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Incorporating spatial structure and stochasticity in endangered Bonelli's eagle's population models: Implications for conservation and management

Alvaro Soutullo[a], *Pascual López-López*[a,b,*], *Vicente Urios*[a]

[a]*Estación Biológica Terra Natura, CIBIO – Fundación Terra Natura, Universidad de Alicante, Apdo. 99 E, 03080 Alicante, Spain*
[b]*Cavanilles Institute of Biodiversity and Evolutionary Biology, Terrestrial Vertebrates Group, University of Valencia, Polígono de la Coma s/n, 46980 Paterna, Valencia, Spain*

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ABSTRACT

Population models have played a chief role informing management decisions for the endangered Bonelli's eagle (*Aquila fasciata*) in Spain. In this paper, we incorporate spatial structure and stochasticity in the construction of individual-based metapopulation models, and use these models to explore the effects of possible management actions on the persistence of the species in Spain. To build the models we used data on seven sub-populations that have experienced different trends in the last decades, and we introduced new estimates of pre-adult survival rate. The elasticity analysis of our models showed that when the interchange of individuals among sub-populations is taken into account, pre-adult mortality plays the key role in determining the overall population trend. This is in contrast to what it has been suggested by previous demographic models that modelled local populations as isolated. Specifically, a 20% decrease in pre-adult mortality during the first two years of life was enough for the stabilization of the metapopulation (i.e., $\lambda \geqslant 1.0$). However, neither a similar decrease in the values of adult mortality, nor an increase in the percentage of breeders, modified the declining trend of our model metapopulation. This reinforces the idea that to ensure the long-term persistence of the species in Spain, management actions should aim at minimizing pre-adult mortality. These include locating and protecting the areas used by juvenile Bonelli's eagles (e.g., temporary settlements), minimizing the risk of electrocution in power lines, and preventing human persecution.

1. Introduction

During the last decades there has been an increasing awareness of the roles of space and environmental and demographic stochasticity in populations' dynamics (e.g., Tilman and Kareiva, 1997; Hanski, 1999; Lande et al., 2003), with computer simulations playing a key role in the analysis of the effects of those factors on populations' trajectories (Lindenmayer et al., 1995; Hanski, 1999). For stage-structured populations an alternative to simulations for projecting population trajectories is the use of matrix population models (e.g., Caswell, 2001). These matrix population models have been influential in the derivation of management recommendations for many endangered species (e.g., Crouse et al., 1987;

* *Corresponding author:* Address: Estación Biológica Terra Natura, CIBIO – Fundación Terra Natura, Universidad de Alicante, Apdo. 99 E, 03080 Alicante, Spain. Tel.: +34 965903400x3202; fax: +34 965903815.
E-mail addresses: Pascual.Lopez@uv.es, lopez.pascual@gmail.com (P. López-López).
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Ferrer and Calderón, 1990; Ferrer and Hiraldo, 1991; Hiraldo et al., 1996; Hitchcock and Gratto-Trevor, 1997; see Caswell, 2001 and references therein). In Spain, population models have played a chief role informing management decisions for the endangered Bonelli's eagle (*Aquila fasciata*) (Real and Mañosa, 1997; Carrete et al., 2002).

Bonelli's eagles are distributed from the European Mediterranean region to south-east Asia (Cramp and Simmons, 1980; Ferguson-Lees and Christie, 2001). The Iberian Peninsula holds approximately 80% of the European breeding pairs (Del Moral, 2006) and yet the species is currently considered as Endangered in Spain (Real, 2004). After a period of decline in the mid-1980s in the Iberian Peninsula (Real and Mañosa, 1997; Real, 2004), it seems to have recovered, although its current status is object of debate (Del Moral, 2006; Cadahía et al., 2008). The Iberian population shows different trends in different parts of the Peninsula. Whereas sub-populations located in the southern and eastern regions seem to be increasing or stable, sub-populations from the central plateau, north-eastern Portugal and northern Spain seem to be decreasing (Balbontín et al., 2003; Real, 2004; pers. obs). There are also differences in the main causes of mortality among regions and age classes. Thus, whereas non-breeding individuals mostly die because of electrocution, adults are mainly the victims of persecution (Real et al., 2001). These differences are associated with differences in the spatial distribution of age classes: persecution is the main cause of death in breeding areas and electrocution in non-breeding areas (Real et al., 2001).

Despite Bonelli's eagles perform large movements during their juvenile dispersal (Balbontín, 2005; Cadahía et al., 2005; Cadahía, 2007), previous demographic models have been based on the unrealistic assumption that sub-populations are isolated, considering no movements of juveniles among them. This is clearly not the case, with a source-sink metapopulation dynamics being a more appropriate description of the dynamics of the species in the Iberian Peninsula (Muñoz et al., 2005). Here, we incorporate spatial structure and stochasticity in the construction of individual-based metapopulation models (as opposed to a fragmented population framework with no connectivity among sub-populations) and use these models to explore the effects of possible management actions on the persistence of the species in Spain.

2. Methods

We used the Vortex simulations software (Lacy, 1993, 2000; Lacy et al., 2005) to develop models of the population dynamics of Bonelli's eagles in Spain that incorporate the effects of spatial structure, and both environmental and demographic stochasticity. Vortex is an individual-based simulation model for population viability analysis (Lacy, 1993, 2000; Miller and Lacy, 2005). It models population dynamics as discrete, sequential events that occur according to probabilities defined by the user. Populations are modelled using constants or random demographic variables that follow specified distributions (actually, once the demographic parameters to be used for the simulations are introduced in Vortex, it also builds a deterministic matrix model of the population). Vortex was originally written to model mammalian and avian populations. The events used for modelling describe the typical life cycle of sexually reproducing, diploid organisms, and it is particularly suitable for species and populations like the one we model here: low fecundity, long lifespan, local populations size less than 500 individuals, less than 20 local populations, estimable age-specific fecundity and survival rates, and monogamous breeding (Lacy, 1993, 2000; Miller and Lacy, 2005).

To explore the role of spatial structure on the dynamics of the population of Bonelli's eagles in Spain we used data on seven sub-populations (defined on the basis of administrative boundaries): Murcia, Toledo, Castellón, Burgos, Navarra, Cádiz and Granada (Fig. 1). Although these do not encompass the whole Iberian population they are representative of the different local trends experienced by the Spanish population in the last decades. We first used demographic parameters from the bibliography (Tables 1 and 2) to create a deterministic matrix population model for each sub-population. Because available estimates on pre-adult mortality are scarce and highly inaccurate, we improved the model using our own data on the mortality of 15 juvenile eagles tracked by satellite telemetry during their juvenile dispersal (Cadahía et al., 2005, 2007). We assumed that birds were dead when signal reception was terminated. This is actually an overestimate of mortality rate, as not all birds were confirmed dead. For computational purposes, the mortality after the 2nd year of dispersal was set as the mean (±SD) adult mortality calculated for the seven sub-populations (see Tables 1 and 2), as for the birds that we were still tracking after the 2nd year of study, signal reception continued for the rest of the juvenile dispersal. Due to the scarcity of available data, heterogeneity in pre-adult survival rate was not incorporated in the models.

To assess the effect on populations' persistence of different levels of connectivity among the local populations we modelled four different scenarios: (a) seven isolated populations, (b) a metapopulation where dispersers have the same probability (14.29%) of settling in any of the seven local populations, (c) a metapopulation where dispersers cannot remain in their natal population but have equal probability (16.67%) of dispersing to any of the other six local populations, and (d) a metapopulation where dispersers cannot remain in their natal population and the probability (ranging from 9% to 36%) of dispersing to any of the other six populations is inversely proportional to the distance from the natal population. Distance among all local populations was calculated as the distance among the centroids of the region encompassing each local population.

We introduced stochasticity in these models by simulating 50-years population trajectories under the four spatial scenarios described (taking 1994 as the fist year of the simulations). A total of 500 simulations were run for each scenario. Simulations were conducted using both our own data on pre-adult mortality, and those from the literature (i.e., 22% for the first year and 59% for the remaining three, assuming for simplicity that for the whole first year survival rate is as high as pre-dispersal survival rate; see Table 1). The effects of environmental variability in survival and reproduction were modelled as non-correlated. The potential effects of inbreeding depression, density-dependent reproduction, catastrophes, harvesting, supplementation, and genetic management (Lacy, 1993,