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

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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;

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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., in press). 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 (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,

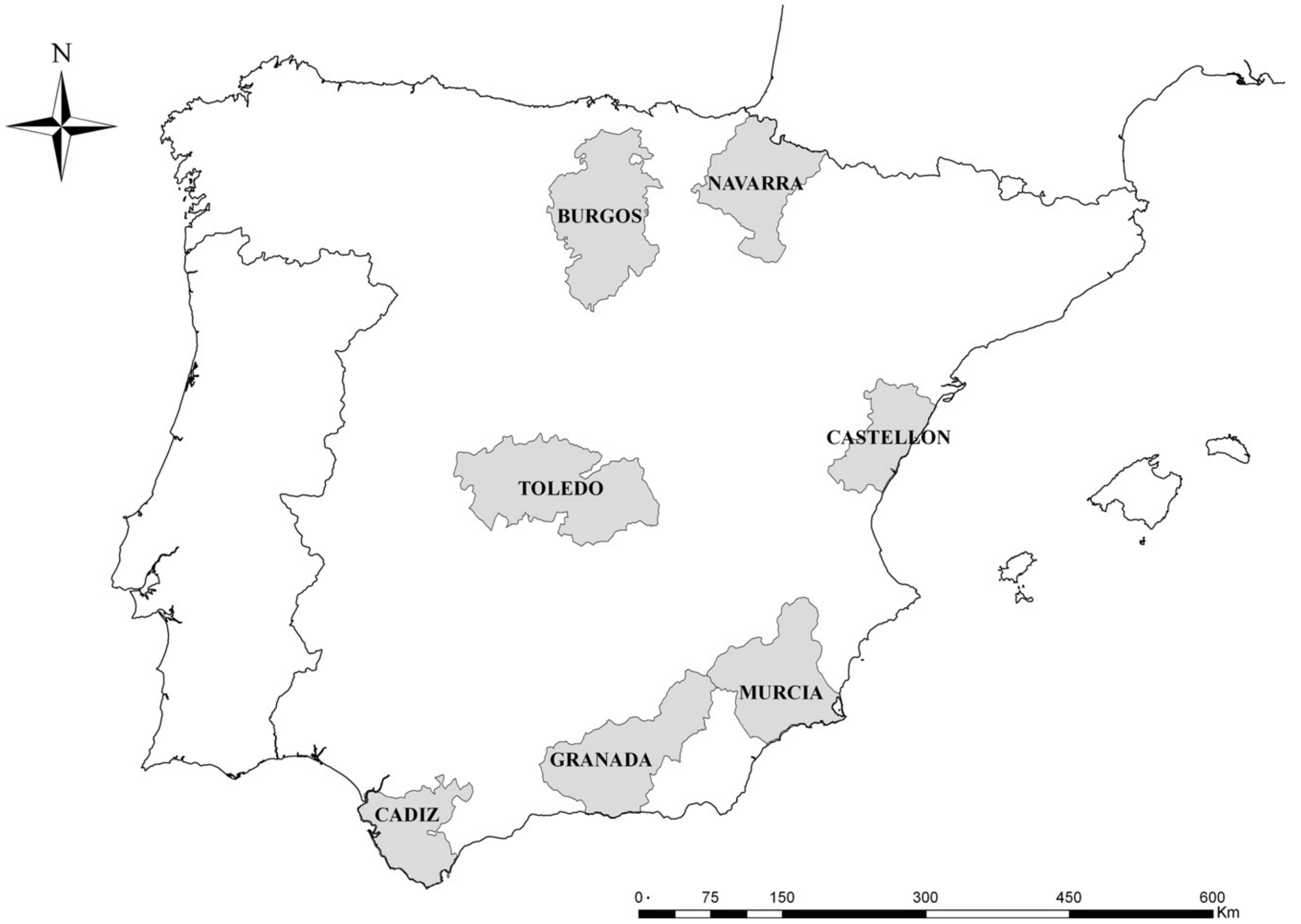

Fig. 1 – The Iberian Peninsula including Spain and Portugal. The seven sub-populations analysed are shown in grey.

2000; Lacy et al., 2005; Miller and Lacy, 2005) were not included in the simulations.

Finally, to evaluate the sensitivity of the projections of the metapopulation models to changes in the demographic parameters estimates, we conducted an elasticity analysis (Caswell, 2001) of the individual-based model built with our data on pre-adult mortality, and the spatial structure of scenario b, characterized by an equal probability of dispersing to any of the populations (including the natal one). Although this is likely unrealistic, in absence of more detailed understanding of the dispersal behaviour of the species, we consider this scenario provides a convenient trade-off for exploring the effects of alternative management decisions (yet, without incorporating sexual stochasticity and density-dependent effects on fecundity, the model is probably too simplistic to derive long-term predictions on population sizes).

Elasticity analyses are a useful tool to explore the convenience of alternative management strategies and provide valuable insights on the effect of estimates inaccuracy on projected population trajectories (Ferrer and Calderón, 1990; Ferrer and Hiraldo, 1991; Mills et al., 1999, 2001; Caswell, 2000; Heppell et al., 2000). Possible management strategies to improve Bonelli's eagle population size include decreasing adult and pre-adult mortality, and increasing the proportion of successful breeders. Therefore, we calculated the effects on population growth rate (λ) of a proportional decrease of 5%, 10%, 20%, 25%, and 30% in the mortality of adults and pre-adults, and the same proportional increases in the proportion of successful breeders. Parameters were modified one at a time. All other parameters of the model (including SD of adult and pre-adult mortality) were kept unchanged. Note that the proportion of successful breeders was never allowed to be higher than 100%.

To estimate population trajectories we evaluated both the probability of population extinction (PE, the proportion of the 500 iterations in which the population went extinct) and the expected annual rate of population growth (λ). Comparisons among models were conducted using the Wilcoxon test (Zar, 1984).

3. Results

For the seven sub-populations, breeding success ranged from 8.30% to 86.59% (mean = 67.27%; SD = 27.02%). The percentage of pairs rising one and two chicks ranged from 33.33% to 75.00% (mean = 47.08%; SD = 15.31%), and from 25.00% to 66.70% (mean = 52.92%; SD = 15.31%), respectively. Annual adult mortality ranged from 3.29% to 16.10% (mean = 8.53%; SD = 4.53%) (Table 2). Considering the seven sub-populations as a single metapopulation, the initial population size was 142 pairs.

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Table 1 – Parameters used to construct individual-based models for the analysis of Bonelli's eagle population viability in Spain

Parameter		Reference
Dispersing classes age range[a]	1–4 years	Ferguson-Lees and Christie (2001)
Survival of dispersers[b]	100%	
Dispersal rates	See text for details	
reproductive system	Monogamous	Ferguson-Lees and Christie (2001)
Age of first offspring[a]	4 years	Ferguson-Lees and Christie (2001)
Maximum age of reproduction	25 years	Real and Mañosa (1997)
Maximum number of progeny per year	2 chicks	Arroyo et al. (1995)
Sex ratio at birth (% males)	50%	
Mean and SD of females breeding (%)	Mean and SD of the% of successful pairs reported for localities within each of the seven regions	Gil-Sánchez et al. (2004), Arroyo et al. (1995), López-López et al. (2007b)
Number offspring per female per year (% in each class)	Mean of the % of nests with 1 or 2 chicks as reported for localities within each of the 5 regions	Balbontín and Ferrer (2005)
Specified age distribution	Equal number of males and females, all with 4 years of age	
Carrying capacity (K)	500 individuals	
Males in breeding pool (%)	100%	
Initial population size	MU:18; TO:10; CS:26; BU:12; NA:6; GR: 30; CA: 40	Del Moral (2006)
Female mortality from age 0 to 1 (%)	22 (0)/50 (0)	Real and Mañosa (1997)[c,d] / own data[d,e]
Female mortality from age 1 to 2 (%)	59 (0)/71 (0)	Real and Mañosa (1997)[c,d] / own data[d,e]
Female mortality from age 2 to 3 (%)	59 (0)/8.53 (4.68)	Real and Mañosa (1997)[c,d] / own data[d,e]
Female mortality from age 3 to 4 (%)	59 (0)/8.53 (4.68)	Real and Mañosa (1997)[c,d] / own data[d,e]
Female mortality after age 4 (%)	Mean and SD of the mortality (1-Sb) reported for localities within the regions considered. For Toledo we calculated it as the mean and SD of the values used for the other six regions	Real and Mañosa (1997)

Abbreviations: MU: Murcia; TO: Toledo; CS: Castellón; BU: Burgos; NA: Navarra; GR: Granada; CA: Cádiz. Se: Young pre-dispersal survival rate; Sn: pre-adult annual survival rate; Sb: annual adult survival rate.

[a] Both sexes.

[b] Dispersers mortality is already considered in the estimate of pre-adult mortality, thus, no additional mortality was introduced.

[c] Survival from age 0 to 1 was assumed as that of pre-dispersal individuals (1-Se). Survival from 1 to 4 as 1-Sn.

[d] Mean (SD).

[e] Survival from age 0 to 1 and 1 to 2 as observed from our data; survival from age 2 to 3 and 3 to 4 was assumed as the mean and SD adult mortality in the seven regions we analyzed.

Table 2 – Summary of demographic parameters employed for modelling seven Spanish populations of Bonelli's eagle

Population	Murcia	Toledo	Castellón	Burgos	Navarra	Granada	Cádiz
Breeding success	74.86	69.36	82.40	8.30	66.70	86.59	82.68
SD breeding success	9.78	24.58	7.70	–	–	6.37	32.50
% Nests with 1 chick	39.70	44.70	61.11	33.33	75.00	35.45	40.30
% Nests with 2 chicks	60.30	55.30	38.89	66.67	25.00	64.55	59.70
Adult mortality (>4 years)	16.10	8.53	12.87	6.73	7.60	3.29	4.61
SD adult mortality	12.25	4.68	6.76	2.24	–	3.24	0.21
No. of pairs in 1994[a]	18	10	26	12	6	30	40
No. of pairs in 2005[a]	22	10	27	3	3	52	40

[a] Del Moral (2006).

When the sub-populations were modelled as isolated (scenario a), the estimated population trends varied significantly depending on the source of the data. Considering the estimates of Real and Mañosa (1997), pre-adult survival (from hatching to first breeding) is only 5.4%, whereas when our data on satellite-tracked individuals is considered, pre-adult survival is 12.1% (see Table 1). Consequently, when data on pre-adult mortality obtained from the literature were used, all the populations showed declining trends ($\lambda < 1.0$). In contrast, when our values of pre-adult mortality were introduced the trend reverted in two of the sub-populations ($\lambda > 1.0$ for Granada and Cádiz) (Table 3). Actually, when the values of pre-adult mortality obtained from the literature were used to construct both the deterministic and stochastic models, population growth rates were slightly lower than those reported by Real and Mañosa (1997) (in both cases: $Z = 1.83$; $p = 0.07$; $n = 4$). In contrast, when they were constructed using our own data on pre-adult mortality, population growth rates were larger than those reported by Real and Mañosa (1997) ($Z = 2.37$; $p = 0.018$; $n = 7$). The probability of extinction (PE)

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Table 3 – Deterministic and stochastic estimates of annual rate of population growth (λ) and probability of extinction (PE) in 50 years of Bonelli's eagles in Spain

	Population	Reported λ^a	Deterministic λ^b	Stochastic λ^b	LCI^b	UCI^b	PE^b	Deterministic λ^c	Stochastic λ^c	LCI^c	UCI^c	PE^c
Scenario a	Murcia	0.912	0.861	0.900	0.879	0.922	1.000	0.920	0.919	0.899	0.939	1.000
	Toledo	–	0.908	0.949	0.927	0.972	0.998	0.965	0.968	0.949	0.987	0.904
	Castellón	0.913	0.881	0.909	0.891	0.928	1.000	0.939	0.933	0.917	0.950	0.964
	Burgos	0.952	0.818	0.938	0.923	0.953	1.000	0.855	0.941	0.928	0.954	1.000
	Navarra	0.973	0.900	0.963	0.941	0.985	1.000	0.952	0.971	0.952	0.991	0.978
	Granada	–	0.965	0.973	0.959	0.987	0.240	1.025	1.029	1.022	1.037	0.000
	Cádiz	–	0.950	0.956	0.937	0.976	0.560	1.009	1.008	0.995	1.021	0.000
Scenario b	Metapopulation	–	–	0.905	0.890	0.920	0.982	–	0.943	0.933	0.952	0.130
	within populations	–	–	0.945	0.910	0.980	0.999	–	0.964	0.928	1.001	0.763
Scenario c	Metapopulation	–	–	0.906	0.891	0.921	0.976	–	0.942	0.932	0.951	0.190
	within populations	–	–	0.946	0.908	0.984	0.999	–	0.965	0.926	1.005	0.789
Scenario d	Metapopulation	–	–	0.904	0.889	0.919	0.976	–	0.942	0.932	0.951	0.168
	within populations	–	–	0.944	0.906	0.982	0.999	–	0.964	0.925	1.004	0.777

Spatial structure and – stochasticity are considered by modelling seven populations as isolated (scenario a) and three scenarios with phylopatry and different probabilities of natal dispersal among populations (scenarios b, c and d; see Methods). Abbreviations: LCI (lower confidence interval), UCI (upper confidence interval).

a Expected λ reported by Real and Mañosa (1997).

b Calculated using values of demographic parameters taken from bibliography (see Methods section).

c Calculated using values of demographic parameters taken from our data and bibliography (see Section 2).

was also lower ($Z = 2.02$; $p = 0.043$; $n = 7$) when we incorporated our estimate of pre-adult mortality, than when we used the values from the literature (Table 3).

One of the consequences of considering sub-populations as isolated is that even with our estimates of pre-adult mortality, the populations of Burgos and Murcia are predicted to become extinct in the next 50 years (PE equal to 100% in both cases) (Table 3), with the chances of those of Toledo, Castellón and Navarra following the same fate (PE higher than 90% in the three cases) (Table 3). In contrast, when sub-populations are modelled as part of a metapopulation (i.e., individuals are allowed to move among populations – scenarios b, c and d), the sub-populations that go extinct are later re-colonized, with the probability of extinction of the whole metapopulation in the next 50 years being less than 20% (range = 13–19%) (Table 3).

The effect on population trajectories of individuals' movement, and more remarkably, the effect of decreasing dispersers' mortality, becomes evident when the elasticity analysis of one of these metapopulation models (scenario b) is considered. Whereas a proportional 20% decrease in the values of pre-adult mortality during the first two years of life allows for the stabilization or increase of the metapopulation (i.e., $\lambda \geqslant 1.0$), neither a decrease in adult mortality, nor an increase in the percentage of breeders changes the declining trend of the metapopulation (Fig. 2). For example, a 5% decrease in pre-adult mortality has an effect on λ that is more than two times that obtained with the same proportional decrease in adult mortality (e.g., $\Delta\lambda = 0.013$ in pre-adult mortality vs. $\Delta\lambda = 0.005$ in adult mortality when changing from 20% to 25%), and more than four times that obtained with an increase in the percentage of breeders ($\Delta\lambda = 0.003$) (Fig. 2), highlighting the importance of pre-adult mortality when stochasticity and the spatial structure of the population are considered.

4. Discussion

Here we present the results of modelling the dynamics of some representative populations of Bonelli's eagles in Spain. As we only consider a fraction of all the pairs breeding in Spain, rather than aiming at projecting the overall trend of the species in the country, what we aim to do here is to evaluate which management strategies may provide the highest reward in terms of population persistence. The main limitations of extant population models in Spain are the assumption of closed populations and the uncertain accuracy of the estimates of pre-adult survival rate they are based on (e.g., Real and Mañosa, 1997). Here we attempt to overcome these limitations incorporating spatial structure and stochasticity in our models, and introducing new estimates of pre-adult survival. The main novelty of our models is the conclusion that pre-adult survival, rather than adult survival, has the largest impact on population growth rate (i.e., on our model metapopulation growth rate). This has important implications for management and conservation at the national scale.

First, a basic expectation of metapopulation models is that local populations eventually go extinct and are re-colonized later (Hanski, 1999). Thus, from conservation point of view, to observe declines at local scales is not a sufficient reason for concern. Moreover, to observe differences in the trajectories of local populations is actually good news, as it suggests that local dynamics are relatively uncoupled, which is a major determinant of metapopulation persistence (Hanski, 1999). Second, the differences in the probability of extinction estimated when we used our data on pre-adult mortality, compared with that obtained when we used the figures provided by Real and Mañosa (1997), highlight the need to be cautious when predicting populations trends and assessing the status of the species in Spain. Unfortunately, reliable estimates of

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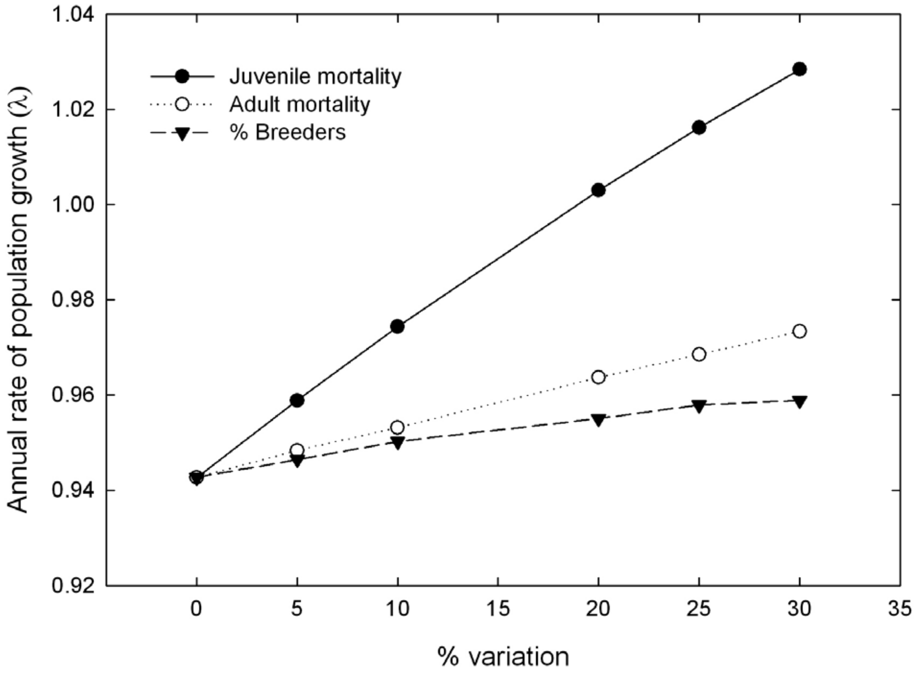

Fig. 2 – Elasticity analysis showing the variation in the annual rate of population growth (λ) resulting from proportional changes in pre-adult mortality, adult mortality and percentage of breeders.

the value of this parameter, which is key to understand the dynamics of the species at a national scale, are not currently available. Although the pre-adult survival of 12.1%, we used is more than twice that estimated from Real and Mañosa (1997) (actually, as two of the 15 individuals tracked were confirmed alive after their fourth year of life, observed survival rate was 13.3%), it is well below the 18.7% estimated by Carrete et al. (2002).

The relevance of pre-adult survival is reinforced by the fact that a 20% decrease in mortality during the first two years of life allowed the stabilization of our metapopulation (i.e., $\lambda \geqslant 1.0$). In contrast, neither a decrease in adult mortality, nor an increase in the percentage of breeders, changed its declining trend. From a management perspective, aiming at improving pre-adult survival is not unreasonable, as the rate currently observed is low for large raptors (e.g., Whitfield et al., 2004 and references therein). This reinforces the idea that it is a consequence of human-mediated activities, rather than a characteristic of the species, and management actions aimed at improving dispersers' survival might boost the population into an upper trend.

In contrast, increasing the proportion of breeders or decreasing adult mortality did not allow the stabilization of our metapopulation (Fig. 2). Furthermore, a proportional increase of 30% in the percentage of breeders is actually impossible, as for some populations this implies that the proportion of breeders would have to be larger than 100%. This has important implications for translating the results of elasticity analysis into sensible management prescriptions. The success of management actions focused on a single parameter depends on whether that parameter is altered in relation to that of a healthy population, and whether it is amenable to human alteration (Hiraldo et al., 1996). This includes how far it is from its potential maximum, and the feasibility and economic cost of implementing actions to take the parameters to the desired values (Hiraldo et al., 1996; Hitchcock and Gratto-Trevor, 1997; Caswell, 2000; de Kroon et al., 2000; Baxter et al., 2006). A parameter giving a low elasticity may even provide the only feasible (or maybe a cheaper) means of increasing the population growth to the desired value (Caswell, 2000; Ehrlén et al., 2001). Thus, the magnitude of the proportional change in the parameters that is needed to achieve a desired population growth is less relevant than the actual possibilities of producing that change, with those parameters further away from their potential maximum being those on which on theoretical grounds it is possible to make a larger improvement.

Unfortunately, despite words of cautions regarding the interpretation of their results for conservation purposes (e.g., Real and Mañosa, 1997; Mills et al., 1999, 2001; Caswell, 2000, 2001; Heppell et al., 2000), the outcomes of matrix population models' elasticity analyses have often been almost blindly interpreted as a clear recommendation of focusing conservation action on the parameter with the highest elasticity. In our case, the recommendation of investing more efforts in enhancing pre-adult Bonelli's eagle's survival in Spain is not only based on the fact that it is the parameter with the highest elasticity, but also on practical grounds, as pre-adult mortality is the parameter with the largest potential to be managed and, consequently, to improve the metapopulation trend. This is a different conclusion from that suggested by previous analyses that identified adult mortality as the main determinant of population trend (Real and Mañosa, 1997; Carrete et al., 2002).

We suggest this difference is because previous studies modelled Bonelli's eagle populations as isolated. Territorial

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occupancy models as that developed by Carrete et al. (2002) are actually more appropriate when the overall population viability is more dependent on within-population dynamics (birth rates and death rates), than on between-population dynamics (patch extinction and colonization rates) (Carrete et al., 2002). Thus, it is not surprising that, given their assumption that within-population processes play the chief role in driving population trends, adult mortality is identified as the parameter with the largest impact on these trends. Yet, in populations interconnected by the flux of dispersers, as it seems to be the case in Bonelli's eagles (Cadahía et al., 2005, in press; Cadahía, 2007), the fate of dispersers has a much larger impact on the populations than expected by closed population models.

Consequently, we suggest that conservation strategies for the species in Spain should seek to ensure that pre-adult mortality decreases. Among other reasons because (a) pre-adult mortality is currently unnaturally high as a consequence of mortality associated with poorly designed electric power lines and other perilous infrastructures (e.g. Ferrer and Hiraldo, 1992; Real and Mañosa, 1997; Ferrer and Janss, 1999; Ontiveros et al., 2004; López-López et al., 2007a, b), and thus, it can be reduced if proper actions are implemented, (b) it is the parameter that the population growth rate seems to be most sensitive to when connectivity among local populations is taken into account, and (c) it is currently further away from its potential maximum than the other parameters analysed. Under a metapopulation point of view, where the different sub-populations are linked through juvenile dispersal (Muñoz et al., 2005), pre-adult mortality plays a key role to ensure the conservation of the species.

Yet, successful conservation action requires mixed strategies aimed at simultaneously improving several parameters (e.g., Hiraldo et al., 1996; Ferrer et al., 2004; Penteriani et al., 2005, 2006), and therefore actions focused on both adults and pre-adults, are needed for the protection of Bonelli's eagles in Spain (Ontiveros et al., 2004). Nevertheless, actions aimed at minimizing pre-adult mortality (e.g., power line and pole correction) have the advantage over actions aimed at decreasing adult mortality (e.g., reducing direct persecution) that the former could be focused in specific areas of the country (e.g., the temporary settlements used by juveniles), whereas the latter should be focused over a large extension of the country (i.e., the extensive breeding areas). Temporary settlements are mostly characterized by the abundance of prey and a low density of adults, and often overlap with important hunting zones and areas with complex patterns of natural vegetation and agricultural lands. In these areas the development of irrigation systems is accompanied by the development of the electricity network, and hence, an increase in the risk of electrocution (Real et al., 2001; Ontiveros et al., 2004). There is already vast information on how to minimize the impact of power lines on raptor populations, including procedures to modify pole design and procedures to identify dangerous lines and poles (Negro and Ferrer, 1995; Ferrer and Janss, 1999; Janss and Ferrer, 1999, 2001; Janss et al., 1999). Thus, locating and protecting the areas used by juveniles Bonelli's eagles as temporary settlements, and putting forward conservation measures aimed at diminishing electrocution and shooting there, are likely to result in sensible improvements on the species' status in Spain.

5. Uncited reference

Wisdom et al. (2000). Q1

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