

# Non-independence of demographic parameters: positive density-dependent fecundity in eagles

Miguel Ferrer<sup>1\*</sup> and Vincenzo Penteriani<sup>2</sup>

<sup>1</sup>Department of Biodiversity Conservation, and <sup>2</sup>Department of Conservation Biology, Estación Biológica de Doñana, CSIC, Avda María Luisa s/n, Pabellón del Perú, 41013 Seville, Spain

## Summary

1. Using information on the Doñana population of Spanish imperial eagles *Aquila adalberti* from 1959 to 2004, we present strong empirical support to theoretical models on the regulation of population trajectories by the relationships between breeder mortality and floater availability.
2. During the study period, the eagle population showed three distinct phases: (i) a population increase with negative density-dependent fecundity; (ii) a period of stability without any relationship between density and fecundity; and (iii) a population decrease with a positive relationship between density and fecundity.
3. A dramatic increase in annual adult mortality due to an increase in poisoning in hunting areas surrounding the Doñana National Park was recorded. The use of poison against generalist predators accounted for more than 54% of the total number of breeding eagles found dead since 1990, increasing annual adult mortality from 6.07 to 12.01%.
4. This high mortality reduced the population annually by 6% during the 1992–2004 period. Also, the population changed from a negative to a positive relationship between density and fecundity (Allee effect). These trends made the population approach extinction due to the double effect of increasing breeder mortality and low availability of floaters.
5. A supplementary feeding programme established in 1990 did not increase fecundity because it was a consequence of high adult mortality rather than low food availability. The high mortality of adults increased the risk of breeding failure and also decreased the availability of floaters, decreasing the likelihood of mate substitution.
6. *Synthesis and applications.* The main target in species conservation management plans is often a single demographic parameter (typically, fecundity in raptor populations). Our research demonstrates, however, that demographic parameters must not be considered as independent variables when formulating management programmes. The essential relationship between adult mortality and the availability of floaters must be better understood to avoid the risk of implementing inefficient management strategies. Although fecundity was low in this eagle population, it was a result of high adult mortality rates. Consequently, management must aim to correct the unusual mortality and recover the floater population.

**Key-words:** Allee effect, *Aquila adalberti*, breeder mortality, demographic parameters, density dependence, fecundity, floater, Spanish imperial eagle

## Introduction

When animal populations with a low number of breeders exhibit a positive relationship between per capita growth rate and population density, they are considered to be affected by the Allee effect (Allee *et al.* 1949; Courchamp, Clutton-Brock

& Grenfell 1999; Stephens, Sutherland & Freckleton 1999; Dennis 2002). The Allee effect increases the likelihood of extinction of a population because of a decrease in reproduction and/or survival. Several factors are associated with such an effect, one of the most common being the reduction in conspecific interactions at low numbers (e.g. decreased sexual reproduction due to shortage of mate encounters when density is too low, Amarasekare 1998). Small populations

\*Correspondence author. E-mail: mferrer@ebd.csic.es

can be dramatically impacted by the Allee effect (Lande 1988) because their small size makes them more sensitive to catastrophic collapses with only slight variations in demographic parameters (Courchamp *et al.* 1999). When the survival of a species depends on the health of its small populations, the Allee effect has the potential to be a primary cause of extinction.

The Spanish imperial eagle *Aquila adalberti*, with its global population of 200 pairs exclusively located in the Iberian Peninsula, is the most endangered bird of prey in Europe and one of the most threatened raptors in the world (Ferrer 2001). The most intensively studied population of this eagle is in Doñana National Park (south-western Spain), which consists of a maximum of 16 pairs (Ferrer 2001). Recently, Penteriani, Ojalora & Ferrer (2006) showed, by individual-based simulations, that a reduced availability of floaters (i.e. juvenile or subadult unpaired eagles) has the potential to strongly affect the breeding portion of the population, provoking a shift in the classical relationship (from negative to positive) between the fecundity (i.e. number of fledglings per pair) and density (i.e. number of pairs) of the population. This low availability is the result of high mortality of floaters (Penteriani *et al.* 2006) or a high level of recruitment provoking a relative decrease in floater number. A decrease in population size and fecundity results in a reduced number of floaters in subsequent years. A positive relationship between density and fecundity is therefore expected when the reduced numbers of floaters do not allow vacancies occurring in the breeding population to be filled.

The Doñana eagles have been studied since 1890, and the birds' unique long-term data set provides a valuable tool to help us in our understanding of the dynamics of small populations. By using the most complete information (from 1959 until 2004) from the available data, we present strong empirical support for the predictions of our previous models on this species (see Ferrer, Ojalora & García-Ruiz 2004 and references therein), showing the occurrence of the Allee effect and analysing possible management action to avoid the extinction of this population. We analysed the trajectory of this small and endangered population, trying to determine which parameters are affecting the recent decline and, consequently, which management actions must be adopted.

## Material and methods

### STUDY AREA

The study was conducted in Doñana National Park (south-western Spain) from 1959 until 2004. Three habitat types can be distinguished in the area: (i) Mediterranean scrublands, formed by shrubs such as *Halimium* spp., *Cistus libanotis*, and *Erica* spp., with scattered cork oaks *Quercus suber* and small stone pines *Pinus pinea* woods; (ii) marshes, principally consisting of *Scirpus* spp., which are flooded during winter and dry during summer; and (iii) coastal sand dunes, characterized by *Ammophila arenaria*, *Corema album*, and *Juniperus phoenicia*. The climate is of Mediterranean type with Atlantic influence (see Rogers & Myers 1980 for a more detailed description of the study area).

### THE SPECIES

The Spanish imperial eagle is a large (2500–3500 g), sedentary and territorial bird of prey, with a low reproductive rate (0.75 chicks per pair per year), an immaturity period of 4–5 years, and an estimated longevity of 21–22 years (Ferrer & Calderón 1990). It can be divided into three easily distinguishable plumage classes: (i) juvenile, with a tawny-coloured plumage that remains until the bird is 3 years old; (ii) subadult, with dark patches over a tawny base, present in 4- to 5-year-old birds; and (iii) adult, that is predominantly dun-coloured with characteristic white markings, present in birds 5 years or older. These differences make the detection of a mixed pair (one member of the pair in non-adult plumage) very easy.

Paired birds show territorial behaviour. Territories, with a mean size of 1200 ha, (range, 980–1870 ha; Ferrer 2001) are exclusive and vigorously defended throughout the year. In contrast, the behaviour of juvenile or subadult unpaired eagles (termed floaters) is radically different (Ferrer 1993). Floaters move between temporary settling areas and return to the natal population continually throughout the dispersal period (Ferrer 1993).

The Spanish imperial eagle population in the Doñana National Park consisted of 15–16 breeding pairs from 1977–1991. This is a very high population density for the species (occupying 20 000 ha of available habitat inside the National Park with a mean territory size of 1200 ha). The eagle population at Doñana is disjunct from other breeding populations of this species, as the nearest nesting eagles are 300 km away (estimate interchange with other population of one eagle each generation, i.e. 16.4 years; see Ferrer 2001).

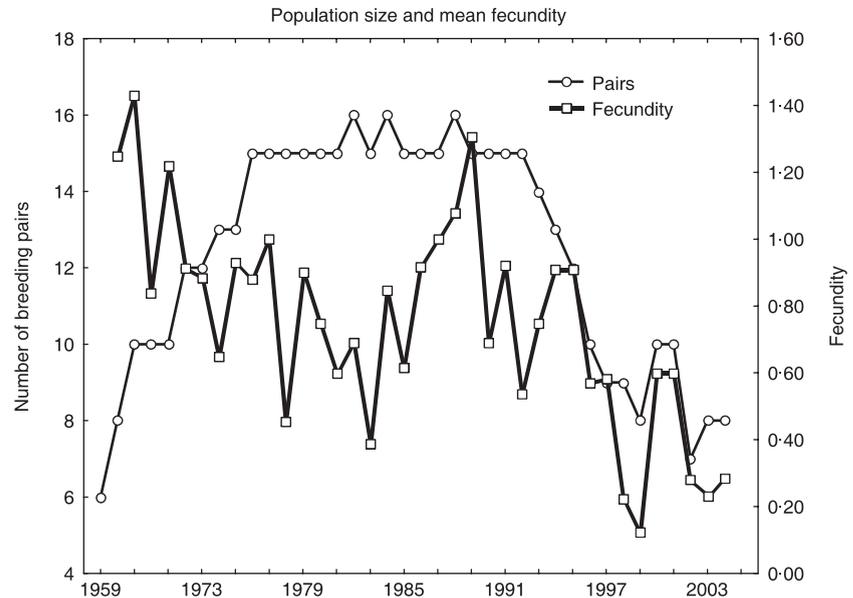
### FIELD DATA

The data used in this study were: (i) obtained from the Doñana Biological Station archives for the years 1959 to 1985; and (ii) collected in the field by one of the authors (M. F.) from 1985 to 2004 inclusive.

The whole National Park area was surveyed at the beginning of each breeding season to determine if pairs were present on breeding territories from the territorial demarcation and nest selection to the courtship period (January–February). The sedentary behaviour of this species and its tendency to call repeatedly greatly facilitates observation of a pair on its territory. Therefore, it is likely that all breeding attempts were detected, as were pairs that did not breed. When age of nestlings allowed visits to nests without any risk, nests were visited regularly to check the progress of reproduction and record the number of fledglings. We considered a breeding attempt as successful when the nestlings reached the age of 50 days (i.e. the age of ringing). Pairs that received less than two visits during the reproductive period were discounted from the calculation of productivity, as well as those years for which data at the beginning of the breeding season were not available. For the purpose of the present work, it was possible to collect information on population size, number of pairs that started breeding and fecundity for 36 years ( $n = 476$  breeding attempts) in the period 1959–2004. The temporal sequence and, consequently, the amount of information within such a data base, represent a unique opportunity to test predictions of population dynamics in birds.

### STATISTICAL METHODS

All the variables were tested for normality. We tested for trends with linear analysis using the *F*-ratio statistic to find whether the slope of the data was significantly different from 0. Variances of the linear



**Fig. 1.** Mean fecundity and breeder numbers in the Spanish imperial eagle population in Doñana (south-western Spain). When the population was increasing, an inverse relationship between population size and fecundity was detected (negative density dependence), no relationship was observed during the period of population saturation, and finally, when the population declined, a positive relationship characterized the link between fecundity and population density (positive density dependence or the Allee effect).

models were tested for homogeneity using Cochran's *C* statistic. Statistical significance was set at  $P < 0.05$  and analyses were conducted using the STATISTICA package.

## Results

### TEMPORAL TRENDS IN THE SIZE OF THE POPULATION FROM 1959 TO 2004

The breeding population of the Spanish imperial eagles in Doñana showed three distinct phases during the study period (Fig. 1): *Phase 1 or the population increase* at the beginning of the 1960s when the number of breeders increased from the six pairs present in 1959 to 15 pairs (1976); *Phase 2 or the stable population* from 1977 to 1991 when the breeding population remained stable at a threshold of 15–16 breeding pairs. This represented a saturated population for Doñana, occupying the 20 000 ha of available habitat inside the National Park with a mean territory size of approximately 1200 ha; and *Phase 3 or the population decrease* after 1992 when this population suffered a notable decline to only eight pairs in 2004.

### TEMPORAL TRENDS IN THE FECUNDITY OF THE POPULATION FROM 1959 TO 2004

Analysing 476 breeding attempts during the study period, the mean fecundity of the Doñana eagles showed (Fig. 1): (1 *or the negative density dependence*) a highly significant decrease (mean annual fecundity = 1.07 fledglings per pair, range = 1.43–0.7;  $F = 16.51$ , d.f. = 9,  $P = 0.003$ , see Ferrer & Donazar 1996) during the 1959–1976 period, when the population increased; (2 *or the high density period*) no trend during the period (1977–1991) of population stability (mean annual fecundity = 0.8 fledglings per pair, range = 0.38–1.08;  $F = 0.06$ , d.f. = 13,  $P = 0.94$ ); and (3 *or the positive density dependence*) a significant decline was observed again during the 1992–2004

period, when the population suffered a decline (mean annual fecundity = 0.59 fledglings per pair, ranging from 0.9 to 0.12 fledglings per pair;  $F = 7.549$ , d.f. = 12,  $P = 0.018$ ). At the beginning of the study, when the population grew, an inverse relationship between population size and fecundity was detected (1959–1976:  $r = -0.81$ , d.f. = 9,  $P = 0.004$ ), no relationship was observed during the period of population stability (1977–1991:  $r = 0.13$ , d.f. = 13,  $P = 0.643$ ), whereas a positive relationship characterized the most recent period when the population decreased (1992–2004,  $r = 0.72$ , d.f. = 12,  $P = 0.005$ ).

There were no differences in fledgling production per successful nest (instead of per nesting pair) between the three periods of population increase, stability and decline (ANOVA, mean number of fledgling per successful nest in *increase period* = 1.581, *stable period* = 1.833, and in *declining period* = 1.622;  $F = 1.34$ , d.f. = 2, 87,  $P = 0.268$ ).

### BREEDER AND FLOATER MORTALITY RATES IN A STABLE VERSUS A DECLINING SITUATION

Data on mortality rates and mate replacement was not available throughout the entire study period. However, it was possible to make comparisons between two samples representing the period of population stability (1974–1985) and the period of population decline (1990–2002).

Mortality records are shown in Table 1. Poisoning of adult eagles showed a significant increase over time with no record during the period 1974–1985, and with more than half of the adult mortality caused by poisoning during the period 1990–2002. Although illegal, the use of poison against generalist predators (typically foxes *Vulpes vulpes*) accounted for more than 54% of the total number of breeding eagles found dead since 1990 (Table 1). Thirteen adults were found dead in the period 1974–1985, the period of population stability. Taking into account that the Doñana population consisted of 15 pairs in those years and the relative isolation of this population

**Table 1.** Causes of mortality affecting the Doñana Spanish imperial eagles during the period of population stability (1974–1985) and the period of population decline (1990–2002). (Floaters, unpaired eagles; Adults, paired eagles)

Period	1974–1985			1990–2002		
	Floaters (%)	Adults (%)	Total	Floaters (%)	Adults (%)	Total
Poisoning	–	–	–	5 (16.6)	11 (52.4)	16
Electrocution	11 (50.0)	6 (46.2)	17	12 (40.0)	2 (9.5)	14
Shooting	7 (31.8)	6 (46.2)	13	4 (13.3)	4 (19.0)	8
Disease	1 (4.5)	–	1	6 (20.0)	1 (4.7)	7
Other causes	2 (9.2)	–	2	1 (3.3)	–	1
Unknown	1 (4.5)	1 (7.6)	2	2 (6.8)	3 (14.4)	5
Total	22	13	35	30	21	51

(only one among the 106 recoveries of ringed eagles in Doñana area was ringed outside Doñana population), this gives an annual adult mortality rate of 3.6%, equivalent to slightly more than half the mortality rate estimated by age-class sightings during these years (6.07%, Ferrer & Calderón 1990). During the 1990–2002 period of population decline, 21 adult eagles were found dead, which gives a minimum annual adult mortality rate of 6.5%. Considering the population size, and assuming that the probability of finding a dead eagle was the same in both periods, we can estimate an annual adult mortality rate of 10.9% during the 1990–2002 period.

Mate replacement primarily involved the substitution in a pair of an individual with adult plumage for one with immature (i.e. juvenile or subadult) plumage. The figure obtained from analysing replacements represents an estimate of the minimum adult mortality level (Ferrer & Calderón 1990). Taking into account the population size and observed replacements during the 1990–2002 period, we deduce an annual mortality rate of 12.01%. In consequence, annual adult mortality would have been increased by 100% with respect to usual values of a stable population.

The number of non-adult birds found dead in the Doñana population was similar between the two periods, after controlling for population size (Table 1). We therefore assumed a pre-adult mortality of 83–84% in both periods (Ferrer & Calderón 1990).

#### ESTIMATED AND REAL POPULATION DECREASES

According to the classic theory of deterministic population dynamics applied to birds of prey (Mertz 1971; Ferrer & Calderón 1990; Ferrer & Hiraldo 1991), the finite index of natural increment ' $\lambda$ ' gives us an idea of the velocity with which the population numerically increases or decreases. This index is defined by the following equation:

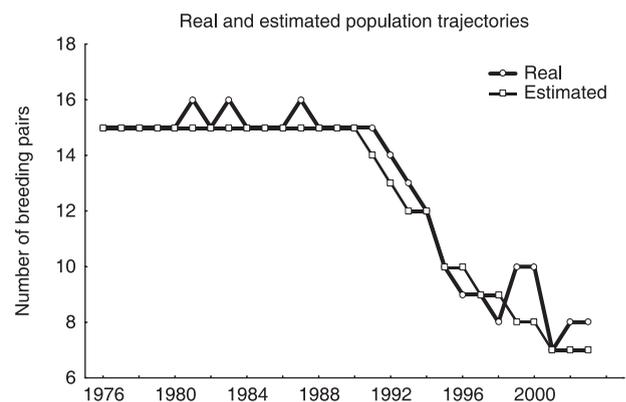
$$1 = \sum \lambda^x l(x)m(x) \quad \text{eqn 1}$$

where ' $x$ ' = the age in years, ' $l(x)$ ' = probability at birth of living to age ' $x$ ', and ' $m(x)$ ' = number of daughter births. If reproductive age is assumed to be 5 years,

$$\lambda^5 - p\lambda^4 - \beta(e/2) = 0 \quad \text{eqn 2}$$

**Table 2.** Basic demographic parameters of the Spanish imperial eagle population of Doñana National Park during the period of population stability (1974–1985) and the period of population decline (1990–2002)

Parameter	1974–1985	1990–2002
Annual adult mortality	6.07%	12.01%
Pre-adult mortality	83.86%	83.86%
Fecundity	0.7525	0.5924
Annual percentage of population change	0%	–6%

**Fig. 2.** Comparison between two population trajectories of Doñana eagle population, one according to estimated demographic parameters and the other the real observed one.

where ' $p$ ' = annual adult survival, ' $\beta$ ' = floater survival until age of breeding, and ' $e$ ' = chick productivity per pair per year.

The percentage annual change in the population equals:

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

Applying the parameters obtained from Table 2, the population would decrease annually by 6% during the 1990–2002 period. Taking into account this figure, we made an estimated trajectory for the population decrease that is nearly identical to the observed one (Fig. 2), supporting the robustness of the parameter estimations.

## RELATIONSHIP BETWEEN ADULT MORTALITY AND FECUNDITY

During the most recent period of the present study (population decline phase, 1992–2004), recorded fecundity was lower than in the previous two periods (population increase and population stability phases) with a mean value of 0.59 fledglings per pair and year. Starting in 1992, the population decreased by about 6% per year (Fig. 1). During the period of population stability, annual adult mortality rate was around 6% and the expected number of adults that died per year was 1.8 for a population of 15 pairs.

The breeding cycle in the eagles lasts for about 8 months, from the beginning of February when egg-laying starts to the beginning of October when the last chicks finally become independent of their parents (Ferrer 2001). Assuming that the probability of death is uniform throughout the year and that both parents are necessary during the whole cycle, with a 6% rate of adult mortality, the eagle population lost one pair during the breeding season each year on average. In consequence, fledgling production of the entire population is expected to change from 11.3 to 10.53. Thus, in a stable population with normal adult mortality, the effect of adult mortality on fecundity could be ignored. Nevertheless, in a population of 15 pairs with an annual adult mortality of 12.01%, as during the 1992–2004 period, the predicted adult mortality rate is 3.6 per year and the expected fecundity is 0.6 fledglings per pair. As adult mortality increases, its effects on fecundity also increases.

## RELATIONSHIP BETWEEN BREEDER MORTALITY AND FLOATER AVAILABILITY

The frequency of breeders in immature (non-adult) plumage varied over the years with a mean value of 1.7 mixed pairs and 2.4 immature eagles breeding per year. The frequency of presence of at least one immature in a breeding pair was the highest in 2001, when mixed pairs represented 42.8% of the total breeding pairs and 30% of the breeding individuals were in immature plumage. The increase in percentage of immature breeders was significantly related to decrease in population size ( $r = -0.654$ ,  $P < 0.001$ ,  $n = 27$ ; Ferrer *et al.* 2003). In addition, a significant relationship was found between adult eagles found dead in Doñana and percentage of immature breeders ( $r = 0.540$ ,  $P = 0.006$ ,  $n = 27$ ; Ferrer *et al.* 2003); that is, a higher proportion of immature breeders were detected in those years characterized by a higher mortality of adult eagles. A significant negative relationship was found between percentage of immature breeders in the population and mean fecundity ( $r = -0.360$ ,  $P = 0.033$ ,  $n = 35$ ), with immature breeders increasing as fecundity decreases.

Taking into account the dynamics of the species, an isolated population of 15 pairs has an annual average of 5.72 floaters between 3 years and 5 years of age that are able to occupy vacancies in the breeding population (Ferrer *et al.* 2004). During the study sample 1990–2002, 52 immature breeders were recorded in breeding pairs (Ferrer *et al.* 2003), with an

annual mean of 4.33 immature breeders. According to the population size, the total floater population available in those years can be estimated at 56 birds with an annual mean value of 4.31, that is 93% of the floaters between 3 years and 5 years old were recruited during these 12 years, with 100% of recruitment during the last 6 years. This incredibly high recruitment rate of immature eagles would have had the same effect on the population as that of a hypothetical increase of floater mortality, that is the appearance of a positive relationship between density and fecundity (Penteriani *et al.* 2006) due to the increasing difficulty of replacing a lost mate in the breeding population. Due to the long breeding cycle in the eagles (nearly 8 months), a delay in mate substitution could result in the loss of the breeding season that year.

## Discussion

The history of the Doñana population of the Spanish imperial eagle that we were able to document for the last 50 years constitutes a rare, well-studied example of how an increasing and then stable population may subsequently show a significant decline due to the double effect of increased breeder mortality and a consequent low availability of floaters (e.g. Allee effects or decline in both number of breeding pairs and fecundity; Penteriani *et al.* 2006). Although floaters were seen to enter the breeding population of the Doñana eagles when the mortality of adult breeding eagles increased (e.g. by poisoning), this did not allow the population to increase to a stable or saturated level. Both increases in adult mortality and decreases in floater availability increased the frequency of vacancies in breeding pairs and the risk of delay in substitution, in turn affecting the fecundity of the population.

During the early 1990s, at the beginning of the period of population decline, the observed 6% per annum decrease in density at Doñana could be explained by the increase in breeder mortality alone. As previous analyses have shown (Ferrer & Calderón 1990), breeder mortality alone can strongly affect the size of the population over a short period. The fact that floaters spend most of their time in the dispersal areas, and that these areas are more than 90 km away from breeding populations with differences in the intensity of human hunting activities among them (Ferrer 2001), could explain different possibilities for young eagles to encounter poisoned baits. The intensity of the effect of adult mortality could be very high in the Doñana population because this population is geographically isolated from the other breeding populations of Spanish imperial eagles due to both distances (i.e. the nearest breeding individuals being approximately 300 km away; Ferrer 2001) and preferences in dispersal routes (Ferrer 1993). Moreover, due to this segregation, the Doñana population strongly depends on the floaters, since these individuals are the most likely source of new breeders where there are empty nesting territories (Ferrer *et al.* 2003, 2004; Ferrer & Penteriani 2003; Penteriani, Otalora & Ferrer 2005a; Penteriani *et al.* 2005b). The importance of immature floaters as replacement mates has been already reported for several species in which a decrease in breeder survival has resulted in

a corresponding decrease in the age of first breeding (e.g. wandering albatross *Diomedea exulans*, Weimerskirch & Jouventin 1987; golden eagles *Aquila chrysaetos*, Steenhof, Kochert & Doremus 1983; and Bonelli's eagle *Hieraetus fasciatus*, Balbontin, Penteriani & Ferrer 2003).

An alternative explanation for the observed decline in eagle fecundity is a decrease in the density of rabbits *Oryctolagus cuniculus* (the main prey for the eagles) due to a new disease, the rabbit haemorrhagic disease (Villafuerte *et al.* 1994; Ferrer & Negro 2004). Although the increase in poisoning was probably related to the decrease in rabbit densities, it is unlikely that the decrease in eagle fecundity could be attributable directly to this disease. During the population decline of the eagles (1992–2004), all nests were provided with supplementary food in order to avoid any effect of decreasing rabbit availability. This management technique is known to be effective in this species by reducing nestling mortality in situations of food shortage (González *et al.* 2006). Secondly, if food shortage was the cause of fecundity decline, we would also expect a decline in the number of young per successful nest. The fact that young per successful nest was the same in both periods strongly suggests that adult mortality and the delay in the replacement of breeding adults were the main driving factors of the unexpected positive relationship between density and fecundity.

### Synthesis and applications

The history of the Doñana population of Spanish imperial eagles illustrates a well-known but sometimes forgotten lesson: demographic parameters are not mathematically independent variables. As we have demonstrated, changes in adult mortality can dramatically affect other demographic parameters such as fecundity, both directly by an increasing risk of a breeding pair failing to breed due to the death of one of the members, or indirectly due to a decrease in the availability of floaters available to occupy the vacancies, increasing the time of substitution and, consequently, decreasing fecundity.

The main target in species conservation management plans is often a single demographic parameter (typically fecundity in raptor populations) and the consequences of management activities for other demographic parameters are often not considered. In the case of the Doñana population of eagles, management activities to attempt to increase fecundity were initiated as soon as fecundity started to decline in 1991. These actions were mainly the provisioning of food close to active nests during the nesting period to try to avoid the loss of nestlings by starvation and through siblicide (González *et al.* 2006). The use of supplementary feeding is recommended as a method of increasing fecundity under a situation of temporal food shortage (Ferrer 2001; González *et al.* 2006). However, as this study has demonstrated, the reduction in fecundity in eagles in Doñana was related to annual adult mortality and a decrease in the availability of floaters, and therefore, it is very unlikely that supplementary feeding would have any observed effect on fecundity. In practice, the effect of food in fecundity became evident with the food provisioning. In light of these

results, a new set of management techniques have been applied since 2006, including 0.5 ha fenced areas with live rabbits provided throughout the year to reduce the movement of adult eagles outside the National Park, thereby avoiding the risk of poisoning and decreasing adult mortality. At the same time, managers have initiated a radio-tracking programme to detect eagle mortality, and they have developed an educational programme to explain the consequences of poisoning to hunters.

This study has demonstrated that demographic variables are not independent parameters when analysing endangered small populations. More detailed analyses are needed to determine the main factors involved in a population trajectory. The essential relationship between adult mortality and the availability of floaters must be better understood to avoid the risk of implementing inefficient management strategies in long-lived species with deferred sexual maturity. Although fecundity was low in this eagle population, it was a result of high adult mortality rates. Consequently, management must aim to correct the unusual mortality and recover the floater population. By concentrating efforts to increase fecundity by food provisioning at the nests, the decline was not controlled. This study has revealed the need for more realistic approaches to management of small and decreasing populations, using for example individual-based simulation models including demographic parameters as non-independent variables and long-term series of field observations.

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