Variations in the age of mates as an early warning signal of changes in population trends? The case of Bonelli's eagle in Andalusia

Javier Balbontín*, Vincenzo Penteriani, Miguel Ferrer

Department of Applied Biology, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Avda. de María Luisa s/n, Pabellón del Perú, Seville 41013, Spain

Abstract

Methods to evaluate population trends have recently received particular attention because of the decreasing patterns shown by several species since the nineteenth century. We have studied demographic traits of the Bonelli's eagle (*Hieraaetus fasciatus*) population of Andalusia (southern Spain) for 20 years (1980–2000). This species is endangered and is suffering a rapid decline in most of its distribution range. Although our study population has remained stable for the last 10 years, both age at first breeding and productivity have decreased during the last 5 years. We propose that age at first breeding could be used as a potential early warning signal to detect possible future changes in population trends of long-lived species with deferred maturation age. In particular, in this species spatial variation in demographic traits could help to detect whether unnatural events such as shooting are decreasing age at first breeding and productivity. If occupation of territories by non-adults is caused by human persecution, conservation efforts in the particular case of Bonelli's eagle have to be directed to protect those breeding territories where an increase in the percentage of pairs containing at least one non-adult individual would be detected.
© 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Age at first breeding; Breeding performance; Demographic traits; Replacing rate; Population monitoring and trends; Early warning signals

1. Introduction

The widespread decline in the range and abundance of many species of birds that has occurred since the nineteenth century has been a subject of great concern for researchers and conservationists. Therefore, there have been many initiatives designed to detect wildlife population trends and to provide effective management and conservation for endangered or threatened species (Tucker and Heath, 1994). The long-term monitoring of animal abundance, the study of animal distribution and the successive examination of the detected patterns have been used as methods to determine the status of populations and their trends. However, census techniques detect changes in population trends once they have already occurred, and therefore lack predictive capability.

The Bonelli's eagle (*Hieraaetus fasciatus* Vecillot, 1822) is a long-lived bird of prey with a maximum life span of 20 years in captivity (Newton, 1979). This species is characterised by a modal clutch size of two eggs (range 1–3) and a mature reproduction age of about 3.5 years (Cramp and Simmons, 1980). It can therefore be included among the ''survival species'', which are characterised by having a late mature reproduction age, a low fecundity rate and a high adult survival rate (Sæther, et al., 1996).

This bird of prey has suffered a rapid decline in its whole distribution range (Rocamora, 1994, France: Cugnasse, 1984; Portugal: Palma et al., 1984; Greece: Hallman, 1985; and Spain: Arroyo et al., 1990; Real and Mañosa, 1997). The European population is currently estimated at between 938 and 1039 breeding pairs (Real et al., 1996) and is classified as endangered (level SPEC 3, Unfavourable Conservation Status and not concentrated in Europe) (Tucker and Heath, 1994).

The Andalusia region (southern Spain) is one of the last strongholds of this species, whose populations are

* Corresponding author. Tel.: +34-95-4232340; fax: +34-95-5621125.
E-mail address: balbonja@ebd.csic.es (J. Balbontín).

nowadays mainly confined to the Iberian Peninsula and northern Africa (Real et al., 1996). The main aim of this study was to investigate whether and how age at first breeding can be used as an early warning signal to predict changes in the breeding performance and viability of bird populations.

2. Species and study area

We studied the whole Bonelli's eagle population of Andalusia (5°32′ W, 36°41′ N), which represents 32.6% of the European population (Balbontín et al., 2000). We monitored the breeding population of the Baetic Mountains, the main mountain system of the region, composed of the Penibaetic massif in the south, close to the Mediterranean Sea, and the Subbaetic one in the north (Fig. 1). The altitude ranges from 80 to 3482 m a.s.l., and the climate is Mediterranean and Sub-arid (Rivas-Martinez, 1986), characterised by mean annual rainfall ranging from 200 to 1500 mm. The landscape is characterised by a mosaic structure of forests (*Quercus*

0   2   4

2 cm = 78.6 km

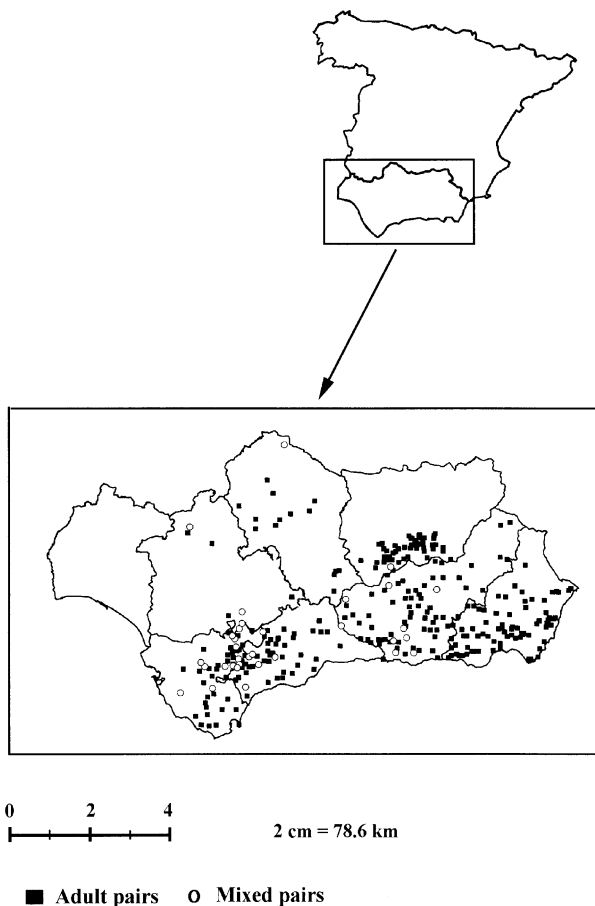■ **Adult pairs**   o **Mixed pairs**

Fig. 1. Distribution range of Bonelli's eagle in Andalusia. Open circles indicate territories occupied by mixed pairs (with at least one non-adult).

suber, *Q. rotundifolia* and *Pinus* spp.), matorral (*Quercus coccifera*, *Thymus vulgaris* and *Rosmarinus officinalis*), calcareous rocks, pastures and fallow lands at lower altitudes.

Bonelli's eagle builds its nests mainly on cliffs, pairs nesting on trees being much less common (Arroyo et al., 1990), except in southern Portugal (Palma et al., 1984). This eagle is sedentary in Europe and its members defend territories throughout the year.

3. Methods

3.1. Data collection

During the 20 years of field work, and with the collaboration of five ornithologist groups, we collected data on breeding biology and productivity of Bonelli's Eagle in Andalusia over a sample of 298 breeding sites. The term "nesting cliff" is used to denote the cliff where a pair attempts to breed, successfully or not. Between January and early February, we checked for territory occupancy (e.g. territorial displays, nests material transfers). During this first check, we also recorded the age of the territory holders. An individual was considered as an adult when its wing feathers did not show pale bars ($>$ 3 1/2 years old; Cramp and Simmons, 1980; Forsman, 1999). Sexing of adults in the field requires considerable experience. To avoid biases associated with differential skills of fieldworkers in sexing eagles, we pooled data from the two sexes and considered the adult and non-adult classes only. We defined a mixed pair as one containing at least one non-adult individual. A second check of the nesting cliffs was made from late February to March to record egg laying, and the third and last visit occurred during April and May, to estimate the number of fledged young. Breeding performances were expressed as percentage of nests that fledged at least one chick, mean number of young fledged per pair occupying a territory (hereafter referred to as *productivity*) and mean number of young fledged per successful pair (Steenhof, 1987). We also calculated the variation in fecundity by the *coefficient of variation* (hereafter CV; Ferrer and Donázar, 1996). We also estimated a measure of mate replacement as a rate of territory occupancy by adult breeders (hereafter RAB) from data of recruitment of non-adults as breeders; that is, when we observed a non-adult replacing an adult, the latter was assumed to be dead or migrating to another breeding site (our set of data never permitted to distinguish among these two cases). We used the frequency of non-adults both within the same territory over the years or within the same year among breeding territories to estimate the RAB as followed:

within territories $\text{RAB} = 1 - (NA/2Y)$

among years $\text{RAB} = 1 - (NA/2BT)$

where NA is the number of non-adults that replaced adults, Y is the number of years a territory was monitored and BT is the number of breeding territories monitored for a given year. We multiply by two because there are two possibilities of replacement within each territory.

3.2. Statistical analysis

Nest site dispersion was analysed by means of the G-statistic, calculated as the ratio between the geometric and the arithmetic mean of the squared nearest neighbour distance (NNDs). The index ranges from 0 to 1: values close to 1 (> 0.65) indicate a uniform distribution of nests (Brown, 1975). We employed a one-way ANOVA to detect possible year-to-year differences in productivity. Several analyses were run on a sub-sample of breeding sites ($n = 37$), for which we had a complete set of data for all the variables of interest, such as variation of demographic traits within territories. Moreover, for these analyses, we only considered those territories where at least a 5-year period of data was available. This set of data was analysed by linear regression or non-parametric correlation to evaluate the possible relationships between the CV of productivity, the mean number of young fledged per breeding pair and the rate of territory occupation by adult breeders. When data were not normally distributed, they were $\log_e$, square-root or arcsine square-root transformed prior to parametric tests (Sokal and Rohlf, 1998). All tests were two-tailed and statistical significance was set at $P < 0.05$. Means are given with ± 1 S.D. All tests were computed using SPSS 10.0.

4. Results

4.1. Population characteristics

Although Bonelli's eagle populations have suffered a notable decline elsewhere in their breeding areas, the population of Andalusia has remained stable for at least the last 10 years ($\chi^2 = 10.98$, d.f. $= 11$, $P > 0.10$) (Table 1). The mean NND was 7000 ± 4079 m ($n = 203$), and the

Table 1
Comparison of the number of occupied territories of Bonelli's eagle in Andalusia: 1990 (Arroyo et al., 1990) vs. 2000

Province	1990	2000	Source (Census, 2000)
Cádiz	36	38–43	Del Junco, O., Paz, J.L. and J. R. Benitez
Málaga	50–58	45–50	Del Junco, O. and J.L. Paz.
Granada	29–37	39–44	Gil-Sánchez, J.M. and collab. D. Ontiveros
Almería	55–72	55–62	Manrrique, J. and collab.
Jaén	43–45	46–57	Madero, A., Rico, J. and P.A. Jódar.
Sevilla	6	7–8	Andalusia Government
Huelva	1	2	Barroso, J.L.

population was uniformly distributed over the region (G-statistic $= 0.75$, $n = 203$).

The mean number of fledged young per breeding pair was 1.39 ± 0.71 ($n = 591$), and the mean number of fledged young per successful pair was 1.59 ± 0.51 ($n = 518$). 12.2% of the breeding pairs did not fledge young, 37.2% fledged one young, 49.7% fledged two young and 0.9% fledged three young. In 13 cases, it was possible to determine the exact causes of reproductive failures: eight failures (61.5%) were due to human disturbance, and the remaining five to egg (7.7%) and young (30.8%) predation.

4.2. Temporal variation in breeding performance

Year to year differences was detected for the mean number of young fledged per breeding pair ($F_{17, 573} = 1.809$, $P = 0.024$): average values were the lowest in 2000, and lower in 1996 than in 1993 and 1998 (LSD Test, $P < 0.05$). The CV of productivity increased significantly in the last 20 years ($F_{1, 16} = 8.769$, $P = 0.009$). There were no year to year differences in the mean number of fledged young per successful pair ($F_{17, 500} = 0.829$, $P = 0.66$). A mean of $92.9 \pm 7.1\%$ of the breeding pairs reproduced successfully each year, but their number decreased significantly during the study period ($\chi^2 = 247.0$, d.f. $= 196$, $P = 0.008$).

4.3. Temporal variation of age at first breeding.

The frequency of territory occupation by non-adults varied over the years ($F_{20, 958} = 4.386$, $P = 0.0001$) and was higher in 1999 and 2000 than before (LSD Test, $P < 0.05$). Starting with 1997, the percentage of adult pairs in the population decreased by about 10%, and between 1997 and 2000 the percentage of pairs with one non-adult ($\bar{x} = 6.6 \pm 4.3\%$) or two non-adults ($\bar{x} = 1.1 \pm 2.2\%$), and of unpaired adults at breeding sites ($\bar{x} = 1.3 \pm 4.0\%$) increased steeply (Fig. 2).

4.4. Spatial variation in RAB

Territories differed in their RAB values. We found an average RAB of $97.5 \pm 4.43\%$. Minimum RAB for a territory was 81.8% and 28 out of 37 (75.6%) territories showed a RAB of 100%. The breeding sites in which we detected the lower RAB rates were also those that produced fewer fledglings and that were more variable in their breeding output (Fig. 3). In fact, RAB and productivity within territory were positively correlated ($r_s = 0.31$, $P = 0.05$, $n = 37$). On the other hand, we also detected a negative correlation between RAB and the coefficient of variation of productivity ($r_s = -0.415$, $P = 0.01$, $n = 37$), as well as between productivity and its coefficient of variation ($r_s = -0.774$, $P < 0.001$, $n = 37$).
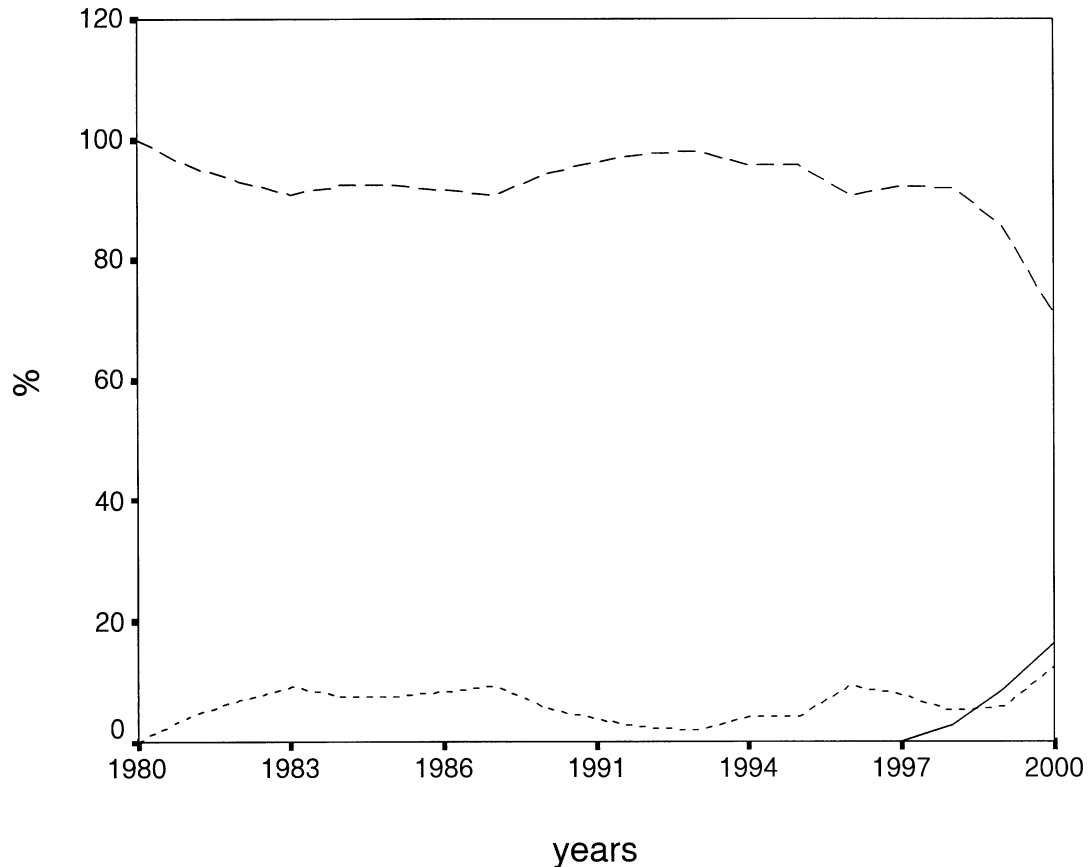
Fig. 2. Variations in pair composition over time (1980–2000) in : (1) percentage of adult pairs (upper broken line), (2) percentage of mixed pairs (lower broken line), and (3) percentage of territories occupied by one unpaired adult (solid line).

5. Discussion

5.1. Population trends

Unlike in other areas of the Bonelli's eagle distribution range, the comparison of the 1990 and 2000 censuses showed that the number of Andalusia breeding pairs has remained relatively stable, at least during the last decade. However, we have detected several changes in age of mates and productivity that could be a first signal of a possible future change in population viability. During recent years, the age at first breeding decreased for many of the monitored breeding pairs. Ten years ago, Arroyo et al. (1990) found that only 2.6% of non-adult individuals were part of breeding pairs, whereas today non-adults occur in 7.3% of pairs. Age at first breeding is an important factor in the population dynamics of avian species (Lack, 1968; Henny et al., 1970; Newton, 1979). There can be two causes of an increase of non-adult individuals in the breeding sector of a population. First, it could be due to an increase in mortality rate, either pre-adult or adult (Valverde, 1960; Novelletto and Petretti, 1980; Ratcliff, 1980; Steenhof et al., 1983); second, it could be due to an increase in availability of resources such as nest sites
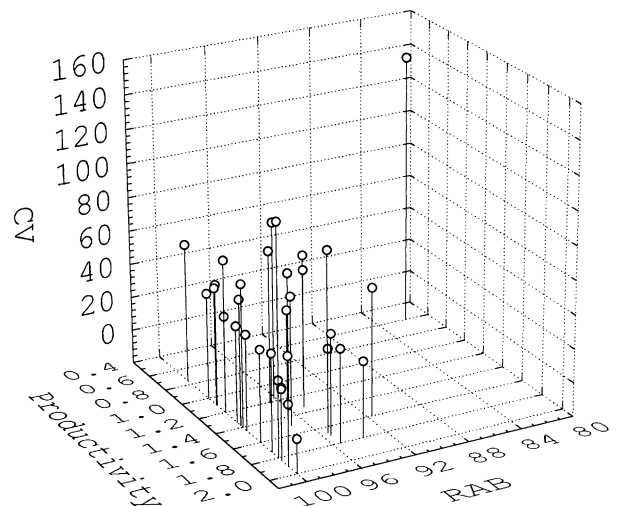

Fig. 3. Classification of territories according to rate of adult breeders (RAB), productivity and coefficient of variation of productivity.

or food (McGowan, 1975; Newton, 1976; Broomer et al., 1998). We were able to obtain data on the pre-adult survival rate from fledging to recruitment of 30 radio-tagged offspring from 1998 to 2000 (Balbontín et al., 2000). The value of 42% so obtained was higher than

for other birds of prey. For example, the pre-adult survival rate was 37% for osprey (*Pandion haliaëtus*) (Poole, 1989), about 30% for Verreaux's eagle (*Aquila verreauxi*) (Gargett, 1990), 26% for peregrine (*Falco peregrinus*) (Wootton and Bell, 1992), 10% for bald eagle (*Haliaëtus leucocephalus*) (Sherrod et al., 1977) and 8–17% for Spanish imperial eagle (*Aquila adalberti*) (Ferrer and Calderon, 1990). Therefore, it seems unlikely that a low pre-adult survival rate would produce a lack of adult individuals in the study population.

On the other hand, no difference was found in the densities of their main prey, rabbits (*Oryctolagus cuniculus*, Gil-Sánchez et al., 1994; Ontiveros and Plaguezuelos, 2000) between occupied and deserted territories in a part of the Andalusia population (Ontiveros and Plaguezuelos, 2000). In addition, rabbits have suffered a rapid decline in Andalusia, as in most parts of their European range, due to diseases such as myxomatosis and viral haemorrhagic disease (Beltrán, 1991; Villafuerte and Moreno, 1991; Villafuerte et al., 1994). Finally, the number of occupied territories has remained stable through the last decade and the territories were evenly distributed over the region. Therefore, neither an increase in food availability nor an increase in nest site availability is likely to have caused the observed increase in the number of non-adults recruited to breeding territories. However, evidence does exist that a decrease in age at first breeding could be due to an increase in adult mortality rate. Recently, Real et al. (2001) recorded 377 cases of death of Bonelli's eagles between 1990 and 1998 in Spain. From eagles of known age, 91 out of 241 cases were adult individuals. Therefore, on the basis of the information presented above, the most probable cause of the presence of non-adult eagles in breeding pairs would be a decrease in adult survival rate rather than either an increase in resource availability or a decrease in pre-adult survival rate. Moreover, the review by Real et al. (2001) showed that adult individuals died mainly in their breeding areas from human persecution (60.4%). Game shooting activities seem to be directly associated with the majority of the causes of death in adult Bonelli's eagle (Real et al., 2001). A decrease in adult survival has also been related to a decrease in the age of first breeding in wandering albatross (Weimerskirch and Jouventin, 1987) and golden eagles (Steenhof et al., 1983). Nevertheless, we could not reject the hypothesis that high pre-adult survival rates in the past (before 1998, when we started monitoring offspring) could be a possible cause of a decrease in age at first breeding. However, in this case, we might expect a decrease in the numbers of territories occupied by non-adult eagles in future years.

In long-lived species, adult survival rate is the factor most closely correlated to future population trends (Stearns, 1976). Thus, environmental factors affecting adult survival are likely to have a higher impact on population trends than factors affecting fecundity or dispersal (Benton and Grant, 1996). In the study population, unnatural events such as human disturbance through electrocution or shooting causalities are directly affecting the most sensitive demographic trait. In agreement with this, previous analyses performed in northern populations have shown that population growth rate is four time less sensitive to changes in pre-adult survival than to changes in adult survival, and about ten times less sensitive to changes in fecundity (Real and Mañosa, 1997).

We also found that a decrease in RAB over time was linked to a simultaneous decrease in productivity. Because of an increase in adult mortality rate, non-adults eagle might be expected to take advantage of the vacancies generated in breeding territories. Due to this phenomenon, and to the availability of non-adult floaters in the study area, the result was a decrease in productivity (probably due to the low breeding experience of non-adults) rather than a loss of breeding territories, as also observed in other raptor species (e.g. Steenhof et al., 1983; Pedrini and Sergio, 2001). Another effect associated with decreased RAB was an increase in the variation in productivity. These results are reinforced by previous studies that suggested that age affected mean and variance of productivity in Bonelli's eagle (Penteriani et al., unpublished data).

5.2. Spatial variation in demographic traits

Territories differed in how demographic traits of breeding individuals were affected by temporal variation of environmental conditions. In territorial species, because of habitat heterogeneity (Wiens, 1976; Turner, 1989; Kotliar and Wiens, 1990), individuals occupying different habitats may experience different probabilities of survival or reproduction, depending on the quality of the habitat they occupy (e.g. Weiss et al., 1988; Ferrer and Donázar, 1996; Newton, 1989; Kadmon, 1993; Penteriani et al., in press). However, few studies have demonstrated spatial variation in demography, though some have shown spatial variation in particular life history traits (e.g. Dhondt et al., 1990; Blondel et al., 1992; Sæther et al., 1999). We found that Bonelli's eagle territories differed in their RAB rate, productivity and variance of productivity. Thus, mates occupying the most productive territories, which we consider as high-quality breeding sites, showed less variability in productivity and were less affected by non-adult presence in the breeding pairs. Conversely, mate changes involving non-adults occurred more frequently in pairs occupying low-quality territories and, consequently, showing lower productivity. A parallel study has shown that territories occupied by non-adult eagles were closer to the nearest source of potential human disturbance, such as built-up

areas and roads (Penteriani et al., unpublished data). Consequently, these territories would be exposed to a higher degree of human persecution or disturbance.

5.3. Conservation implications

Our results show the importance of long-term studies of demographic traits, especially age at first breeding and productivity, in long-lived territorial avian species characterised by deferred maturity. In territorial species, data collected in such a way could be used in early detection of temporal changes in adult survival rate, once other possible causes that might provoke a decrease in age at first breeding have been rejected. Actually, regular monitoring of the age-structure of territorial pairs can be a potentially reliable method to forecast changes in population viability. Such a method may have better predictive power than the simpler and more common surveys of the number of pairs that are present each year on the breeding territories. Moreover, it is crucial to locate precisely where an increase in mate replacement by non-adults has taken place before planning interventions. This kind of analysis therefore provides a potentially useful tool in conservation biology. On the other hand, if the cause of a decrease of age at first breeding was an increase in resource availability, monitoring of demographic data could also indicate a future increase in population size, and would therefore represent highly valuable information from a conservationist point of view.

If occupation of territories by non-adults is caused by human persecution, conservation guidelines might be directed primarily at protecting those breeding territories where recruitment of non-adult eagles is detected. In the specific case of Bonelli's eagle, priority efforts might be made to protect those areas by increasing vigilance during the hunting season. On the other hand, the high values found in some demographic trait such as productivity and pre-adult survival rate seem to indicate that, in a metapopulation context characterised by a source-sink system (Pulliam, 1988), the Andalusian subpopulation has most probably been working as a source where births have exceeded deaths. However, if human persecution continues to erode the number of adult breeders, this situation could affect population growth rates in this important portion of the European population. In addition, as a sink population depends on immigration of individuals from source subpopulations (Pulliam, 1988; Pulliam and Danielson, 1991), severe effects in source dynamics might cause a rapid decline elsewhere in the breeding range.

Acknowledgements

References

Arroyo, B., Ferreiro, E., Garza, V., 1990. Inventario de la población Española de Águila Perdicera Hieraaetus fasciatus y sus áreas de cría. ICONA, Madrid.

Balbontín, J., Penteriani, V., Ferrer, M., 2000. El águila perdicera en Andalucía: situación actual y tendencias en las áreas de reproducción y de dispersión juvenil. Junta de Andalucía/Consejo Superior de Investigaciones Científicas.

Beltrán, J.F., 1991. Temporal abundance pattern of the wild rabbit in Doñana, SW Spain. Mammalia 55, 591–599.

Benton, T.G., Grant, A., 1996. How to keep fit in the real world: elasticity analyses and selectiom pressures on life histories in a variable environment. American Naturalist 147, 115–139.

Blondel, J., Pradel, R., Lebreton, J.D., 1992. Low fecundity insular blue tits do not survive better as adult than high fecundity mainland ones. Journal of Animal Ecology 61, 205–213.

Broomer, J.E., Pietiäinen, H., Kolunen, H., 1998. The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. Journal of Animal Ecology 67, 359–369.

Brown, D., 1975. A test of randomness of nest spacing. Wildfowl 26, 102–103.

Cramp, S., Simmons, K.E.L., 1980. Handbook of the Birds of Europe, the Middle East and North Africa—Vol. 2. Oxford University Press, Oxford.

Cugnasse, J.M., 1984. L'Aigle de Bonelli Hieraaetus fasciatus en Languedoc-Roussillon. Nos Oiseaux 37, 223–232.

Dhondt, A.A., Adriansen, F., Matthysen, E., Kempenaers, B., 1990. Nonadaptative clutch size in tits. Nature 348, 723–725.

Ferrer, M., Donázar, J.A., 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. Ecology 77, 69–74.

Ferrer, M., Calderon, J., 1990. The Spanish Imperial Eagle Aquila adalberti in Doñana National Park south west Spain: a study of population dynamics. Biological conservation 51, 151–161.

Forsman, D., 1999. The Raptors of Europe and The Middle East. A Handbook of Field Identification. T and AD Poyser, London.

Gargett, V., 1990. The Black Eagle. A Study. Acorn Books, Randburg.

Gil-Sánchez, J.M., Molino, F.M., Valenzuela, G., 1994. Parámetros reproductivos y alimentación del Águila Real Aquila chrysaetos y del Águila Perdicera Hieraaetus fasciatus en la Provincia de Granada. Aegypius 12, 47–51.

Hallmann, B. 1985. Status and conservation of birds of prey in Greece. In: Newton, IY, Chancellor, RD. (eds.), Conservation Studies on Raptor, ICBP Technical Publication 5, 55–59.

Henny, C.J., Overton, W.S., Wight, H.M., 1970. Determining parameters for population using structure models. Journal of Wildlife management 34, 690–703.

Kadmon, R., 1993. Population dynamic consequences of habitat heterogeneity: an experimental study. Ecology 74, 816–825.

Kotliar, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59, 253–260.

Lack, D., 1968. Ecological Adaptations for Breeding in Birds. Methuen and Co, London.

McGowan, J.D., 1975. Distribution, Density and Productivity of Goshawk in Interior Alaska. Alaska Dept. Fish and Game, Juneau, Alaska.

Newton, I., 1976. Breeding of Sparrowhawk *Accipiter nisus* in different environments. Journal of Animal Ecology 45, 831–849.

Newton, I., 1979. Population Ecology of Raptors. Buteo Books, Vermillion, South Dakota.

Newton, I., 1989. Lifetime Reproduction in Birds. Academic Press, London.

Novelletto, S., Petretti, F., 1980. Ecologia dell'Aquila reale negli Appennini. Rivista italiana di Ornitologia 50, 249–262.

Ontiveros, D., Pleguezuelos, J.M., 2000. Influence of prey densities in the distribution and breeding success of Bonelli's eagle *Hieraaetus fasciatus*: management implications. Biological Conservation 93, 19–25.

Palma, L., Cancelada, F., Oliveira, L., 1984. L'alimentation de l'aigle de Bonelli *Hieraaetus fasciatus* dans la côte portugaise. Rapinyaires Mediterranis 2, 87–96.

Pedrini, P., Sergio, F., 2001. Density, productivity, diet, and human persecution of Golden eagle *Aquila chrysaetos* in the Central-eastern Italian Alps. Journal of Raptor Research 35, 40–48.

Penteriani, V., Gallardo, M., Roche, P. Landscape structure and food supply affect eagle owl *Bubo bubo* density and breeding performance: a case of intra-population heterogeneity. Journal of Zoology (in press).

Poole, A.F., 1989. Ospreys: a Natural and Unnatural History. Cambridge University Press, Cambridge.

Pulliam, H.R., 1988. Source, sinks, and population regulation. American Naturalist 132, 652–661.

Pulliam, H.R., Danielson, B.J., 1991. Source, sinks and habitat selection: a landscape perspective on population dynamics. American Naturalist 137, S50–S56.

Ratcliffe, D., 1980. The Peregrine Falcon. Buteo Books, Vermillon, SD.

Real, J., Grande, J.M., Mañosa, S., Sánchez-Zapata, J.A., 2001. Geographic variation of the causes of death of Bonelli's eagle *Hieraaetus fasciatus* in Spain. Bird Study 48, 221–228.

Real, J., Mañosa, S., 1997. Demography and conservation of western European Bonelli's eagle *Hieraaetus fasciatus* populations. Biological Conservation 79, 59–66.

Real, J., Mañosa, S., Codina, J., 1996. Estatus, demografía y conservación del Aguila perdicera *Hieraaetus fasciatus* en el Mediterráneo. In: Muntaner, J., Mayol, J. (Eds.), Biología y Conservación de las Rapaces Mediterráneas, Monografía no. SEO, pp. 83–89.

Rivas-Martínez, S., 1986. Memoria del Mapa de las Series de Vegetación de España. ICONA, Madrid.

Rocamora, G., 1994. Bonelli's Eagle *Hieraaetus fasciatus*. In: Tucker, G.M., Heath, F.M. (Eds.), Birds in Europe. Their Conservation Status. Birdlife International, Cambridge.

Sæther, B.-E., Ringsby, T.H., Bakke, Ø., Solberg, E.J., 1999. Spatial and temporal variation in demography of a house sparrow metapopulation. Journal of Animal Ecology 68, 628–637.

Sæther, B.-E., Ringsby, T.H., Roskaft, E., 1996. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. Oikos 77, 217–226.

Sherrod, S.K., White, C.M., Williamson, F.S.L., 1977. Biology of the bald eagle on Michitka Island, Alaska. Living bird 15, 143–182.

Sokal, R.R., Rohlf, F.J., 1998. Biometry. Third ed. W.H. Freeman, New York, NY.

Stearns, S.C., 1976. Life history tactics. A review of the ideas. Quarterly Review of Biology 51, 3–47.

Steenhof, K., 1987. Assessing raptor reproductive success and productivity. In: Giron Pendleton, B.A., Millsap, B.A., Cline, K.W., Bird, D.M. (Eds.), Raptor Management Techniques Manual. National Wildlife Federation 10, Washington DC, pp. 157–170.

Steenhof, K., Kochert, M.N., Doremus, J.H., 1983. Nesting of sub-adult Golden eagles in Southwestern Idaho. Auk 100, 743–747.

Tucker, G.M., Heath, M.F., 1994. Birds in Europe: Their Conservation Status. Birdlife International. Birdlife Conservation Series no. 3, Cambridge, UK.

Turner, M.G., 1989. Landscape ecology: the effect of pattern on processes. Annual Review of Ecology and Systematics 20, 171–197.

Valverde, J.A., 1960. La population d'Aigles Imperiaux *Aquila heliaca adalberti* des marismas du Guadalquivir: son evolution depuis un siècle. Alauda 28, 20–26.

Villafuerte, R., Moreno, S., 1991. Rabbit Haemorragic Disease RHD in Doñana National Park SW Spain. Congr. Int. UN. Game Biol, Gödöllö, Hungary.

Villafuerte, R., Calvete, C., Cortázar, C., Moreno, S., 1994. First epizzotic of rabbit haemorragic disease in free living population of *Oryctolagus cuniculus* at Doñana National Park Spain. Journal of Wildlife Disease 30, 176–179.

Weimerskirch, H., Jouventin, P., 1987. Population dynamics of the wandering albatross, *Diomedea exulans*, of the Crozet Island: causes and consequences of the population decline. Oikos 49, 315–322.

Weiss, S.B., Murph, D.D., White, R.R., 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. Ecology 69, 1486–1496.

Wiens, J.A., 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7, 81–120.

Wootton, J.T., Bell, D.A., 1992. A metapopulation model of the peregrine falcon in California: viability and management strategies. Ecological Application 23, 307–321.