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

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ARTICLE INFO

Key words: Agent-based models Aquila fasciata Electrocution Population dynamics Power lines

ABSTRACT

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

1. Introduction

Wildlife is increasingly affected by mortality from multiple anthropogenic sources (Hill et al., 2020; Loss et al., 2015), including legal harvesting (e.g., overfishing; Hill et al., 2019), direct persecution (Inskip and Zimmermann, 2009; Madden et al., 2019), bycatch (Hall et al.,

2000) and interactions with infrastructures (Bernardino et al., 2018; Forman and Alexander, 1998; Marques et al., 2014). Such mortality may have far-reaching consequences on population dynamics, potentially leading to local extinctions (Diffendorfer et al., 2021; Grilo et al., 2021). In particular, long-lived top predators should be highly vulnerable to additional mortality, due to their relatively low intrinsic population

https://doi.org/10.1016/j.ecolmodel.2024.110752

Received 12 January 2024; Received in revised form 20 April 2024; Accepted 6 May 2024 Available online 21 May 2024

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growth rates, large home ranges, small population sizes, and low carrying capacity (Ripple et al., 2014). Therefore, a detailed understanding is needed on how additional mortality can affect the population dynamics of these species, providing information to design cost-effective strategies for avoiding and mitigating impacts (Chevallier et al., 2015; Loveridge et al., 2017).

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

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

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

2. Material and methods

2.1. Model species

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

Our study focused on the Bonelli's eagle population of southern Portugal (south of the Tagus River), which has been steadily increasing in numbers and expanding in range since the early 1990s, from 33 up to over a hundred breeding pairs at present (Dias et al., 2017; Palma et al., 2013). Breeding pairs typically establish home ranges with a mean of 141.6 \pm 71.1 km² (Marques et al., 2022). Data collected from this population over a 20-year period allowed to estimate its demographic parameters and revealed that it acts as a source within the Western European metapopulation, comprising Portugal, Spain and France (Hernández-Matías et al., 2013).

2.2. Model description

We implemented an Individual-Based Modelling (IBM) framework

using NetLogo (Tisue and Wilensky, 2004; Wilensky, 1999) to estimate the impacts of anthropogenic mortality on Bonelli's eagle populations. A complete, detailed model description, following the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2020, 2010, 2006) is presented in the Appendix A. The code is available here: https://github. com/TCrispimMendes/IBM Anthropogenic Mortality on Territorial Predators

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

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

The model included three entities, characterised by the state variables listed in Table 1: Patches (grid cells) representing spatial units used by Bonelli's eagles (i.e., territories for breeding birds), Birds (agents) representing individual Bonelli's eagles, and the Global Environment (i. e., Observer in NetLogo), the only entity at the system level, which controlled the submodels and the probabilities of additional mortality, while also keeping track of simulated time. The model spatial extent simulated the geographical context of the population, including 131 Patches potentially used by breeding pairs (type "A" Patches), and another 50 Patches that can only be used by non-territorial individuals

Table 1

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

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

(type "B" Patches). As we lack detailed empirical data about the range and settlement areas and the size of home ranges used by the nonterritorial birds of the Bonelli's' eagle population in southern Portugal, we chose a number of patches of type "B" that was sufficient to accommodate the non-breeding birds predicted for a population of 131 pairs with a stable age distribution (the defined carrying capacity in the model). This calculation was conducted assuming a delay in recruitment as a density-dependant mechanism, which occurs when the carrying capacity of patches occupiable by territorial individuals (type "A") is reached. In this scenario, we assumed that recruitment only takes place in the 4th year of life, rather than being able to occur in the 2nd and 3rd years. In this case, considering the basal recruitment probability of 0.93 for individuals aged 4 years, for a population of 262 territorial individuals (131 pairs) with a stable age distribution, it is anticipated that there will be 236 non-territorial individuals. Given our model's carrying capacity of 5 non-territorial individuals per Patch, this suggests the need for at least 48 type "B" Patches to accommodate all non-territorial individuals. Additionally, considering the potential reduction in recruitment probability for individuals aged 4, we chose to conservatively include 50 "B" Patches in the model to ensure adequate space for the maximum expected population when the carrying capacity of "A" Patches is reached.

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

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

2.3. Key assumptions and model parametrization

We specified an IBM framework considering a generalisation of the spatial and social structures of the Bonelli's eagle, which is akin of that of many other territorial birds of prey. First, we considered a study area divided according to a regular grid of Patches, some of which can be occupied by a breeding pair or, transitorily, by a single territorial adult. This assumption implies that all territories are geometrically equivalent, though real home ranges vary widely in shape and size. This simplification is reasonable because our model does not require Birds to interact with environmental features within their home-ranges, e.g., to forage or nest. Second, although we assumed that all Patches have the same size and shape, we considered that habitat conditions of the Patches can be of either type "A" or "B", according to whether they are suitable or not for setting breeding territories. Specifically, we assumed that only type "A" Patches can be used by breeding individuals, while both type "A" Patches unoccupied by breeders and type "B" Patches can be used by up

to a maximum of five non-territorial individuals. This assumption was taken to mimic the spatial organisation of territorial versus nonterritorial individuals in real populations, where the later tend to occupy areas less suitable to the former (Newton, 1992). It ignores however other sources of variation in habitat quality potentially affecting population viability, which were incorporated implicitly by specifying random variation in the values of demographic parameters across territories. Third, Patches occupied by territorial pairs can only house the members of the couple and their annual offspring, thus mirroring the behaviour of territorial birds. We assumed that territorial individuals reproduce and stay within the same Patch until dying. We believe this assumption is warranted, because there are few reported instances of breeders shifting across territories or losing their territorial status (Martínez-Miranzo et al., 2016).

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

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

Following Hernández-Matías et al. (2013), we specified a life-cycle structure with five age classes (Fig. 1), with the demographic parameters of individuals determined by age class membership. Briefly, each year breeding females produce fledglings according to age-class specific

fecundity rates, and each member of the breeding pair survives to the next year according to age-class specific survival rates. Fledglings are integrated into the non-territorial fraction of the population, staying there until dying or recruiting to the territorial breeding population according to age-class specific survival and recruitment rates. We limited the breeding population to a total of 131 pairs (i.e., carrying capacity), corresponding to 110 % of the breeding population of southern Portugal in 2019, which was considered close to saturation (Dias et al., 2017). The model parameters were assigned based on empirical data from our focal population or, when not available, they were inferred from other Western Europe populations (Table 2).

To model the effects of electrocution on the population dynamics, we

Table 2

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

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



Fig. 1. Structure of the Bonelli's eagle life cycle. The solid arrows represent the transitions between age classes and territorial state, while the dashed arrows represent productivity, based on fertility values. S represents the survival rates of individuals during their first (S1), second and third (S23), fourth (S4), and fifth and subsequent (adult) years of life (SA). AMNT and AMT represent the exposure to additional mortality for non-territorial and territorial individuals, respectively. R represents the propensity to become territorial in immature birds (R2), subadults (R3), first-year adults (R4), and adults (RA). F represents fertilities for any given age class (F2, F3, and FA being fertility of two- and three-year olds and adults, respectively).

considered exposure to additional mortality by reducing the baseline survival rate by a given probability, which varied across simulated scenarios (see Section 2.4 for details). The additional mortality affects the overall probability of mortality according to the formula:

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

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

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

2.4. Model validation and simulation experiments

The sensitivity analysis was performed by estimating the impact on annual population growth rates of varying the input parameters (initial population size, number of patches of types "A" and "B", recruitment, survival and fertility) between 10 % above and below their default value following a randomised one-factor-at-a-time design (Campolongo et al., 2007; Morris, 1991). The analysis used the Morris screening method because of its low computational effort requirements (Morris, 1991). For each parameter, the method evaluates its relative importance, linear and additive or nonlinear effect, and interactions with other parameters (Campolongo et al., 2007; Morris, 1991; Thiele et al., 2014). Specifically, for each parameter we estimated: (i) μ - the overall influence; and (ii) σ - the standard deviation of the elementary effects, as an estimate of non-linear and/or interaction effects. The number of tested settings is determined by the formula $r \times (K + 1)$, where *r* represents the number of elementary effects or trajectories computed per parameter (K). With our selection of 1000 trajectories, this resulted in $1000 \times (7 + 1) = 8000$ runs. These runs were conducted with four different random seeds, totalling 32,000 simulations.

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

We ran a set of experiments simulating the effects of exposure to additional mortality on: (i) only territorial birds; (ii) only non-territorial birds; or (iii) both classes. While scenarios where both territorial classes were affected are most likely in a wild population, analysing each class separately may provide deeper insights into the population impacts of additional mortality within each class. In each case, we simulated additional mortality affecting 0 % (used as a reference value), 25 %, 50 % or 75 % of the Patches. Also, we varied the probability of additional mortality within each from 0 to 100 %, with intervals of 10 %. Models were run for 50 time-steps (50 years) and each experiment was completed with 1000-replicates. We used declines in annual population growth rate, number of pairs and the number of years of population persistence (i.e., number of years that the population persisted until its eventual extinction) as a proxy for negative impacts resulting from exposure to additional mortality.

3. Results

3.1. Sensitivity analysis and model validation

According to the Morris screening method, the population is most sensitive to variation in adult survival (SA), which showed much higher μ and μ^* values than the other parameters (Fig. 2). However, the high value of σ suggests that some of the other demographic parameters also have a relevant role in the population dynamics. Survival rate from juveniles and immatures (S23) is the second most influential parameter, followed by fledgling survival (S1). The initial population size and the number of available Patches (both types) exhibit a limited but nonmonotonic influence, indicating a degree of dependence on other model parameters.

Regarding the model validation, the baseline scenario (comprising 131 type "A" and 50 type "B" Patches) provided a reasonable approximation to the number of Bonelli's eagle breeding pairs observed in southern Portugal between 1991 and 2019 (Fig. 3). Regarding the scenarios with a 10 % variation in the number of patches (Fig. 3), we found that the population increase is consistent irrespective of the scenario simulated, with variations only occurring close to the carrying capacity. We also tested a fourth scenario, changing the number of type "B" Patches from 50 (baseline scenario) to 100 (Fig. B.1). The population growth curve was similar in both scenarios, suggesting that the sensitivity of the model to this parameter was low.

3.2. Impacts of exposure to additional mortality

The impacts of exposure to additional mortality on populational parameters varied widely depending on whether it affected territorial or non-territorial birds, or both (Fig. 4).

When additional mortality affects only territorial birds, the population growth rate decreases with an increasing proportion of Patches affected, with the population declining (λ) for > 50 % of Patches affected and the additional mortality probability > 0.20 (Fig. 4a). Surprisingly, while population growth rate decreased with increasing additional mortality probability up to about 0.20, it levelled off or very slightly increased thereafter (Fig. 4a). Exposure to additional mortality impacted in the number of the breeding pairs, irrespective of the number of affected Patches, though the population size remained constant when the probability of additional mortality was > 0.20 (Fig.4b). During the 50-year simulation, population extinction occurred only when 75 % of the territories were exposed to additional mortality (Fig. 4c). Unexpectedly, the mean annual survival rate of the territorial birds remained constant with increasing probability of additional mortality (Fig. B.2a), while the proportion of territorial birds dying in Patches exposed to additional mortality decreased (Fig. B.2b). Such results reflect the fact that the Patches tend to become vacant with increasing both the exposure to and the probability of additional mortality (Fig. B.2c).

When additional mortality affects only non-territorial birds, population growth rate also decreased strongly with both increasing proportion of Patches affected and increasing exposure to additional mortality, though remaining with $\lambda > 1$ up to about 25 % of Patches affected and additional mortality probability up to about 0.70 (Fig. 4a). In comparison with territorial birds only, population impacts (growth rate; Fig. 4a, population size; Fig. 4b) of exposure to additional mortality of non-territorials were slightly lower for low probabilities of additional mortality (< 0.20), but higher for higher mortality probabilities. Additionally, population extinction occurred across a broader range of mortality thresholds (Fig. 4c). Also, as expected, the mean annual survival of non-territorial birds was lower than that of territorial birds (Fig. B.2a), and the proportion of non-territorial birds dying in Patches exposed to additional mortality increased with increasing exposure and probability of additional mortality, being higher than the one resulting from the simulations that assumed effects on territorial birds only (Fig. B.2b).



Fig. 2. Results of the sensitivity analysis, using the Morris screening method. μ and μ^* are indicators of the overall influence of the parameter on the annual population growth rate, but when μ^* is high and μ is low, it indicates that there is a non-monotonic effect on the output; σ is an indicator of dependency of the other input factors (Thiele et al., 2014). NI represents the number of the breeding pairs of the initial population. NPA and NPB represent the number of available type "A" and type "B" Patches, respectively. S represents the survival rates of individuals during their first (S1), second and third (S23), fourth (S4), and fifth and subsequent (adult) years of life (SA). F represents fertilities for any given age class (F2, F3, and FA being fertility of two- and three-year olds and adults, respectively).



Fig. 3. Estimated growth of the Bonelli's eagle population of southern Portugal during a 50-year period, considering three scenarios for the number of Patches (type "A" and "B") available in the study area: the baseline, used in further analyses, consists of 131 "A" Patches and 50 "B" Patches, while two other scenarios include a 10 % variation in the number of available Patches. The lines and shadowed areas represent the mean number of breeding pairs and the standard deviation. The black diamonds represent the empirical value for the number of breeding pairs in 1991 and 2019 (28 years apart).



Fig. 4. Impact of exposure to additional mortality in 25 %, 50 % and 75 % of the Patches on the a) annual growth rate ($\lambda = 1$ represents the population trend threshold: if $\lambda > 1$ the population increases and if $\lambda < 1$ the population declines), b) number of breeding pairs in year 50 and c) number of years of population persistence (number of years that the population persisted until eventual its extinction), when affecting territorial, non-territorial and both territorial and non-territorial birds. Additional mortality values represent a percentage increase in the mortality probability. Lines are mean values and the shadowed areas represent the 95 % confident-interval.

Overall, the strongest impacts of exposure to additional mortality were observed when both territorial and non-territorial birds were affected, with the population declining (λ < 1) even for relatively small proportion of Patches affected and low probability of exposure to additional mortality (Fig. 4a). Steep population declines (λ < 0.9) and quick population extinction (Fig. 4b and c) were predicted when the proportion of Patches affected was > 75 % and exposure to additional mortality probability > 0.20, with the population declining (both in terms of number of territorial and non-territorial birds) mainly in the first 10-years of the simulation period in these scenarios (Fig. B.3). When additional mortality affects the entire population, the patterns of annual survival for both territorial and non-territorial birds, as well as the proportion of deaths occurring in patches exposed to additional mortality (Fig. 5), are similar to those observed when each territorial class is affected individually (Fig. B.2).

When analysing the probability of dispersion and recruitment into patches exposed to additional mortality affecting the entire population, it is possible to observe that patches with additional mortality attract a higher number of dispering birds, particularly when mortality affects 25 % or 50 % of the patches (Fig. 6). Additionally, low levels of mortality (25 % of patches exposed to a probability of 0.10 additional mortality) are also responsible for higher recruitment than expected into these patches (Fig. 6).

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

4. Discussion

Our study provides a framework based on an Individual-Based Model (IBM) specifically designed to evaluate the impacts of exposure to additional anthropogenic mortality on populations of territorial species. The application of the framework to a specific case study focusing on Bonelli's eagles in Southern Portugal, clearly illustrated the importance



Fig. 5. Impact of exposure to additional mortality in 25 %, 50 % and 75 % of the Patches on the a) mean annual survival of territorial of territorial and non-territorial birds, b) proportion of deaths in Patches exposed to additional mortality during the 50-year simulation, and c) proportion of individuals in Patches exposed to additional mortality at the end of the 50-year simulation period, when affecting both territorial and non-territorial birds. Additional mortality values represent a percentage increase in the mortality probability. Lines are mean values and the shadowed areas represent the 95 % confident-interval.

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

4.1. Consequences of anthropogenic mortality on a Bonelli's eagle population

The results suggest that our IBM provided a reasonable approximation to the dynamics of the focal Bonelli's eagle populations, thereby supporting the inferences drawn from the model. In particular, we found that the model was able to replicate the increase of the Bonelli's eagle population in southern Portugal over a 28-year period. This was accomplished even when considering different scenarios of available patches, a parameter for which less precise empirical data were available (Fig. 3 and Fig. B1). Such results suggest that our model achieved its intended purpose of simulating the population dynamics of this population.

In line with previous studies, the sensitivity analysis of our model clearly identified adult survival (broadly corresponding to territorial birds) as a key parameter for this population, as previously described for the Bonelli's eagle (Hernández-Matías et al., 2013). Overall, this result



Fig. 6. Impact of exposure to additional mortality in 25 %, 50 % and 75 % of the Patches on the: (i) probability of dispersal (proportion of juvenile Birds dispersing) and (ii) probability of recruitment (proportion of non-territorial birds recruiting) into Patches exposed to additional mortality over the 50-year simulation period, when affecting both territorial and non-territorial birds. Additional mortality values represent a percentage increase in the mortality probability. Lines are mean values and the shadowed areas represent the 95 % confident-interval.

agrees with the widely accepted idea that population growth rate of long-lived vertebrate species with delayed maturity and reduced fertility, such as large raptors, is most sensitive to changes in breeding adult survival rate (Sæther and Bakke, 2000; Tack et al., 2017). Still, survival rates for other age classes were also relevant to the population trend, especially if compared with other demographic parameters as adult fertility. This confirms the high relevance of the non-breeding component of animal populations for their overall dynamics and persistence, as previously identified by other studies (reviewed by Penteriani et al., 2011).

Given the sensitivity of the population dynamics to adult survival, the strong impact of additional mortality on the non-territorial fraction of the population might seem surprising. While our simulations aligned with expectations by showing the greatest impacts when both territorial and non-territorial individuals faced additional mortality, it also produced a counterintuitive result showing that impacts were higher when only non-territorial individuals, as opposed to territorial individuals, were exposed to additional mortality risk. This is probably a consequence of territorial behaviour, because exposure to additional mortality risk within territories affects at most the annual survival probability of the two breeding adults. In contrast, the same level of exposure to additional mortality risk may affect multiple non-territorial individuals using each Patch. This idea aligns with empirical data indicating that mortality due to electrocution disproportionately affects juveniles and immatures rather than adults in the Bonelli's eagle (Hernández-Matías et al., 2015; Sousa, 2017) and other birds of prey (Hunt et al., 2017; Mojica et al., 2018). From a population demography perspective, this implies that for a given level of exposure to a mortality risk source, the effective decline in the population survival rate is greater when it affects non-territorial individuals compared to territorial individuals (as confirmed by our simulations; Fig. 5a), because more non-territorial than territorial individuals tend to be exposed to the risk.

Different exposures to the same mortality risk likely influenced the key role revealed by our simulations on the importance of non-territorial birds (i.e., non-breeders) to sustain this population under anthropogenic mortality risks. First, the population starts to decline (λ < 1) with intermediate or high levels of exposure of non-territorial individuals to additional mortality. This result suggests that such exposure compromises the pool of non-territorial individuals within the population, i.e., there is a shortage of non-territorial individuals to recruit into established territories whenever there is a vacancy, and thereby leading to population decline. Second, the availability of a large pool of non-territorial individuals is the responsible for the persistence of the population (λ > 1) when intermediate or large levels of exposure to additional mortality affects a small fraction (25 %) of the breeding

territories, as the pool of non-territorial birds are rapidly recruited to the affected territories, buffering the impact of mortality. This is confirmed by the simulations of cumulatively impacting 25 % of the area used by both territorial classes, showing that the population can only buffer (λ > 1) relatively small additional mortality probabilities (0.10). Conversely, when only 25 % of the breeding territories were affected, the population still exhibited increasing trends, even with a 0.90 additional mortality probability, if the non-territorial class was not affected.

The mechanisms linked to territorial behaviour also explain the unforeseen similarity in populational outputs when the same fraction of territories is affected by intermediate and high mortality probabilities (> 0.20), as evidenced by horizontal curves in both the annual growth rate (Fig. 4a) and the number of breeding pairs (Fig. 4b). In fact, in territories with higher mortality risk, there is an increased likelihood that both members of the breeding pair will die in the same year, leading to the vacancy of the territory. Conversely, in areas with low to intermediate exposure to mortality risk, it is more likely that only one member of the breeding pair will die in a given year, with the surviving member remaining in the territory and attracting a new member (Fig. 6).

In the long run, a larger number of birds are likely to die at territories with low to intermediate mortality risk when compared to territories with higher mortality (Fig. 5b and Fig. 6). Such lower to intermediate mortality values thus appear to function as an ecological trap, constantly attracting non-territorial birds to recruit into these territories. However, over time, territories with intermediate and high mortality levels tend to become vacant of territorial birds, a phenomenon predicted by our simulations and supported by empirical data from populations of this species (Carrete et al., 2002). In this scenario, non-territorial birds are attracted to disperse into these patches exposed to additional mortality and vacated by territorial birds, which also appear to function as an ecological trap (Fig. 6).

4.2. Importance of explicitly modelling territorial behaviour processes

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

Despite these advancements, territoriality remains poorly addressed

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

4.3. Model generalization

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

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

Further enhancements to the IBM could encompass the integration of new submodels simulating ecological processes such as movement patterns, migration (both inbound and outbound), and interactions with other species. Currently, the IBM only considers birds to be exposed to additional mortality in their settlement areas (Patches to where Birds dispersed) and breeding territories (Patches to where Birds recruited), without accounting for risks during the movements between these areas. Exposure to risks may be particularly significant during the dispersal

period, when individuals typically use multiple settlement areas and large movements across them are expected (Balbontín and Ferrer, 2009; Real and Mañosa, 2001). Therefore, a submodel addressing movements trajectories (both dispersal and migratory movements) across the study area could be developed within a spatially explicit framework, providing insights into individual movements and identifying locations with heightened threats and risks. This approach could be useful to, for instance, identify critical mortality hotspots for long-lived territorial species, and prioritize areas for mitigation (Barbosa et al., 2020). Another enhancement to the IBM model would involve further developing the migration process, specifically by incorporating the flow of individuals to and from the modelled population, as individual exchanges across populations are expected in many territorial species. The model developed in this study only accounts for emigration when all available patches are fully occupied, and immigration has not been implemented. Finally, potential future upgrades might involve considering interactions with other species to address intra-specific competition. This ecological dynamic could restrict the population growth of a territorial species, and was not implemented in the model.

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

4.4. Recommendations for minimizing bird electrocutions at power lines

As highlighted in our study (Fig. 2; see Section 4.1), electrocutions at power lines have a negative and direct impact on the studied population survival rate, which is the most important demographic parameter in raptors population dynamics (Tack et al., 2017). Electrocutions are a source of significant mortality in many raptor populations (González et al., 2007; Martínez et al., 2016; Mojica et al., 2018; Real et al., 2001), thus reducing such mortality may be the most far-reaching conservation measure (Hernández-Matías et al., 2015). This might be achieved by retrofitting distribution lines, through the insulation of conductors or burying the lines, measures that have been implemented worldwide, successfully reducing the electrocution risk for several raptor species (Chevallier et al., 2015; Dixon et al., 2018; López-López et al., 2011).

The fact that intermediate or high mortality rates within the same territories have the same impact on the population growth rate and population size (Fig. 4a and b) and that territories with intermediate and high mortality risk tend to become vacant (Fig. 5c), suggests that each breeding territory should be considered as a mitigation unit, where all pylons posing electrocution risk should be intervened whenever mitigation actions are put in place.

Our results highlight the importance of taking into consideration all individuals' life stages in a population, juveniles, floaters and breeding birds, i.e., both breeding and pre-adult settlement areas, when planning the mitigating of electrocutions. Conservation practices traditionally favour breeding home ranges, and management actions aiming at reducing mortality rates of the non-territorial component of populations are frequently relegated to a secondary role (Penteriani et al., 2011). Our IBM simulations show that this may be an ineffective strategy, as additional sources of mortality, either affecting the territorial or the non-territorial fractions of the population, always have important population impacts (Fig. 4). In reality, our study highlights the key role of non-territorial individuals in sustaining populations of territorial species facing anthropogenic mortality sources, strongly suggesting that conservation and land planning strategies should account this fraction of the population.

Funding

Work co-funded by the project NORTE-01-0246-FEDER-000063, supported by Norte Portugal Regional Operational Programme (NORTE2020), under the Portugal 2020 Partnership Agreement, through the European Regional Development Fund (ERDF); and by FCT/

R&D structural funds to MED (https://doi.org/10.54499/UIDB/05183/ 2020; https://doi.org/10.54499/UIDP/05183/2020) and CHANGE (https://doi.org/10.54499/LA/P/0121/2020). PB and ATM were funded by the EDP Biodiversity Chair. TCM was funded by FCT doctoral grant SFRH/BD/145156/2019 (https://doi.org/10.54499/SFRH/BD/ 145156/2019). FM was funded by the REN Biodiversity chair and FCT (IF/01053/2015). LP was supported by InBIO Programático FUI 2020-2023, Ref.^a UIDP/50027/2020 from FCT. RP was supported by the FCT research contract 2022.02878.CEECIND.

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Ana Teresa Marques: Writing – original draft, Methodology, Formal analysis, Conceptualization. Tiago Crispim-Mendes: Writing – original draft, Software, Methodology, Formal analysis, Conceptualization. Luís Palma: Writing – review & editing, Methodology. Ricardo Pita: Writing – review & editing, Methodology. Francisco Moreira: Methodology, Conceptualization, Writing – review & editing. Pedro Beja: Conceptualization, Methodology, Writing – original draft.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ana Teresa Margues reports financial support was provided by Commission of the Coordination and Regional Development of the North. Ana Teresa Marques reports financial support was provided by EDP Biodiversity Chair. Pedro Beja reports financial support was provided by EDP Biodiversity Chair. Francisco Moreira reports financial support was provided by REN Biodiversity Chair. Tiago Crispim-Mendes reports financial support was provided by Fundação para a Ciência e Tecnologia - FCT. Francisco Moreira reports financial support was provided by Fundação para a Ciência e Tecnologia - FCT. Luis Palma reports financial support was provided by Fundação para a Ciência e Tecnologia - FCT. Ricardo Pita reports financial support was provided by Fundação para a Ciência e Tecnologia - FCT. Pedro Beja reports a relationship with EDP Biodiversity Chair that includes: funding grants. Francisco Moreira reports a relationship with REN Biodiversity Chair that includes: funding grants. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The code for our IBM model is available at: https://github .com/TCrispimMendes/IBM_Anthropogenic_Mortality_on_Territorial_ Predators.

Acknowledgements

We are grateful to Nuno Queiroz, Marisa Vedor and Ivo Costa for providing assistance and a server to run the models.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2024.110752.

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