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DEMOGRAPHY AND CONSERVATION OF WESTERN EUROPEAN BONELLI'S EAGLE *Hieraaetus fasciatus* POPULATIONS

Joan Real & Santi Mañosa

Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Avinguda Diagonal 645, 08028 Barcelona, Catalonia, Spain

Abstract

The basic demographic parameters of six Bonelli's eagle Hieraaetus fasciatus *populations in Spain and France were calculated from field data obtained in the last 15 years. Average annual productivity ranged from 0.36 to 1.24 young/pair and average annual adult survival from 84% to 96%. Preadult survival (from fledging to recruitment) was estimated at 10%. All the populations were declining at annual rates ranging from −7.3 to −1.1%. Although no statistically significant disagreement was observed between the predictions of a Leslie matrix model fitted to the population parameters and the real trends, some populations declined faster and others more slowly than expected. These differences were interpreted as a result of differential emigration, recruitment rates or preadult survival not accounted for by the model. Since the intrinsic population growth rate was about four times less sensitive to changes in preadult survival than to changes in adult survival, and about ten times less sensitive to changes in fecundity and predispersal survival, conservation efforts must be primarily directed towards increasing adult and preadult survival. Power line casualties and direct persecution must be eliminated in order to reduce mortality. Priorities on research should address dispersal, mortality and habitat relationships involving these two parameters. Monitoring should be extended to other populations. Copyright © 1996 Elsevier Science Limited*

INTRODUCTION

Bonelli's eagle *Hieraaetus fasciatus* is an endangered raptor whose populations have experienced a marked decline in Europe, involving both a loss of range and numbers (Rocamora, 1994). The European population is estimated to be between 938 and 1039 breeding pairs, 75–93% of which are found in the Iberian Peninsula and south-eastern France (Real *et al.*, in press).

In spite of this situation, there is little information on detailed population trends, or on the most relevant life history parameters of this species. This information is essential for the proper design of conservation strategies. Using these data, demographic models can help to understand the factors involved in population decline (Lebreton & Clobert, 1991; McDonald & Caswell, 1993), or to evaluate conservation strategies (Ferrer & Calderón, 1990; Wootton & Bell, 1992; Wood & Collopy, 1993), and they may be also used as an alternative tool to detect population trends before it is too late (Taylor & Gerrodette, 1993). The aims of this paper are (1) to describe population trends of six Bonelli's eagle populations and to estimate their most relevant life history parameters; (2) to build a demographic matrix model including these parameters in order to give additional support to the observed population trends and (3) to use the model to show the value of different conservation strategies and to suggest future trends in management and research.

METHODS

Study areas and population change

We studied the long-term population change of six Bonelli's eagle populations for 10–14 years up to 1994 in Spain and France, ranging from the northern limit of the species' distribution to southern Iberian peninsula (Fig. 1). The study included subpopulations located within the core distribution (El Vallès-Penedès in Catalonia, Murcia, Castelló), as well as some isolated subpopulations (Burgos, Navarra, Provence). Some areas held high eagle densities, such as Castelló (0.48 pairs/100 km²) and Murcia (0.40 pairs/100 km²), while others had only medium or low eagle densities, such as El Vallès-Penedès (0.32 pairs/100 km²), Provence (0.30 pairs/100 km²), Burgos (0.25 pairs/100 km²) and Navarra (0.13 pairs/100 km²). These densities were computed from the starting number of pairs and the area occupied on a 10×10 km² UTM (Universal Transverse Mercator) grid.
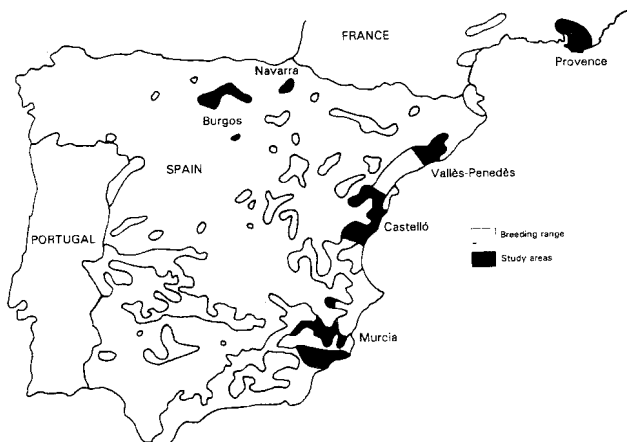
Fig. 1. The distribution of Bonelli's eagle in Spain and France (light shade) and location of the six study areas (dark shade). Redrawn from Arroyo *et al.* (1990) and Cheylan and Siméon (1984).

Each population was initially censused by searching for occupied and deserted territories (revealed by unoccuppied nests) in potential breeding habitats (Mediterranean sierras with rocky cliffs, rocky ranges and river canyons, see Del Hoyo *et al.*, 1994). Subsequent population changes were monitored by checking all the previously detected occupied or deserted territories, to determine possible disappearance or reestablishment of birds. Censuses were carried out from January to March. The lack of bird observations and the absence of arranged nests, prey remains and droppings on perches revealed the disappearance of a pair. When only a single bird was observed in a breeding territory, the loss of half a pair was recorded. When a pair was not recorded in its traditional site, we searched within a radius of several kilometers for suitable breeding habitats in order to exclude the possibility of a pair having moved to a new breeding site.

Productivity
Pairs holding territories were visited to determine how many of them laid eggs, hatched chicks and fledged young. We considered a young as fledged when it had attained 8–9 weeks of age, which was judged from feather development or hatching date. The number of fledglings produced per occupied territory was then calculated for each population and year, and the average and the standard deviation of these annual values were calculated for every population. In Provence 188 breeding attempts were monitored from 1982 to 1994, 141 in El Vallès-Penedès from 1980 to 1994, 156 in Murcia from 1983 to 1994, 25 in Navarra from 1984 to 1994, 79 in Burgos from 1980 to 1994, and 313 in Castelló from 1982 to 1994.

Annual survival rate for territorial birds
For each population, annual survival rate for a given year was computed as the proportion of birds present in

the population at the start of the breeding season which were still present at the start of the following breeding season. From these annual values, an average was then calculated for each population. The death of a bird was assumed when it disappeared from its breeding site from one year to the next or when it was replaced by a bird of a different age class. Where there was the loss of a pair, and the eagles were not found in neighbouring previously unoccupied areas, we assumed death. Otherwise, we assumed that the pair had moved from one breeding area to another. Differential plumage colour during the first four years of life (Parellada, 1984) allowed the assessment of replacement. Since very few birds, if any, seem to wait to acquire adult plumage to enter the breeding population, replacement of adult birds by other adult birds, which might be undetectable by our method, was assumed to be rare. This was based on the fact that all the Bonelli's eagles banded in Catalonia and France that have subsequently entered the breeding population did so between one and four years old. Because birds were not marked, the movement of an adult bird from one breeding area to another with a previous vacancy would have been recorded as a death, resulting in an overestimate of the adult mortality rate. The proportion of breeding territories held by a single individual in Catalonia from 1992 to 1995 was 5% ($n = 167$), so this is the maximum bias that this sort of movement would produce. Estimates of adult survival were based on 228 bird-years in Provence from 1987 to 1994, 240 in El Vallès-Penedès from 1980 to 1994, 262 in Murcia from 1983 to 1992, 74 in Burgos from 1992 to 1994, 670 in Castelló from 1982 to 1994, and 92 in Navarra from 1976 to 1994 (Fernández-León, 1994).

Survival rate during the dependence period
Survival of young during the dependence period was estimated from the radiotracking of six chicks which were continuously followed in El Vallès-Penedès in 1986 and 1987 from fledging to dispersal. Dispersal was assumed to occur when contact could not be established with the young for four consecutive complete days within the breeding area. To base our estimate on a larger sample, we combined our results with those of Arroyo *et al.* (1992).

Survival rate for non-territorial birds
Preadult survival rate was estimated from a wing-tagging study conducted in two areas. We wing-tagged 76 chicks in El Vallès and Penedès districts (Catalonia, Spain) from 1986 to 1992, and 24 in Provence (France) in 1990. Nestlings aged 40–50 days were provided with TXN-80 tags wrapped around the humerus, between the tertials and scapulars in each wing, with colour coding for year and natal area (see Young & Kochert, 1987). All these birds reached potential breeding age by January 1995, so we estimated minimum preadult survival rate using the proportion that were recruited into the studied breeding populations by the 1995 breeding

season. This survival rate is a minimum estimate, since recruits to remote unsampled breeding populations may have remained undetected. Consequently, our estimate for preadult mortality may contain a component of emigration. Although loss of both tags never occurred before dispersal, tags may have been lost afterwards, also causing an underestimate of survival rate. To obtain an independent estimate of the annual tag-loss rate from dispersal to recruitment, we conducted a census in central Catalonia in 1991–1993. This area affords refuge to an important number of non-breeding eagles before they recruit into the breeding population and can be described as a juvenile eagle dispersal area (González *et al.*, 1989; Ferrer, 1990). During the autumns of 1991, 1992 and 1993 we conducted car transects in this area (1018 km in 1991, 3356 km in 1992 and 3477 km in 1993), and counted the number of tagged and untagged young and immature eagles (according to the plumages described in Parellada, 1984) belonging to the 1991 and 1992 cohorts observed. If there were no tag loss, we should expect the proportion of tagged birds to be equal for young and for immature birds, whereas with tag loss, we should expect the former to be higher than the latter. Immigration of untagged birds from remote areas into the dispersal area would only change the initial 'tag composition' of the cohort, but not the subsequent change in 'tag rate'. Comparison of these two ratios would therefore provide an estimate of the annual tag-loss rate during the first year of life, defined as the proportion of tagged birds that, having survived a year interval, lose both tags.

If Y is number of tagged young observed from a given cohort and y the number of untagged young observed from the same cohort, then the number of immature tagged birds, I, observed from that cohort equals the number of tagged young, Y, that survive minus those that have lost their tag, that is:

$$I = YS - YSL$$

where S is the annual survival rate, and L the proportion of tagged birds that, having survived a year interval, lose the tags.

The number of immature untagged birds, i, observed from that cohort equals the number of untagged young, y, that survive plus those tagged young that have lost their tags, that is:

$$i = yS + YSL$$

Then:

$$\text{Tag ratio for young} = \frac{Y}{y}$$

and

$$\text{Tag ratio for immature} = \frac{I}{i} = \frac{YS - YSL}{yS + YSL} = \frac{Y - YL}{y + YL}$$

The quotient between these two expressions gives:

$$C = \frac{\text{Tag ratio young}}{\text{Tag ratio immature}} = \frac{y + YL}{y - yL}$$

from where

$$L = \frac{y(C - 1)}{Y + Cy} \qquad (1)$$

Model definition, assumptions and statistical analyses

We modelled the population change in every studied population by means of a Leslie matrix model structured into three age classes (Table 1). Bird ages in months were calculated from the average fledging date, which was assumed to be 1 June. Dispersal from the natal place was assumed to occur after a three-month dependence period (see Results), on 1 September. At census time (conventionally 1 January), age classes were defined as *Young*: birds 7 months old (in their second calendar year); *Immature*: birds 19 months old (in their third calendar year); *Subadult/adult*: birds 31 months old or more (in their fourth calendar year or older). As is usual, we only modelled the dynamics of females. We assumed that all birds were first censused as breeders 2.3 years after dispersal.

Three different survival rates were assumed in the model: (1) survival from fledging to dispersal (S_e). The same value for this parameter was used to model all the populations. (2) Annual survival rate for non-territorial birds (those not holding a breeding territory) from dispersal to age 2.3 (S_n), computed as (survival from dispersal to age 2.3)$^{1/2.3}$. The same value for this parameter was used to model all the populations. (3) Annual survival rate for birds already settled on a breeding territory, after age 2.3 (S_b). A specific value was used to model each population.

As sex-ratio was assumed to be 1:1 in all life stages, fecundity (F) was calculated as half the productivity of each population.

Observed λ (annual population growth rate) and observed percentage of annual change were computed as:

$$N_t = N_0 \lambda^t, \text{ to give } \lambda = (N_t/N_0)^{1/t}$$

Table 1. Matrix model for the Bonelli's eagle population

$$\begin{bmatrix} 0 & 0 & FS_e(S_n^{4/12}) \\ S_n & 0 & 0 \\ 0 & S_n & S_b \end{bmatrix} * \begin{bmatrix} Y_t \\ I_t \\ B_t \end{bmatrix} = \begin{bmatrix} Y_{t+1} \\ I_{t+1} \\ B_{t+1} \end{bmatrix}$$

Where Y = number of *Young* females, I = number of *Immatures* females, B = number of *Breeding* females, F = number of female chicks fledged per territorial female (maximum value = 1), S_e = young survival from fledging to dispersal (3 months; maximum possible value = 1), S_n = annual survival in the dispersal areas (preadult survival; maximum possible value = 1), S_b = annual survival in the breeding areas (breeders survival) and t = year t (0 to ∞).

and

$$\text{Percentage annual change} = 100(\lambda - 1)$$

where N_t is the final population size, N_0 is the initial population size, and t is the time between the two censuses. For λ values < 1 the population declines, while values > 1 indicate a growing population. Approximate 95% confidence intervals of λ estimates were $\pm$ twice its standard deviation, which was computed following Lande (1988). The approximate estimates of standard deviations for S_e, S_n and S_b needed to perform these computations were obtained by assuming a binomial distribution for these survival variables (Lande, 1988). To assess the effect of changes in each parameter on population growth rate, a sensitivity analysis was conducted following Lande (1988). This gave indexes reflecting the unit change in λ per unit change in the parameter. Both the model and the sensitivity analysis were run on the ULM software (Legendre, 1992). When performing simulations, the starting number of breeding birds was taken from the actual number at the start of the simulation. From that, and using the actual values of fecundity, predispersal and preadult survival, the starting numbers of young and immature birds were calculated and entered into the model. Statistics were performed on the SPSS/PC package (SPSS-INC., 1990). One-tailed probabilities were use to check the significance of correlation tests. The model does not take into account factors such as stochasticity, exchanges between populations or density dependence. This has to be remembered when interpreting the results of our model, as well as possible differences between populations in relation to these factors.

RESULTS

Population trends

The numbers of pairs of Bonelli's eagles in the six populations at the start of the monitoring periods ranged from 4.5 in Navarra, with a density of 0.13 pairs/100 km^2, to a maximum of 46 in Castelló, with a density of 0.48/100 km^2 (Table 2). Over 10–14 years the number of breeding pairs declined in all populations (Fig. 2). The trend was steepest in Murcia (–7.3% per year) and Navarra (–5.7%), intermediate in Castelló (–4.1%) and Burgos (–3.9%), and low in El Vallès-Penedès (–2.7%) and Provence (–1.1%) (Table 2).

Productivity and adult annual mortality

Average annual production of young (P) in the studied populations ranged from 0.36 ± 0.23 young/pair to 1.24 ± 0.30 young/pair, and annual adult survival ranged from 83.91% to 96.07% (Table 2). One-way ANOVA tests showed the existence of significant variation in productivity ($F = 8.604$, d.f. $= 5$, $p < 0.001$) and annual mortality ($F = 3.175$, d.f. $= 4$, $p = 0.023$) between the studied populations. A Tukey test ($p = 0.05$) revealed that the Burgos population showed significantly lower productivity than the Navarra, El Vallès-Penedès, Provence, and Murcia populations, and that productivity in Murcia and El Vallès-Penedès was significantly higher than in Castelló. The only two populations

Table 2. Summary of demographic parameters and model results for the populations. Preadult annual survival rate (S_n) was set at 41%, and young predispersal survival rate (S_e) was set to 78% for all populations

	Burgos	Navarra	Vallès	Castelló	Murcia	Provence
Density pairs/100 km^2	0.25	0.13	0.32	0.48	0.40	0.30
Starting-ending years	1980–94	1984–94	1980–94	1982–94	1983–94	1982–94
Starting-ending no. pairs	21–12	4.5–2.5	14–9.5	46–28	37–16	16–14
Average annual productivity (P)	0.36	0.96	1.09	0.71	1.24	1.02
Minimum-maximum annual productivity	0–0.62	0–1.66	0.43–1.58	0.35–1.04	0.78–1.66	0.75–1.28
SD annual productivity	0.23	0.52	0.32	0.34	0.30	0.21
Expected lifetime productivity	5.17	12.15	12.43	5.16	7.09	25.45
Adult survival % (S_b)	93.27	92.4[a]	91.16	87.13	83.91	96.07
SD adult survival	2.24	—	7.88	6.76	12.25	24.95
Average breeding longevity	14.36	12.66	11.40	7.27	5.72	24.95
Observed % annual change	–3.9	–5.7	–2.7	–4.1	–7.3	–1.1
Observed λ	0.961	0.943	0.973	0.959	0.927	0.989
Expected λ	0.952	0.973	0.968	0.913[b]	0.912[b]	1.009
SE of Exp. λ	0.031	0.037	0.026	0.024	0.031	0.020
Sensitivity to S_b	0.96	0.91	0.89	0.92	0.86	0.91
Sensitivity to S_n	0.11	0.25	0.29	0.22	0.36	0.25
Sensitivity to S_e	0.02	0.06	0.06	0.05	0.08	0.06
Sensitivity to F	0.10	0.09	0.09	0.11	0.10	0.09
S_b Equilibrium value	98	95	95	97	94	95
S_n Equilibrium value	73	51	52	72	63	37
P Equilibrium value	1.40	1.58	1.82	—	—	0.82

[a]Taken from Fernández-León (1994).
[b]Significant difference from equilibrium.
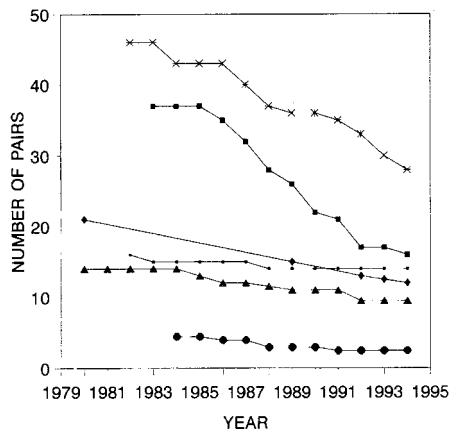
Fig. 2. Population trends in the six study areas. – ■ –, Provence; – ▲ –, Valles-Pendés, – * –, Castelló, – ■ –, Murcia; – ● –, Navara; – ◆ –, Burgos.

showing significant differences in annual adult survival were Murcia and Provence, at opposite extremes of the mortality range.

The cause of adult mortality was known for 16 birds that were found dead in El Vallès-Penedès. Shooting accounted for 53% of deaths, and power line casualties (electrocution and collision) for another 41%. In Navarra, of seven birds found dead, five had been shot and another two were electrocuted (Fernández-León, 1994). In Provence, two birds were found dead, both of them killed by power lines (Cheylan, Bayle and Lucchesi, pers. comm.). In Murcia, shooting and trapping accounted for 92% of 13 birds found dead, and power line casualties for the remaining 8% (Sánchez *et al.* pers. comm.). In Castelló all birds for which the cause of death was known ($n = 24$) had been shot (79%), trapped (17%) and poisoned (4%) (Ramia & Bort, 1995).

Survival rate during the dependence period

Five of the six of our radiotracked birds survived to disperse, while the other was killed by an eagle owl *Bubo bubo*, giving a 0.83 survival rate for this period which, on average, lasted for 96.2 ± 15.1 days ($n = 5$). The average date of dispersal for these birds was 16 September (range: 22 August–10 October). In combination with the results of Arroyo *et al.* (1992), who obtained a survival rate of $17/22 = 0.77$ for 22 radiotagged birds, a rate of $22/28 = 0.78$ was obtained.

Survival rate for non-territorial birds

During counts in the dispersal areas we observed 52 untagged young birds, 26 untagged immature birds, 18 tagged young and six tagged immature birds. Although no statistically significant difference in the ratio of tagged to untagged birds was observed for young versus immature birds ($\chi^2 = 0.59$, d.f. = 1, $p = 0.44$), evidence for tag loss existed from the observation of seven young birds carrying a single tag. The tagged to untagged ratio for young birds was 0.35, while the ratio for immature

birds was 0.23. As expected for tag loss, the tag ratio for young birds was higher than the tag ratio of immature birds. From eqn 1, a tag loss rate of 27% (or 73% annual tag survival rate) was thus obtained.

Five of the tagged birds were observed as breeders with the tags on them and another was recovered dead without tags, but with a leg-band, at breeding age. As 100 chicks were tagged, this gives a preadult survival rate of $5/100 = 0.05$. Allowing for mortality from fledging to dispersal and tag loss rate gives a survival rate value of $(0.05/0.78) / 0.73^{2.3} = 0.13$ from dispersal to recruitment age. A lower limit for preadult survival rate is obtained if we consider that a total of six birds were recorded dead or alive after breeding age, with or without tags, giving a value of $6/(100 \times 0.78) = 0.08$.

Evidence from raptor studies suggest that preadult survival rate declines after the first year of life (Newton, 1979), but in order to run the model an average annual survival rate for non-territorial birds after dispersal was computed; assuming that recruitment occurs 2.3 years after dispersal gives an annual survival rate value of $0.13^{1/2.3} = 0.41$ for non-territorial birds after dispersal.

The causes of preadult mortality were analysed based on birds found dead in different dispersal areas. In Catalonia, electrocution accounted for 44% of 23 deaths, shooting for 30%, starvation for 13% and other causes accounted for 13%. In France (Provence and Languedoc), electrocution caused 74% of 27 recorded deaths, while shooting and starvation caused 11% and 4% respectively. In southern Iberia power line casualties caused 63%, shooting and trapping 32% and poisoning 5% of 19 recorded deaths.

Population models and sensitivity analysis

Although the studied populations showed values of observed growth rate < 1, the significance of the difference between these observed values and 1 (stability) could not be statistically tested. However, the number of pairs did not increase from one year to the next for any of the six populations throughout the study period. The 95% confidence interval for estimated growth rates was below 1 only in Castelló and Murcia. Thus, the model predicted that only these two populations were significantly below demographic equilibrium. As pointed out by Taylor and Gerrodette (1993), however, statistical power (probability of rejecting the null hypothesis of no decline when it is false) is low, so the fact that we were unable to detect a statistically significant departure from $\lambda = 1$ in some populations does not necessarily imply that they were in equilibrium, but may be a result of the small size of these populations or low parameter estimate accuracy. In all cases observed population growth rates lay within the 95% confidence interval of expected growth rates, but correlation between both variables was not quite significant ($r = 0.70$, $n = 6$, $p = 0.059$). Whereas in Provence and Navarra observed growth rates were smaller than those derived from the model, in Burgos, El Vallès-Penedès,

Castelló and Murcia observed growth rates were higher than predicted by the model, indicating that the latter declined at a slower rate than expected from our model.

All populations were most sensitive to changes in adult annual mortality rates (sensitivities ranging from 0.86 to 0.96) and preadult mortality rates (sensitivities from 0.10 to 0.36), and much less to changes in fecundity (sensitivities from 0.06 to 0.11) or predispersal mortality (sensitivities from 0.02 to 0.09).

Equilibrium values for the parameters, i.e. the value that a particular parameter has to take in order to attain a growth rate of 1 without altering the other parameters, ranged from 0.94 to 0.98 for adult annual survival rate (S_b), and from 0.37 to 0.73 for preadult annual survival rate (S_n). The Provence, El Vallès-Penedès, Burgos and Navarra populations were liable to be led to equilibrium by manipulation of productivity (P), although the value needed in Navarra and El Vallès-Penedès (Table 2) was larger than the maximum ever observed for the species (1.5, Gil *et al.*, 1994).

DISCUSSION

Several non-exclusive hypotheses have been put forward to explain the decline in Bonelli's eagle populations in recent decades, such as habitat destruction (Arroyo *et al.*, 1990; Rocamora, 1994; Real *et al.*, in press), persecution (Arroyo *et al.*, 1990), decline in prey availabity (Cugnasse, 1989; Real, 1991), power line casualties (Cheylan, 1994), disturbance at nesting sites (Rocamora, 1994) and competition with other raptors (Fernández & Insausti, 1990). For a species which lays two eggs, a value of one young produced per occupied territory and year can be considered as a threshold for good or bad productivity. The results of our study showed very low productivity values in Burgos, and low in Castelló. In Burgos, at the limit of the species' distribution range, this may be caused by low prey availability or habitat constraints (Fernández *et al.*, 1993). Action to increase productivity should therefore concentrate on increasing prey availability by appropriate habitat and game management in areas with low or intermediate values (i.e. Burgos, El Vallès-Penedès, Navarra, Provence), and reducing human disturbance at nest sites. In Castelló, high adult mortality may be the main reason for the low production of young.

Estimates of adult survival were based on mate replacement and disappearance of breeders, and might be subject to underestimation (Ferrer & Calderón, 1990). However, estimates ranged from 83.91 to 96.07%, which are of a similar order of magnitude to those obtained for other long-lived raptors of similar size: 94% for the Spanish imperial eagle *Aquila adalberti* (Ferrer & Calderón, 1990), 83–90% for ospreys *Pandion haliaetus* (Poole, 1989) and 91–95% for the black eagle *Aquila verreauxi* (Gargett, 1990). Also, they are in agreement with the 20 years maximum longevity reported for the species in captivity (Newton, 1979). Except in Provence, all populations showed adult annual survival rates below equilibrium values. Our results showed particularly low adult survival values in levant populations (i.e. Murcia, Castelló), which are related to high human persecution. This seems to be the main reason for the sharp population decline found in these areas. The elimination of intense persecution by hunters, gamekeepers and pigeon fanciers is a central goal in order to achieve a sensible reduction in adult mortality in eastern Iberian populations. Mitigation measures to reduce collision and electrocution in power lines is the most important action we can undertake to reduce adult mortality in northern populations (i.e. El Vallès-Penedès, Provence). This could be achieved by detecting the main dangerous points in the power lines and correcting them (Bevanger, 1994; Negro & Ferrer, 1995), as well as by implementing new law regulations to forbid dangerous power pole designs in the future.

Our preliminary estimate of juvenile survival from fledging to recruitment ($0.78 \times 0.41^{2.3} = 10\%$), may be subject to some error, mainly because of some birds passing undetected. It is lower than the 30–33% in *Aquila verrauxi* (Gargett, 1990), 37% in *Pandion haliaetus* (Poole, 1989), 62–73% (first year) in the buzzard *Buteo buteo* (Kenward & Walls, 1994), 26% for peregrine falcon *Falco peregrinus* (Wootton & Bell, 1992), but similar to 10% in the bald eagle *Haliaetus leucocephalus* (Sherrod *et al.*, 1977) and the 8–17% for *Aquila adalberti* (Ferrer & Calderón, 1990). In areas such as El Vallès-Penedès, Provence or Navarra, where adult mortality is not extremely high, and production of young not extremely low, the slow decline observed might be the consequence of low recruitment rates, caused by high preadult mortality (power line casualties, persecution, low prey availability), long-distance dispersal, and reduction of habitat suitability in the breeding areas. Reduction of preadult mortality needs a global approach. Accelerating agricultural intensification and bad game management are reducing the potential range for young to disperse, and eagles are increasingly shot or trapped in the few good areas remaining. Moreover, in these areas, rural development has led to a spectacular increase in the power line network, leading to an increasing risk of electrocution. Improving the habitat of dispersal areas next to breeding areas may reduce dispersal and increase recruitment in the most isolated populations (i.e. Burgos, Navarra, Provence).

These points of view are supported by the results of our model and sensitivity analysis. The outputs of our model may be affected by constraints in model assumptions and biases in parameter estimates, mainly adult and preadult survival, to which λ is more sensitive. An additional problem was that we assumed equal preadult survival values for all populations, even though different populations may have different values for this parameter if they use differerent dispersal areas and are subject to different mortality factors. Our model was

also constrained by the fact that it treats each population as closed, which is obviously false. Taking all the above into account, the magnitude and sign of the deviation between the observed and expected trends may indicate to what extent each particular population was open and in which direction. Some populations (Provence and Navarra) showed a steeper decline than expected, which may be the consequence of high emigration rates or higher levels of preadult mortality than estimated. The first possibility is supported by the particular dispersal patterns of young Bonelli's eagles, which involve the movement of a large proportion of birds from northern populations to the south (unpublished data). On the other hand, in Provence, the large incidence of electrocution in the dispersal areas would produce a lower juvenile survival rate than the one we used. The situation in Provence and Navarra would be made more critical because of their isolation and small size, which would make them vulnerable to stochastic events and would make recruitment difficult. Other populations (Castelló, Murcia and Burgos), showed a smaller decline than expected. This might be the consequence of immigration from other populations in southern and western Spain (Andalusia, Extremadura), or even from birds coming from Provence or Navarra.

Sensitivity analysis showed the intrinsic population growth rate to be about four times less sensitive to changes in preadult survival than to changes in adult survival, and about 10 times less sensitive to changes in fecundity and predispersal survival. The immediate implication for the conservation of western European Bonelli's eagle populations is that efforts must be primarily directed towards increasing adult survival, rather than to increasing production of young. Increasing preadult survival and/or recruitment was shown to be essential to reduce population decline in some areas. However, some populations may show very specific problems of low productivity, and here efforts to increase adult survival and fecundity seems a sensible approach. The Burgos population would be a good example.

Although our model is very simple, it suggests the importance of dispersal, recruitment, spatial structure and movements for the understanding of the population dynamics of certain species (Court *et al.*, 1989; Wootton & Bell, 1992), and that these aspects should be the subject of future research. It is worthwhile noting that our analysis involves only populations located in the north and east Iberian peninsula and in France. No long-term data exist on the demography of southern Iberian populations. However, recent monitoring of some populations in Andalusia (Gil *et al.*, 1994) and Extremadura (Real *et al.*, in press; A. Sanchez, pers. comm.), indicate that they are stable or even increasing. Future research is needed to understand the dynamics of these populations and their relationship with the others. Other priorities for research should address dispersal, philopatry, mortality causes and habitat relationships

with these parameters. However, important urbanistic and transport plans (motorways, high speed railways, industrial estate and housing development) are being developed in some areas (El Vallès-Penedès and Provence), that will irreversibily change the shape of the breeding and hunting territories of the eagles. Research and conservation efforts to improve the demographic parameters of the eagles will be wasted if no appropriate landscape planning is undertaken in order to ensure enough space is kept for the eagles free from human interference.

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