom and top bars represent the minimum (First quartile minus 1.5 * Interquartile range) and maximum (Third quartile plus 1.5 * Interquartile range) values, respectively. Circles outside the first and third quartiles range are outliers.

Moreover, considering the high degree of philopatry, adult short-distance movements and the isolated location of the BSPA Shag population, source-sink/interchange dynamics with scattered pairs breeding along the Portuguese shore near the Berlengas is possible while breeding in the closest colony – Cíes Islands, Galicia, >300 km away – seems highly unlikely (Potts, 1969; Martínez-Abraín *et al*., 2001; Barlow *et al*., 2013; Orta *et al*., 2020).

Our results highlight the potential benefits of rat eradication and fisheries control, by removing bycatch, for Shag conservation (Table 3 and Table S4 in Supporting Information Appendix S5) (Jouventin, Bried & Micol, 2003; Bell *et al*., 2016; Avery *et al*., 2017). In fact, rats are present on most of the world's major islands and are known to negatively affect island biota, exacerbated by endemism or small population sizes that are inherently susceptible to extinction (Atkinson, 1996; Oliveira *et al*., 2019). Recent efforts to eradicate rats from the archipelago should show its results in the next years (Oliveira *et al*., 2019) as many successful examples point to the benefits of rat removal from islands for seabird conservation and insular ecosystem restoration (Russell & Holmes, 2015; Jones *et al*., 2016). Actually, the maintenance of a rat-free BSPA could result, according to our simulations, in more than 100 additional breeding pairs of Shag over the next decade but might also be responsible for the recent increase in Cory's shearwater population or the recent colonization by the Band-rumped Storm-petrel (Mendes, 2013; Andrade *et al*., 2019; Nascimento *et al*., 2019; Fagundes, 2021). Furthermore, endemic plant species, such as Berlengas thrift *Armeria berlengensis*, Berlengas rupturewort *Herniaria berlengiana* and Berlengas fleabane *Pulicaria microcephala* (Tauleigne *et al*., 2004) and reptiles, such as Berlengas wall lizard *Podarcis carbonelli berlengensis* are clearly benefitting from this eradication (Howald *et al*., 2007; Jones *et al*., 2016; Nascimento *et al*., 2019).

On the other hand, removing bycatch mortality is highly unlikely to be implemented, due to the importance of the BSPA for fisheries and the local socio-economy (Melvin, Parrish & Conquest, 1999). We used conservative effects of this factor on Shag population dynamics but we must not forget that exceptionally high mortality events can occur and these random events can be extremely important for future population trajectories and even cause extinction in small populations (Boyce, 1992). Different mitigation measures (visual, acoustic signals, setting time, setting depth) have been tested, although with inconclusive results for Shag (Martin & Crawford, 2015; Oliveira *et al*., 2020). Therefore, to minimize fishing gear bycatch, halting fisheries in shallow areas and reducing fishing pressure could be considered effective measures, which ultimately could also contribute to increased fish stocks and the conservation of other species (e.g. seabirds, sea mammals) (Melvin *et al*., 1999). These actions might be exceptionally relevant for species such as the critically endangered Balearic shearwater, whose time to extinction was recently estimated to be approximately 60 years (Genovart *et al*., 2016), Northern gannet and Cory's shearwater (Faria, 2014; Oliveira *et al*., 2020; Calado *et al*., 2021). Interestingly, our simulations seem to demonstrate that combining both strategies, eradication of rats and reduction of bycatch, produces increases in the population that might have not been anticipated by summing results when each is implemented independently (83.6% vs. 48.5% and 13.5%). This agrees with studies demonstrating that only one strategy might not be enough to halt seabird declines, advocating combined actions, such as rat removal in combination with bycatch taxes, as effective approaches (Donlan & Wilcox, 2007; Finkelstein *et al*., 2008; Igual *et al*., 2009).

Disturbance caused by tourism and oil spills had minor effects on the population trends, probably because visits occur mostly in July and August when chicks are no longer in the nest (Silva, 2015; Fernandes, 2016) and the low probability of oil spills considered for the simulated period. However, tourism in natural areas continues to increase with negative consequences (Marcella *et al*., 2017), and a single oil spill event might have dramatic consequences for this relict population (Velando *et al*., 2005; Munilla *et al*., 2011).

Environmental and oceanographic change

Our model did not explicitly evaluate the impacts of global climate or oceanographic change and sandeel abundance on the population dynamics, because the inter-annual variation predicted for the next decade should be higher than the expected trend (Cook & Reeves, 1993; Frederiksen *et al*., 2005; Cury *et al*., 2011; IPPC, 2018). In this way, extreme event occurrence and prey abundance were considered stochastic environmental phenomena within all scenarios. We have considered factors emerging from that variation, such as the mortality of chicks associated with adverse weather conditions and juvenile and chick mortality rates related with prey abundance (Velando *et al*., 1999; Furness & Tasker, 2000). In fact, *chick mortality due to extreme meteorological events* was considered a determinant parameter in the OAT sensitivity analysis (Supporting Information Appendix S4, Table S6). Despite the fact that a 10- year simulation period only allows very incipient conclusions to be drawn, the prediction of more extreme climate events in the future, namely increasing days with heavy rains and strong winds and a decrease in the main food source, might have detrimental effects on chick survival (Grémillet & Boulinier, 2009). Even though seabird declines have been correlated with ocean warming, more investigation is needed to uncover direct and indirect interactions and causalities (Jenouvrier *et al*., 2018).

Evaluation of model assumptions and potential biases

When compared to other modelling methodologies, such as the widely used Species Distribution Models (SDM), System Dynamics (SD) frameworks are considered more flexible, transparent and easy to understand, and able to simulate processes at local scales (Santos *et al*., 2015). Also, the custom-made nature, grey-box structure and hysteresis of SD might complement generic programs used for Population Viability Analysis, by selecting the most appropriate scales, which parameters should be reproduced, link relevant parameters with outcomes and, in this way, contribute to uncovering details within population dynamics (Reşit Akçakaya & Sjögren-Gulve, 2000; Morrison, Wardle & Castley, 2016; Chaudhary & Oli, 2020). That said, evaluation of assumptions made during the conceptualization of demographic models is of utmost importance (Sydeman *et al*., 2017; Sæther & Engen, 2019). In fact, even if the trends depicted seem consistent, some parameters and state variables, such as the inherently imprecise initial population size (Neto, 1997; Pereira & Oliveira, 2019) or the mortality rate due to stochastic events, could have influenced the obtained results. Moreover, not all parameters and/or data included in the model were obtained from our local population and region. To minimize these drawbacks, instead of using specific values that could unduly impact the results, we used ranges of values, estimated from minimum and maximum values (from the literature), and conservative probabilities of phenomena occurrences. Another potential weakness in demographic models may be the assumption of anthropogenic mortality as additive to natural mortality (Péron, 2013). Clearly separating natural from anthropogenic mortality is itself dubious and some authors assume general rates for both types (Aanes *et al*., 2007).

Complementary ideas and uncertainties

Cost-effective monitoring and management of conservation areas is regularly achieved using umbrella and/or indicator species (Simberloff, 1998; Hawkes *et al*., 2019). As a marine top predator, Shag could play a relevant role by indicating the ecological status of rocky shore marine areas such as the BSPA (Hunter *et al*., 2016). In fact, the species is sensitive to a wide range of socio-ecological factors such as invasive mammals, human disturbance, fisheries competition and overlapping with feeding areas, as well as climate/oceanographic changes. In this way, the species is capable of capturing the complexities of the ecosystem, and it can be easily monitored by standard methodologies (Siddig *et al*., 2016).

On the other hand, dynamic models such as the one developed in our study have been recognized as appropriate to guide management decisions (Cuddington *et al*., 2013) and, therefore, could assist in implementing European directives of the Natura 2000 Network (Directive 1992/43 EC; Directive 2009/147/EC) to marine SPAs, by selecting cost-effective management policies for habitats and species. This type of frameworks could help envision the ecological consequences of conservation actions. Even though our results are linked with a specific area of the Iberian-Atlantic arc and seabird species, the methodology presented could be easily parametrized to other areas, species and challenges (Bastos *et al*., 2012; Arosa *et al*., 2017; Petrescu Bakış *et al*., 2021).

We have described and analysed the probable impacts of ongoing disturbances on the trends of a small relict population (Highlights in Supporting Information Appendix S6). However, effective conservation should move forward relentlessly trying to anticipate new threats or investigate those we do not yet know about. Recent studies show new stress factors, particularly microplastics, which have been found in more than 60% of Shag pellets and whose effects are mostly unknown (Álvarez, Barros & Velando, 2018). Also, projected offshore windfarms for this coast, which are particularly attractive to Shags (but also to other seabirds) could produce an additional source of mortality (Dierschke, Furness & Garthe, 2016). Finally, we cannot forget the unique situation of the small population of Shag in BSPA, susceptible to genetic drift and inbreeding depression (Velando, Barros & Moran, 2015).

Based on the results obtained, we suggest investigating the following management recommendations: (1) interrelate, using monitored data, the breeding population of Shag, meteorological/oceanographic conditions and fish populations in the BSPA; (2) monitor invasive mammals in BSPA and respond rapidly with pertinent actions if a re-invasion occurs; (3) apply mitigation measures in fishing gear and consider closing specific Shag foraging areas to fisheries during the breeding season; (4) reduce the number of tourists visiting BSPA, especially during the breeding season. These actions might contribute to improve both our knowledge and the conservation of Shags and the broader ecosystem of the BSPA.

Conclusions

The ability to accurately predict species responses to environmental change is crucial for conservation planning and to support key ecosystem management actions (Kandziora, Burkhard & Müller, 2013). Despite all the assumptions and weaknesses that this academic work may present, the dynamic model developed integrates disperse information concerning the biology and ecology of Shag, estimating the likely outcome of different conservation actions available for a relict population. The results obtained stress the importance of controlling invasive mammals and bycatch to conserve and recover Shag populations and concomitant coastal ecosystems (Bull, 2007; Oliveira *et al*., 2019) (Fig. S1 in Supporting Information Appendix S6).

Acknowledgements

This study was supported by the International Internship Grant Program of the University of Cadiz (EDUCA), Spain for conducting research in internationally renowned centres and the Centre for the Research and Technology of Agro-Environmental and Biological Sciences (CITAB) of the Universidad de Trás-os-Montes e Alto Douro (UTAD), Vila Real, Portugal.

In addition, the following entities contributed to this work: European Investment Funds by FEDER/COMPETE/POCI – Operational Competitiveness and Internationalization Programme, under Project POCI-01-0145-FEDER-006958, National Funds by FCT – Portuguese Foundation for Science and Technology, under the project UIDB/04033/2020 and INTERACT, Integrative Research in Environment, Agro-Chains and Technology, Project Norte 2020 45/2015/02. R. B. received support from POPH/FSE, funds and by National Funds through FCT Foundation for Science and Technology under the Portuguese Science Foundation through Doctoral grant FCT_SFRH/BD/102428/2014.

References

Aanes, S., Engen, S., Sæther, B.-E. & Aanes, R. (2007). Estimation of the parameters of fish stock dynamics from catch-at-age data and indices of abundance: can natural and fishing mortality be separated? *Can. J. Fish. Aquat. Sci.* **64**, 1130–1142.

Aebischer, N.J. (1985). *Aspects of the biology of the shag (Phalacrocorax aristotelis)*. Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/7880/

Aebischer, N. (1986). Retrospective investigation of an ecological disaster in the Shag, *Phalacrocorax aristotelis*: a general method based on long-term marking. *J. Anim. Ecol.* **55**, 613–629.

Aebischer, N. & Wanless, S. (1992). Relationships between colony size, adult non-breeding and environmental conditions for Shags *Phalacrocorax aristotelis* on the Isle of May, Scotland. *Bird Study* **39**, 43–52.

Alonso, H., Teodósio, J., Andrade, J., Mendes, R. & Marques, P. (2019). *O estado das aves em Portugal, 2019*. Lisboa: Sociedade Portuguesa para o Estudo das Aves.

Álvarez, G., Barros, Á. & Velando, A. (2018). The use of European Shag pellets as indicators of microplastic fibers in the marine environment. *Mar. Pollut. Bull.* **137**, 444–448.

Anderson, C.M., Iverson, S.A., Black, A., Mallory, M.L., Hedd, A., Merkel, F. & Provencher, J.F. (2018). Modelling demographic impacts of a growing Arctic fishery on a seabird population in Canada and Greenland. *Mar. Environ. Res.* **142**, 80–90.

Andrade, J., Leitão, D., Costa, L., Domingues, J., Fernandes, M.J., Morais, L., Correia, A.J., Veríssimo, R., Cativo, N., Bertino, H., Ministro, M., da Silva, C.P., Fonseca, C., Nogueira, R.M. & Leandro, S. (2019). *Life Berlengas*. Relatório Não-técnico.

Arcos, J.M., Louzao, M. & Oro, D. (2008). Fisheries ecosystem impacts and management in the mediterranean: seabirds point of view. In *Reconciling Fish. with Conserv. Proc. Fourth World Fish. Congr. Fish. Soc. Symp*: 1471–1479. Vol. **49**. Bethesda: American Fisheries Society.

Arosa, M.L., Bastos, R., Cabral, J.A., Freitas, H., Costa, S.R. & Santos, M. (2017). Long-term sustainability of cork oak agro-forests in the Iberian Peninsula: a model-based approach aimed at supporting the best management options for the montado conservation. *Ecol. Modell.* **343**, 68–79.

Atkinson, I.A.E. (1996). Introductions of wildlife as a cause of species extinctions. *Wildl. Biol.* **2**, 135–141.

Avery, J.D., Aagaard, K., Burkhalter, J.C. & Robinson, O.J. (2017). Seabird longline bycatch reduction devices increase target catch while reducing bycatch: a meta-analysis. *J. Nat. Conserv.* **38**, 37–45.

Banos-González, I., Terrer, C., Martínez-Fernández, J., Esteve-Selma, M.A. & Carrascal, L.M. (2016). Dynamic modelling of the potential habitat loss of endangered species: the case of the Canarian houbara bustard (Chlamydotis undulata fuerteventurae). *Eur. J. Wildl. Res.* **62**, 263–275.

Barlow, E.J., Daunt, F., Wanless, S., Álvarez, D., Reid, J.M. & Cavers, S. (2011). Weak large-scale population genetic structure in a philopatric seabird, the European Shag *Phalacrocorax aristotelis*. *The Ibis* **153**, 768–778.

Barlow, E.J., Daunt, F., Wanless, S. & Reid, J.M. (2013). Estimating dispersal distributions at multiple scales: within-colony and among-colony dispersal rates, distances and directions in European Shags *Phalacrocorax aristotelis*. *The Ibis* **155**, 762–778.

Barros, Á., Álvarez, D. & Velando, A. (2013). Climate influences fledgling sex ratio and sex-specific dispersal in a seabird. *PLoS One* **8**, e71358.

Bastos, R., D'Amen, M., Vicente, J., Santos, M., Yu, H., Eitelberg, D., Gonçalves, J., Civantos, E., Honrado, J. & Cabral, J.A. (2016). A multi-scale looping approach to predict spatially dynamic patterns of functional species richness in changing landscapes. *Ecol. Indic.* **64**, 92–104.

Bastos, R., Santos, M., Ramos, J.A., Vicente, J., Guerra, C., Alonso, J., Honrado, J., Ceia, R.S., Timóteo, S. & Cabral, J.A. (2012). Testing a novel spatially-explicit dynamic modelling approach in the scope of the laurel forest management for the endangered Azores bullfinch (*Pyrrhula murina*) conservation. *Biol. Conserv.* **147**, 243–254.

Bell, E., Bell, B. & Merton, D. (2016). The legacy of Big South Cape: rat irruption to rat eradication. *N. Z. J. Ecol.* **40**, 212–218.

Bennett, A.E., Preedy, K., Golubski, A., Umbanhowar, J., Borrett, S.R., Byrne, L., Apostol, K., Bever, J.D., Biederman, L., Classen, A.T., Cuddington, K., Graaff, M., Garrett, K.A., Gross, L., Hastings, A., Hoeksema, J.D., Hrynkiv, V., Karst, J., Kummel, M., Lee, C.T., Liang, C., Liao, W., Mack, K., Miller, L., Ownley, B., Rojas, C., Simms, E.L., Walsh, V.K., Warren, M. & Zhu, J. (2019). Beyond the black box: promoting mathematical collaborations for elucidating interactions in soil ecology. *Ecosphere* **10**, 1–16.

BirdLife International. (2018). *Gulosus aristotelis*. The IUCN Red List of Threatened Species 2018: e.T22696894A133538524. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22696894A133538524.en

Boyce, M.S. (1992). Population viability analysis. *Annu. Rev. Ecol. Syst.* **23**, 481–497.

Buchadas, A., Vaz, A.S., Honrado, J.P., Alagador, D., Bastos, R., Cabral, J.A., Santos, M. & Vicente, J.R. (2017). Dynamic models in research and management of biological invasions. *J. Environ. Manage.* **196**, 594–606.

Bull, L.S. (2007). Reducing seabird bycatch in longline, trawl and gillnet fisheries. *Fish Fish.* **8**, 31–56.

Cairns, D.K. (1992). Population regulation of seabird colonies. In *Current ornithology*: 37–61. Power, D.M. (Ed.). Boston: Springer US.

Calado, J.G., Ramos, J.A., Almeida, A., Oliveira, N. & Paiva, V.H. (2021). Seabird-fishery interactions and bycatch at multiple gears in the Atlantic Iberian coast. *Ocean Coast. Manag.* **200**, 105306.

Chastel, O., Weimerskirch, H. & Jouventin, P. (1995). Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* **76**, 2240–2246.

Chaudhary, V. & Oli, M.K. (2020). A critical appraisal of population viability analysis. *Conserv. Biol.* **34**, 26–40.

Cohen, J. (1988). *Statistical power for the social sciences*: 98–101. Hillsdale, NJ: NJ Laurence Erlbaum Assoc.

Colomer, M.À., Margalida, A. & Pérez-Jiménez, M.J. (2013). Population Dynamics P System (PDP) models: a standardized protocol for describing and applying novel bio-inspired computing tools.*PLoS One* **8**, e60698.

Cook, R. & Reeves, S. (1993). Assessment of North Sea industrial fish stocks with incomplete catch-at-age data. *ICES J. Mar. Sci.* **50**, 425–434.

Crawley, M.J. (1993). *GLIM for ecologist*. Oxford, UK: Blackwell Science.

Crookes, D.J. & Blignaut, J.N. (2019). An approach to determine the extinction risk of exploited populations. *J. Nat. Conserv.* **52**, 125750.

Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A. & Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv. Int.* **22**, 1–34.

Cuddington, K., Fortin, M.-J., Gerber, L.R., Hastings, A., Liebhold, A., O'Connor, M. & Ray, C. (2013). Process-based models are required to manage ecological systems in a changing world. *Ecosphere* **4**, art20.

Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A., Murphy, E.J., Osterblom, H., Paleczny, M., Piatt, J.F., Roux, J.-P., Shannon, L. & Sydeman, W.J. (2011). Global seabird response to forage fish depletion. One-third for the birds. *Science* **334**, 1703–1706.

Dehnhard, N., Skei, J., Christensen-Dalsgaard, S., May, R., Halley, D., Ringsby, T.H. & Lorentsen, S.H. (2020). Boat disturbance effects on moulting common eiders Somateria mollissima. *Mar. Biol.* **167**, 1–11.

del Moral, J.C., Oliveira, N. (2019). *El cormorán moñudo en la península ibérica. Población reproductora en 2017 y método de censo*. Madrid: SEO/BirdLife.

Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Borboroglu, P.G. & Croxall, J.P. (2019). Threats to seabirds: a global assessment. *Biol. Conserv.* **237**, 525–537.

Dierschke, V., Furness, R.W. & Garthe, S. (2016). Seabirds and offshore wind farms in European waters: avoidance and attraction. *Biol. Conserv.* **202**, 59–68.

Donald, P.F. (2007). Adult sex ratios in wild bird populations. *The Ibis* **149**, 671–692.

Donlan, C.J. & Wilcox, C. (2008). Integrating invasive mammal eradications and biodiversity offsets for fisheries bycatch: conservation opportunities and challenges for seabirds and sea turtles. *Biol. Invasions* **10**, 1053–1060.

Douglas Steel, R.G., Shigenobu, A. & Mei, W. (2017). *Steel.Dwass.test: Steel-Dwass pairwise ranking test*. R package version 1.0.0.

Drechsler, M. (2020). Model-based integration of ecology and socio-economics for the management of biodiversity and ecosystem services: state of the art, diversity and current trends. *Environ. Model. Softw.* **134**, 104892.

Fagundes, I. (2021). *The use of the Portuguese coast by migratory seabirds*. Évora: Universidade de Évora.

Faria, J. (2014). *Using a seabird top predator to assess the adequacy of the Berlengas marine protected area using a seabird top predator to assess the adequacy of the Berlengas marine protected area*. Coimbra: Universidade De Coimbra.

Fernandes, A. (2016). *A utilização recreativa da Berlenga e as implicações para a sua gestão*. Lisboa: Universidade de Lisboa.

Finkelstein, M., Bakker, V., Doak, D.F., Sullivan, B., Lewison, R., Satterthwaite, W.H., McIntyre, P.B., Wolf, S., Priddel, D., Arnold, J.M., Henry, R.W., Sievert, P. & Croxall, J. (2008). Evaluating the potential effectiveness of compensatory mitigation strategies for marine bycatch. *PLoS One* **3**, e2480.

Fiúza, A.F.G. (1983). Upwelling patterns off Portugal. In *Coast. Upwelling Its Sediment Rec*: 85–98. Suess, E. & Thiede, J. (Eds). Boston, MA: Springer US.

Frederiksen, M., Wright, P., Harris, M., Mavor, R., Heubeck, M. & Wanless, S. (2005). Regional patterns of kittiwake Rissa tridactyla breeding success are related to variability in sandeel recruitment. *Mar. Ecol. Prog. Ser.* **300**, 201–211.

Furness, R.W. & Camphuysen, K.C.J. (1997). Seabirds as monitors of the marine environment. *ICES J. Mar. Sci.* **54**, 726–737.

Furness, R.W. & Tasker, M. (2000). Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Mar. Ecol. Prog. Ser.* **202**, 253–264.

Galbraith, H., Russell, S. & Furness, R.W. (1981). Movements and mortality of isle of may Shags as shown by ringing recoveries. *Ringing Migr.* **3**, 181–189.

García-Barcelona, S., Macías, D., Ortiz De Urbina, J.M., Estrada, A., Real, R. & Báez, J.C. (2010). Modelling abundance and distribution of seabird by-catch in the Spanish mediterranean longline fishery. *Ardeola* **57**, 65–78.

Genovart, M., Arcos, J.M., Álvarez, D., McMinn, M., Meier, R., B. Wynn, R., Guilford, T. & Oro, D. (2016). Demography of the critically endangered Balearic shearwater: the impact of fisheries and time to extinction. (H. Österblom, Ed.). *J. Appl. Ecol.* **53**, 1158–1168.

Genovart, M., Doak, D.F., Igual, J.M., Sponza, S., Kralj, J. & Oro, D. (2017*a*). Varying demographic impacts of different fisheries on three Mediterranean seabird species. *Glob. Chang. Biol.* **23**, 3012–3029.

Genovart, M., Oro, D. & Tavecchia, G. (2017*b*). Science, technology, and society initiative to minimize unwanted catches in European fisheries. In *WP3. Impact Assess. minimizing unwanted catches discarding. MINOUW.* European Project. http://minouw-project.eu/

Gillson, L., Biggs, H., Smit, I.P.J., Virah-Sawmy, M. & Rogers, K. (2019). Finding common ground between adaptive management and evidence-based approaches to biodiversity conservation. *Trends Ecol. Evol.* **34**, 31–44.

Giudici, A., Navarro, J., Juste, C. & González-Solís, J. (2010). Physiological ecology of breeders and sabbaticals in a pelagic seabird. *J. Exp. Mar. Biol. Ecol.* **389**, 13–17.

Glantz, S.A. & Slinker, B.K. (2001). *Primer of applied regression & analysis of variance*. New York: McGraw-Hill Inc.

Gonzalez, D., Cabral, J.A., Torres, L. & Santos, M. (2015). A cohort-based modelling approach for managing olive moth Prays oleae (Bernard, 1788) populations in olive orchards. *Ecol. Modell.* **296**, 46–56.

Gössling, S., Hall, C. & Scott, D. (2018). Coastal and ocean tourism. In *Handb. Mar. Environ. Prot.*: 773–790. Salomon, M. & Markus, T. (Eds). Cham: Springer.

Grémillet, D. & Boulinier, T. (2009). Spatial ecology and conservation of seabirds facing global climate change: a review. *Mar. Ecol. Prog. Ser.* **391**, 121–137.

Hall, M.A., Alverson, D.L. & Metuzals, K.I. (2000). By-catch: problems and solutions. *Mar. Pollut. Bull.* **41**, 204–219.

Hamilton, S. & Moller, H. (1995). Can PVA models using computer packages offer useful conservation advice? Sooty shearwaters *Puffinus griseus* in New Zealand as a case study. *Biol. Conserv.* **73**, 107–117.

Harris, M.P. & Wanless, S. (1996). Differential responses of Guillemot Uria aalge and Shag *Phalacrocorax aristotelis* to a late winter wreck. *Bird Study* **43**, 220–230.

Hawkes, R.W., Smart, J., Brown, A., Jones, H., Lane, S., Wells, D. & Dolman, P.M. (2019). Multi-taxa consequences of management for an avian umbrella species. *Biol. Conserv.* **236**, 192–201.

Hénin, R., Ramos, A.M., Pinto, J.G. & Liberato, M.L.R. (2021). A ranking of concurrent precipitation and wind events for the Iberian Peninsula. *Int. J. Climatol.* **41**, 1421–1437.

Howald, G., Donlan, C.J., Galván, J.P., Russell, J.C., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi, P., Pascal, M., Saunders, A. & Tershy, B. (2007). Invasive rodent eradication on islands. *Conserv. Biol.* **21**, 1258–1268.

Howells, R.J., Burthe, S.J., Green, J.A., Harris, M.P., Newell, M.A., Butler, A., Wanless, S. & Daunt, F. (2018). Pronounced long-term trends in year-round diet composition of the European Shag *Phalacrocorax aristotelis*. *Mar. Biol.* **165**, 1–15.

Hunter, M., Westgate, M., Barton, P., Calhoun, A., Pierson, J., Tulloch, A., Beger, M., Branquinho, C., Caro, T., Gross, J., Heino, J., Lane, P., Longo, C., Martin, K., McDowell, W.H., Mellin, C., Salo, H. & Lindenmayer, D. (2016). Two roles for ecological surrogacy: indicator surrogates and management surrogates. *Ecol. Indic.* **63**, 121–125.

Igual, J.M., Forero, M.G., Gomez, T., Orueta, J.F. & Oro, D. (2006). Rat control and breeding performance in Cory's shearwater (*Calonectris diomedea*): effects of poisoning effort and habitat features. *Anim. Conserv.* **9**, 59–65.

Igual, J.M., Tavecchia, G., Jenouvrier, S., Forero, M.G. & Oro, D. (2009). Buying years to extinction: is compensatory mitigation for marine bycatch a sufficient conservation measure for long-lived seabirds? *PLoS One* **4**, e4826.

IPPC. (2018). Summary for policymakers IPPC Special Report on Global Warming of 1.5°C. IPPC Spec. Rep. Glob. Warm. 1.5 °C.

ITOPF. (2007). *Oil tanker spill statistics: 2006*.

Jenouvrier, S., Desprez, M., Fay, R., Barbraud, C., Weimerskirch, H., Delord, K. & Caswell, H. (2018). Climate change and functional traits affect population dynamics of a long-lived seabird. *J. Anim. Ecol.* **87**, 906–920.

Jones, H.P., Holmes, N.D., Butchart, S.H.M., Tershy, B.R., Kappes, P.J., Corkery, I., Aguirre-Muñoz, A., Armstrong, D.P., Bonnaud, E., Burbidge, A.A., Campbell, K., Courchamp, F., Cowan, P.E., Cuthbert, R.J., Ebbert, S., Genovesi, P., Howald, G.R., Keitt, B.S., Kress, S.W., Miskelly, C.M., Oppel, S., Poncet, S., Rauzon, M.J., Rocamora, G., Russell, J.C., Samaniego-Herrera, A., Seddon, P.J., Spatz, D.R., Towns, D.R. & Croll, D.A. (2016). Invasive mammal eradication on islands results in substantial conservation gains. *Proc. Natl. Acad. Sci. USA* **113**, 4033–4038.

Jones, H.P., Tershy, B.R., Zavaleta, E.S., Croll, D.A., Keitt, B.S., Finkelstein, M.E. & Howald, G.R. (2008). Severity of the effects of invasive rats on seabirds: a global review. *Conserv. Biol.* **22**, 16–26.

Jørgensen, S.E. & Fath, B.D. (2011). *Fundamentals of ecological modelling: application in environmental management and research*. Amsterdam: Elsevier.

Jouventin, P., Bried, J. & Micol, T. (2003). Insular bird populations can be saved from rats: a long-term experimental study of white-chinned petrels Procellaria aequinoctialis on Ile de la Possession (Crozet archipelago). *Polar Biol.* **26**, 371–378.

Kandziora, M., Burkhard, B. & Müller, F. (2013). Interactions of ecosystem properties, ecosystem integrity and ecosystem service indicators: a theoretical matrix exercise. *Ecol. Indic.* **28**, 54–78.

Labocha, M.K. & Hayes, J.P. (2012). Morphometric indices of body condition in birds: a review. *J. Ornithol.* **153**, 1–22.

Lakens, D. (2013). Calculating and reporting effect sizes to facilitate cumulative science: a practical primer for t-tests and ANOVAs. *Front. Psychol.* **4**, 1–12.

Lambert, C., Laran, S., David, L., Dorémus, G., Pettex, E., Van Canneyt, O. & Ridoux, V. (2017). How does ocean seasonality drive habitat preferences of highly mobile top predators? Part I: the north-western Mediterranean Sea. *Deep Res. Part II Top. Stud. Oceanogr.* **141**, 115–132.

Lambert, S., Ezanno, P., Garel, M. & Gilot-Fromont, E. (2018). Demographic stochasticity drives epidemiological patterns in wildlife with implications for diseases and population management. *Sci. Rep.* **8**, 1–14.

Lande, R., Engen, S. & Saether, B.-E. (2003). *Stochastic population dynamics in ecology and conservation*. New York: Oxford University Press.

Lecoq, M. (2003). *Censo das Populações de Aves Marinhas Nidificantes no Arquipélago da Berlenga em 2002: Calonectris diomedea, Phalacrocorax aristotelis e Uria aalge*. Relatório II (Final): Censo da População em 2002.

Lee, J.-S., Filatova, T., Ligmann-Zielinska, A., Hassani-Mahmooei, B., Stonedahl, F., Lorscheid, I., Voinov, A., Polhill, G., Sun, Z. & Parker, D.C. (2015). The complexities of agent-based modeling output analysis. *J. Artif. Soc. Soc. Simul.* **18**, 1–26.

Li, Y., Sun, M., Evans, K.S., Ren, Y. & Chen, Y. (2020). Rethinking marine conservation strategies to minimize socio-economic costs in a dynamic perspective. *Biol. Conserv.* **244**, 108512.

Ligmann-Zielinska, A. (2013). Spatially-explicit sensitivity analysis of an agent-based model of land use change. *Int. J. Geogr. Inf. Sci.* **27**, 1764–1781.

Lilliendahl, K. & Solmundsson, J. (2006). Feeding ecology of sympatric European Shags *Phalacrocorax aristotelis* and great cormorants *P. carbo* in Iceland. *Mar. Biol.* **149**, 979–990.

Lucas, T.C.D. (2020). A translucent box: interpretable machine learning in ecology. *Ecol. Monogr.* 1–17.

Marcella, T.K., Gende, S.M., Roby, D.D. & Allignol, A. (2017). Disturbance of a rare seabird by ship-based tourism in a marine protected area. *PLoS One* **12**, 1–23.

Margalida, A., Colomer, M.À., Oro, D., Arlettaz, R. & Donázar, J.A. (2015). Assessing the impact of removal scenarios on population viability of a threatened, long-lived avian scavenger. *Sci. Rep*. **5**, 16962.

Martín, B., Delgado, S., De la Cruz, A., Tirado, S. & Ferrer, M. (2015). Effects of human presence on the long-term trends of migrant and resident shorebirds: evidence of local population declines. *Anim. Conserv.* **18**, 73–81.

Martin, G.R. & Crawford, R. (2015). Reducing bycatch in gillnets: a sensory ecology perspective. *Glob. Ecol. Conserv.* **3**, 28–50.

Martínez-Abraín, A., Oro, D., Conesa, D. & Jiménez, J. (2008). Compromise between seabird enjoyment and disturbance: the role of observed and observers. *Environ. Conserv.* **35**, 104–108.

Martínez-Abraín, A., Oro, D., Jiménez, J., Martinez-Abrain, A. & Jimenez, J. (2001). The dynamics of a colonization event in the European Shag: the roles of immigration and demographic stochasticity. *Waterbirds* **24**, 97–102.

Martínez-Abraín, A., Velando, A., Oro, D., Genovart, M., Gerique, C., Bartolomé, M.A., Villuendas, E. & Sarzo, B. (2006). Sex-specific mortality of European Shags after the Prestige oil spill: demographic implications for the recovery of colonies. *Mar. Ecol. Prog. Ser.* **318**, 271–276.

Meirinho, A., Barros, N., Oliveira, N., Catry, P., Lecoq, M., Paiva, V., Geraldes, P., Granadeiro, J.P., Ramírez, I. & Andrade, J. (2014). *Atlas das Aves Marinhas de Portugal*. Lisboa: Sociedade Portuguesa Para o Estudo das Aves.

Melvin, E.F., Parrish, J.K. & Conquest, L.L. (1999). Novel tools to reduce seabird bycatch in coastal gillnet fisheries. *Conserv. Biol.* **13**, 1386–1397.

Mendes, A.R. (2013). *Status and conservation of Madeiran Storm-petrel Oceanodroma castro in Farilhão Grande, Berlengas, Portugal: relevance to the management plan of this protected area*.

Mendes, S., Franco, I., Fagundes, I., Oliveira, N., Crisóstomo, P., Morais, L., Afonso, C. & Mouga, T. (2018). The vegetation of Berlengas' island: an attempt to promote the recovery of *Armeria berlenguensis* (Plumbaginaceae). *Front. Mar. Sci.* **5**, 10–13.

Miller, J.A.O., Furness, R.W., Trinder, M. & Matthiopoulos, J. (2019). The sensitivity of seabird populations to density-dependence, environmental stochasticity and anthropogenic mortality. *J. Appl. Ecol.* **56**, 2118–2130.

Monteiro, P.V. (2017). The purse seine fishing of sardine in Portuguese waters: a difficult compromise between fish stock sustainability and fishing effort. *Rev. Fish. Sci. Aquac.* **25**, 218–229.

Moon, K., Guerrero, A.M., Adams, V.M., Biggs, D., Blackman, D.A., Craven, L., Dickinson, H. & Ross, H. (2019). Mental models for conservation research and practice. *Conserv. Lett.* **12**, 1–11.

Morinha, F., Bastos, R., Carvalho, D., Travassos, P., Santos, M., Blanco, G., Bastos, E. & Cabral, J.A. (2017). A spatially-explicit dynamic modelling framework to assess habitat suitability for endangered species: the case of Red-billed Chough under land use change scenarios in Portugal. *Biol. Conserv.* **210**, 96–106.

Morley, C.L. (1982). A simulation study of the powers of three multiple comparison statistics. *Aust. J. Stat.* **24**, 201–210.

Morris, W.F. & Doak, D.F. (2002). *Quantitative conservation biology. Theory and practice of population viability analysis*. Sunderland, Massachusetts: Sinauer Associates, Inc. Publishers.

Morrison, C., Wardle, C. & Castley, J.G. (2016). Repeatability and reproducibility of population viability analysis (PVA) and the implications for threatened species management. *Front. Ecol. Evol.* **4**, 1–7.

Munilla, I., Arcos, J.M., Oro, D., Álvarez, D., Leyenda, P.M. & Velando, A. (2011). Mass mortality of seabirds in the aftermath of the Prestige oil spill. *Ecosphere* **2**, 1–14.

Munilla, I. & Barros, Á. (2019). El cormorán moñudo en Galicia en 2017. In *El cormorán moñudo en la península ibérica. Población Reprod. en 2017 y método censo*: 54–64. del Moral, J.C. & Oliveira, N. (Eds). Madrid: SEO/BirdLife.

Naimi, B. & Voinov, A. (2012). StellaR: a software to translate Stella models into R open-source environment. *Environ. Model. Softw.* **38**, 117–118.

Nascimento, T., Oliveira, N., Fagundes, A.I., Tejada-Baena, C. & Luís, A. (2019). Diet selection of introduced black rats

Rattus rattus L. in relation to plant availability on Berlenga Island. *Portugal. Ecol. Mediterr.* **45**, 15–30.

Naveda-Rodríguez, A., Vargas, F.H., Kohn, S. & Zapata-Ríos, G. (2016). Andean Condor (*Vultur gryphus*) in ecuador: geographic distribution, population size and extinction risk. *PLoS One* **11**, e0151827.

Neto, J. (1997). Contribuiçao para o conhecimento da biologia reprodutiva do Corvo-marinho-de-crista *Phalacrocorax aristotelis* na Reserva Natural da Berlenga. *Airo Port. Soc. Study Birds* **8**, 16–24.

Newell, M., Wanless, S., Harris, M. & Daunt, F. (2015). Effects of an extreme weather event on seabird breeding success at a North Sea colony. *Mar. Ecol. Prog. Ser.* **532**, 257–268.

Oliveira, N. (2019). Resultados generales Portugal. In *El cormorán moñudo en la península ibérica. Población Reprod. en 2017 y método censo*. del Moral, J.C. & Oliveira, N. (Eds). Madrid: SEO/BirdLife.

Oliveira, N., Almeida, A., Alonso, H., Constantino, E., Ferreira, A., Gutiérrez, I., Santos, A., Silva, E. & Andrade, J. (2020). A contribution to reducing bycatch in a high priority area for seabird conservation in Portugal. *Bird Conserv. Int.* 1–20.

Oliveira, N., Almeida, A., Constantino, E., Ferreira, A., Gutiérrez, I., Santos, A., Silva, E. & Andrade, J. (2018). *Avaliação do impacto das pescas sobre aves marinhas na ZPE das Ilhas Berlengas*. Relatório final da Ação C6 do Projeto LIFE Berlengas (relatório não publicado). *Soc. Port. para o Estud. das Aves*.

Oliveira, N., Almeida, A., Santos-Torres, A., Fagundes, I., Rodrigues, P. & Andrade, J. (2016). *Updated Information on the Breeding Status of Berlengas Archipelago Seabirds Updated Information on the Breeding Status of Berlengas Archipelago Seabirds*. Report of the Action A1, Project Life Berlengas.

Oliveira, N., Geraldes, P., Fagundes, P., Oliveira, P. & Andrade, J. (2019). Rat eradication from Berlengas Island. In *Island invasives: scaling up to meet the challenge. Proceedings of the international conference on island invasives 2017*. Veitch, M.N, Martin, A.R., Russell, J.C. & West, C.J. (Eds). Switzerland: IUCN. https://doi.org/10.2305/IUCN.CH.2019.SSC-OP.62.en

Oro, D., Aguilar, J.S., Igual, J.M. & Louzao, M. (2004). Modelling demography and extinction risk in the endangered Balearic shearwater. *Biol. Conserv.* **116**, 93–102.

Oro, D., Álvarez, D. & Velando, A. (2018). Complex demographic heterogeneity from anthropogenic impacts in a coastal marine predator. *Ecol. Appl.* **28**, 612–621.

Orta, J., Garcia, E., Jutglar, F., Kirwan, G.M. & Boesman, P.F.D. (2020). European shag (*Phalacrocorax aristotelis*). In *Birds of the world*. Vol. **8235**. Keeney, B.K. (Ed.). Ithaca: Cornell Lab of Ornithology. https://doi.org/10.2173/bow.eursha1.01.2

Paleczny, M., Hammill, E., Karpouzi, V. & Pauly, D. (2015). Population trend of the World's monitored seabirds, 1950–2010. *PLoS One* **10**, e0129342.

Pereira, A.T. & Oliveira, N. (2019). Censo nacional de galheta, 2017. In *O estado das aves em Port*: 50–52. Alonso, H., Teodósio, J., Andrade, J. & Leitao, D. (Eds). Liboa: Sociedade Portuguesa Para o Estudo das Aves.

Péron, G. (2013). Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. *J. Anim. Ecol.* **82**, 408–417.

Petrescu Bakış, A.-L., Macovei, I., Barros, P., Gomes, C., Carvalho, D., Cabral, J.A., Travassos, P., Torres, L., Aranha, J., Galațchi, L.-D. & Santos, M. (2021). Is biodiversity linked with farm management options in vineyard landscapes? A case study combining ecological indicators within a hybrid modelling framework. *Ecol. Indic.* **121**, 1–12.

Pohlert, P. (2020). *PMCMRplus: Calculate Pairwise Multiple Comparisons of Mean Rank Sums Extended*. R package version 1.4.4.

Potts, G.R. (1969). The influence of eruptive movements, age, population size and other factors on the survival of the Shag (*Phalacrocorax aristotelis* (L.)). *J. Anim. Ecol.* **38**, 53.

Provencher, J.F., Borrelle, S., Sherley, R.B., Avery-Gomm, S., Hodum, P., Bond, A., Major, H.L., McCoy, K.D., Crawford, R., Merkel, F., Votier, S., Reynolds, M., Hatfield, J., Spatz, D. & Mallory, M. (2019). Seabirds. In *World Seas an Environ. Eval*. 2nd edn.: 133–162. Elsevier. https://doi.org/10.1016/B978-0-12-805052-1.00007-3, https://www.sciencedirect.com/book/9780128050521/world-seas-an-environmental-evaluationbook-info

R Development Core Team. (2020). *R: a language and environment for statistical computing*. Viena, Austria: R Found. Stat. Comput.

Ramírez, I., Geraldes, P., Meirinho, A., Amorim, P. & Paiva, V. (2008). *Áreas importantes para as Aves Marinhas em Portugal*. Lisboa: Sociedade Portuguesa Para o Estudo das Aves.

Reşit Akçakaya, H. & Sjögren-Gulve, P. (2000). Population viability analyses in conservation planning: an overview. *Ecol. Bull.* **48**, 9–21.

Rodrigues, N.V., Mendes, S., Franco, J.N., Castanheira, M., Castro, N. & Maranhão, P. (2011). Fish diversity in the Berlengas Natural Reserve (Portugal), a marine protected area. *Rev. Ecol.* **43**, 35–43.

Russell, J.C. & Holmes, N.D. (2015). Tropical island conservation: rat eradication for species recovery. *Biol. Conserv.* **185**, 1–7.

Sæther, B.-E. & Engen, S. (2019). Towards a predictive conservation biology: the devil is in the behaviour. *Philos. Trans. R. Soc. B Biol. Sci.* **374**, 20190013.

Santos, M., Bastos, R. & Cabral, J.A. (2013). Converting conventional ecological datasets in dynamic and dynamic spatially explicit simulations: current advances and future applications of the Stochastic Dynamic Methodology (StDM). *Ecol. Modell.* **258**, 91–100.

Santos, M., Bastos, R., Vicente, J., Berger, U., Filho, S.S., Rodrigues, H., Alonso, J., Guerra, C., Martins, J., Honrado, J. & Cabral, J.A. (2015). Anticipating invasions and managing impacts: a review of recent spatio-temporal modelling approaches. In *Biol. Invasions Aquat. Terr. Syst. Biogeogr. Ecol. Impacts, Predict. Manag*: 389–410. Canning-Clode, J. (Ed.). Warsaw/Berlin: De Gruyter Open Ltd.

Santos, M., Ferreira, D., Bastos, R., Vicente, J., Honrado, J., Kueffer, C., Kull, C.A., Berger, U. & Cabral, J.A. (2016). Linking landscape futures with biodiversity conservation strategies in northwest Iberia — a simulation study combining surrogates with a spatio-temporal modelling approach. *Ecol. Inform.* **33**, 85–100.

Santos, M., Silva, S., Bastos, R., Carvalho, D. & Cabral, J.A. (2018). How good are the ecological assumptions and predictions made in the past? Insights from a dynamic modelling approach applied to changing landscapes. *Ecol. Indic.* **90**, 226–230.

Siddig, A.A.H., Ellison, A.M., Ochs, A., Villar-Leeman, C. & Lau, M.K. (2016). How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. *Ecol. Indic.* **60**, 223–230.

Silva, E. (2015). *Contribuição para o estudo da biologia reprodutora e ecologia de galheta, Phalacrocorax aristotelis*, do arquipélago das Berlengas. Aveiro: Universidade de Aveiro.

Silva, E., Luís, A. & Oliveira, N. (2017). Contribution to the study of the breeding biology of the European Shag (*Phalacrocorax aristotelis*) in Berlengas archipelago, Portugal. *Airo Port. Soc. Study Birds* **24**, 3–16.

Simberloff, D. (1998). Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? *Biol. Conserv.* **83**, 247–257.

Snow, B. (1960). The breeding biology of the Shag *Phalacrocorax aristotelis* on the island of Lundy, Bristol Channel. *The Ibis* **102**, 554–575.

Spelt, A. & Pichegru, L. (2017). Sex allocation and sex-specific parental investment in an endangered seabird. *The Ibis* **159**, 272–284.

Steger, C., Hirsch, S., Cosgrove, C., Inman, S., Nost, E., Shinbrot, X., Thorn, J.P.R., Brown, D.G., Grêt-Regamey, A., Müller, B., Reid, R.S., Tucker, C., Weibel, B. & Klein, J.A. (2021). Linking model design and application for transdisciplinary approaches in social-ecological systems. *Glob. Environ. Change* **66**, 102201.

Sutherland, W. (2006). Predicting the ecological consequences of environmental change: a review of the methods*. *J. Appl. Ecol.* **43**, 599–616.

Sydeman, W.J., Thompson, S.A., Anker-Nilssen, T., Arimitsu, M., Bennison, A., Bertrand, S., Boersch-Supan, P., Boyd, C., Bransome, N.C., Crawford, R.J.M., Daunt, F., Furness, R.W., Gianuca, D., Gladics, A., Koehn, L., Lang, J.W., Logerwell, E., Morris, T.L., Phillips, E.M., Provencher, J., Punt, A.E., Saraux, C., Shannon, L., Sherley, R.B., Simeone, A., Wanless, R.M., Wanless, S. & Zador, S. (2017). Best practices for assessing forage fish fisheries-seabird resource competition. *Fish. Res.* **194**, 209–221.

Tam, J.C., Link, J.S., Rossberg, A.G., Rogers, S.I., Levin, P.S., Rochet, M.J., Bundy, A., Belgrano, A., Libralato, S., Tomczak, M., Van De Wolfshaar, K., Pranovi, F., Gorokhova, E., Large, S.I., Niquil, N., Greenstreet, S.P.R., Druon, J.N., Lesutiene, J., Johansen, M., Preciado, I., Patricio, J., Palialexis, A., Tett, P., Johansen, G.O., Houle, J. & Rindorf, A. (2017). Towards ecosystem-based management: identifying operational food-web indicators for marine ecosystems. *ICES J. Mar. Sci.* **74**, 2040–2052.

Tauleigne, C., Draper, D., Marques, I. & Rosseló-Graell, A. (2004). *Componente Vegetal do Plano de Ordenamento da Reserva Natural das Berlengas: Flora e Vegetação do Arquipélago Das Berlengas*. Lisboa: MNHN-Jardim Botânico.

Torchiano, M. (2020). effsize: efficient effect size computation. R package version 0.8.1. https://CRAN.R-project.org/package=effsize

Trappey, A.J.C., Trappey, C.V., Hsiao, C., Ou, J.J.R. & Chang, C. (2012). System dynamics modelling of product carbon footprint life cycles for collaborative green supply chains. *Int. J. Comput. Integr. Manuf.* **25**, 934–945.

Troisi, G., Barton, S. & Bexton, S. (2016). Impacts of oil spills on seabirds: unsustainable impacts of non-renewable energy. *Int. J. Hydrogen Energy* **41**, 16549–16555.

Tucker, A.M., McGowan, C.P., Mulero Oliveras, E.S., Angeli, N.F. & Zegarra, J.P. (2020). A demographic projection model to support conservation decision making for an endangered snake with limited monitoring data. *Anim. Conserv.* **24**, 1–11.

Velando, A., Barros, Á. & Moran, P. (2015). Heterozygosity-fitness correlations in a declining seabird population. *Mol. Ecol.* **24**, 1007–1018.

Velando, A. & Freire, J. (1999). Intercolony and seasonal differences in the breeding diet of European Shags on the Galician coast (NW Spain). *Mar. Ecol. Prog. Ser.* **188**, 225–236.

Velando, A. & Freire, J. (2002). Population modelling of European Shags (*Phalacrocorax aristotelis*) at their southern limit: conservation implications. *Biol. Conserv.* **107**, 59–69.

Velando, A. & Munilla, I. (2008). *Plan de conservación del cormorán moñudo en el Parque Nacional de las Islas Atlánticas*. Vigo: Departamento de Ecoloxía e Bioloxía Animal, Universidade de Vigo.

Velando, A. & Munilla, I. (2011). Conservación del Cormorán moñudo en el Parque Nacional de las Islas Atlánticas de Galicia. *Boletín GIAM* **35**, 9–18.

Velando, A., Munilla, I. & Leyenda, P.M. (2005). Short-term indirect effects of the "Prestige" oil spill on European Shags: changes in availability of prey. *Mar. Ecol. Prog. Ser.* **302**, 263–274.

Velando, A., Ortega-Ruano, J.E. & Freire, J. (1999). Chick mortality in European Shag Stictocarbo aristotelis related to food-limitations during adverse weather events. *Ardea* **87**, 51–59.

Warwick-Evans, V., Atkinson, P., Robinson, L. & Green, J. (2016). Predictive modelling to identify near-shore, fine-scale seabird distributions during the breeding season. *PLoS One* **11**, 1–17.

Weller, F., Sherley, R.B., Waller, L.J., Ludynia, K., Geldenhuys, D., Shannon, L.J. & Jarre, A. (2016). System dynamics modelling of the Endangered African penguin populations on Dyer and Robben islands, South Africa. *Ecol. Modell.* **327**, 44–56.

White, E.R. (2019). Minimum time required to detect population trends: the need for long-term monitoring programs. *Bioscience* **69**, 26–39.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Stella software conceptual diagrams of the model used to predict Shag dynamics in the Berlengas SPA.

Appendix S2. Mathematical equations associated with the model used to predict Shag dynamics in the Berlengas SPA.

Appendix S3. Details and explanation of the dynamic model used to predict Shag population dynamics in the Berlengas SPA.

Appendix S4. Additional information on the biology and ecology of European Shag (*Gulosus aristotelis*).

Appendix S5. Effect size comparison results (Cohen's *d*), generalized linear model (GLzM), post-hoc comparisons for pairwise of all scenarios, one-parameter-at-a-time technique (OAT) sensitivity analysis and global sensitivity analysis.

Appendix S6. Highlights and graphical abstract of the main results.

Appendix S7. Effect of fixed sandeels' abundance in the European Shag *Gulosus aristotelis* population estimates.