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Authors: Margalida, Antoni, Mañosa, Santi, Mariano González, Luis, Ortega, Enric, Sánchez, Roberto, et al.

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Breeding of non-adults and effects of age on productivity in the Spanish Imperial Eagle *Aquila adalberti*

Antoni Margalida^{1,*}, Santi Mañosa², Luis Mariano González³, Enric Ortega², Roberto Sánchez⁴ & Javier Oria⁵

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We studied annual and geographical variation in the proportion of breeding non-adult (<4.5 years old) Spanish Imperial Eagles *Aquila adalberti* in relation to the species' recent demographic recovery. The proportion of non-adult breeders in the populations studied increased significantly during 1983–2004 in parallel with the population increase. Non-adult pairs were more often associated with 'young' territories (occupied recently) than with territories that had already been occupied for longer time (mostly used by adult pairs). Adult pairs produced significantly more chicks than mixed adult–non-adult pairs, which in turn had a higher productivity than pairs in which both male and female were non-adult. Adult pairs attempted breeding more often than non-adult pairs, and clutch and brood size were larger. The poorest reproductive output was found in pairs with non-adult males. These differences were not associated with differences in fledging rates. Once the influence of territories was controlled for (comparing the productivity between adult pairs and non-adult pairs present in the same territory) the age effect on productivity was significant. Our results emphasise the important role which the recruitment of non-adult birds into the breeding population may have played in the recent population recovery of the Spanish Imperial Eagle.

Key words: *Aquila adalberti*, breeding parameters, productivity, Spanish Imperial Eagle, non-adult pairs, territory quality

¹Bearded Vulture Study & Protection Group, Apdo. 43, E-25520 El Pont de Suert, Lleida, Spain; ²Departament de Biologia Animal, Universitat de Barcelona. Facultat de Biologia, Avinguda Diagonal, 645. E-08028 Barcelona, Spain; ³Dirección General para la Biodiversidad, Ministerio de Medio Ambiente, c/ Ríos Rosas 24, 28003, Madrid, Spain; ⁴TRAGSA-División Servicios Medioambientales, c/ Velázquez, 36 Madrid; ⁵Boscage S.L., c/San Agustín 22, E-40001 Segovia, Spain;

*corresponding author (margalida@inf.entorno.es)

INTRODUCTION

In birds, delayed acquisition of definitive adult plumage is associated with deferred breeding and

has been interpreted as an evolutionary strategy to gain experience and, in the long run, to increase individual fitness (Newton 1979). Recent studies have suggested that delayed maturity might be

favoured if the costs of early reproduction outweigh the benefits (Stearns 1992, Weimerskirch 1992, Pyle *et al.* 1997, Tavecchia *et al.* 2001). In most bird species, reproductive performance appears to increase with age (Lunn *et al.* 1994, Forslund & Pärt 1995, Reid *et al.* 2003) and in raptors pairs with non-definitive plumage have lower breeding success (e.g. Sánchez-Zapata *et al.* 2000, Pedrini & Sergio 2001, Penteriani *et al.* 2003, Margalida *et al.* 2007a). The age at first breeding appears to be a trait affected by a complex interplay between costs and benefits of early reproduction mediated by habitat heterogeneity and population density (Krüger 2005).

In breeding populations of raptors a variable percentage is generally made up of individuals with non-adult plumage (Newton 1979). Three explanations for the occurrence of non-adults in breeding populations are: 1) an increase in adult mortality which enables younger birds to breed (Ferrer *et al.* 2003); 2) an increase in resource availability (nest sites or food supply), which can boost the number of non-adult (and adult) breeders (Wyllie & Newton 1991, Brommer *et al.* 1998); and 3) when an increasing population has not yet reached saturation levels (Newton 1998).

The Spanish Imperial Eagle *Aquila adalberti* is a threatened species (Birdlife International 2004), with around 200 breeding pairs in 2004 (González & Oria 2004). It occurs in the southwestern quadrant of the Iberian Peninsula in five population aggregations, also named subpopulations. The species was on the verge of extinction in the 20th century (González *et al.* 2008) but, since the 1980s, has increased in numbers by 4% annually (González & Oria 2004, Ortega *et al.* in press). The species is characterised by delayed acquisition of definitive plumage and begins to breed at an average age of 3.5 years (González *et al.* 2006). The occurrence of non-adult individuals in the breeding populations of this species has been studied in various parts of their range (González 1991, Margalida *et al.* 2007a), particularly in the Doñana population (Valverde 1960, Ferrer *et al.* 2003). In that population non-adult breeding pairs, if in excess of 10% of the population, are suggested to

be an early warning signal of population decline (Ferrer *et al.* 2003). On other hand, in the Spanish Imperial Eagle age seems to have an effect on productivity (González 1991, Margalida *et al.* 2007a). However, Ferrer & Bisson (2003) suggested that age and territory quality are interrelated such that when territory quality is corrected for, the effect of age on productivity disappears.

The objectives of this study are: 1) to analyse the proportion of non-adult birds in the breeding segment of Spanish Imperial Eagle in relation to the growth of the population; 2) to analyse the geographic and temporal variations of reproductive parameters of non-adult and adult pairs; 3) to evaluate differences in breeding output between breeding pairs of different age composition and to test whether these differences persist after controlling for territory effects; and 4) to discuss the factors which influence the occurrence of non-adult breeders in the populations of Spanish Imperial Eagle.

STUDY AREA AND METHODS

Between 1981 and 2004 we monitored 220 territories belonging to 168 breeding pairs, accounting for 85% of the species' entire population (González *et al.* 2008), and covering the entire distribution range of the species in Spain (Fig. 1), except the Doñana area, which has already been studied (Ferrer & Bisson 2003). The work was carried out within the framework of Recovery Plans of the autonomous communities of Castilla y León, Extremadura, Madrid and Castilla-La Mancha, added with own data for Andalucía (Fig. 1).

We monitored the territories 5–7 times annually during the breeding season of the species (Margalida *et al.* 2007a). We recorded the frequency of territory occupation, its occupation by one or more individuals, the number of times that an individual or pair was observed, and the breeding behaviour. We defined a pair as territorial if it was observed in courtship, nesting or in territorial defence (Steenhof 1987, González 1991, Margalida *et al.* 2007a). We also recorded the sex and



Figure 1. Outline of Spanish Imperial Eagle populations considered in the present study.

age-class of the birds based on their plumages (González 1991, González *et al.* 2008). Individuals in adult plumage (age class >5.5 years old) and in subadult plumage (age class 4.5–5.5 years old, because most of these individuals reproduced, unlike younger age classes) were considered to be *adults* and individuals in the age-classes of 1.0–4.5 years were considered *non-adults*. In order to detect the formation of new pairs, we monitored peripheral areas adjacent to the nuclei with potential habitat for the species on an annual basis (González *et al.* 2006, González *et al.* 2008).

The proportion of non-adult breeding pairs in the population was defined as the proportion of territorial pairs with at least one non-adult member. The percentage of non-adult breeding birds was calculated for each subpopulation, separately for four regions (Northern, Central, Western and Southern, Fig. 1) previously established on the basis of habitat and geography (González *et al.* 2006, Ortega *et al.* in press), and for three periods of population growth (Ortega *et al.* in press): 1981–93 (population increase), 1994–99 (population stability) and 2000–04 (population increase).

We calculated three breeding parameters for each territory or series of data: 1) *Proportion of pairs laying*, estimated as the percentage of territories in which eggs were laid; 2) *Fledging rate*, i.e.

the number of fledglings per successful pair, and 3) *Productivity*, i.e. the number of fledglings per territorial pair. In addition, during the monitoring we were able to determine the contents of the nests on several occasions (clutch size and brood size).

To analyse the influence of age of the territories (date of first occupancy) on the current reproductive parameters and proportion of non-adult birds, we considered four territory categories: ancient territories, already established in 1981; old territories, established between 1981 and 1993; new territories, established between 1994 and 1999; and young territories, established between 2000 and 2004. The analyses were restricted to those territories for which the year of establishment was known.

For each group of breeding attempts being considered, we calculated the averages and their corresponding variances for each of the breeding parameters and for the percentage of non-adult pairs in each subpopulation.

Statistical analysis

Statistical analyses were carried out at a significance level of 0.05, using the statistical package SPSS 11.5 (SPSS 1996). We tested for differences in reproductive parameters between age classes and between territories using ANOVA, or Kruskal-Wallis tests when data were not normally distributed (Sokal & Rohlf 1981). In order to remove age effects, we conducted Kruskal-Wallis tests for adult-adult pairs only. In addition, in order to remove the effect of territory quality, we compared breeding parameters between non-adults and adult pairs present in the same territory using the Wilcoxon signed-rank test in 81 territories. A Mann Whitney U-test was used to test differences between periods and the Spearman rank correlation to test the relationship between the percentage of non-adult breeders and productivity or years. Means are reported \pm SD.

RESULTS

Breeding of non-adults in the population

The 220 territories were occupied 2363 times. The frequency of occupation of each territory varied from 36.8% occupied 1–5 times, 34.1% occupied 6–15 times and 29.1% occupied 16–24 times. In 77.5% of the cases, the territory was occupied by a pair, 0.1% by a solitary male, 0.4% by a solitary female, and 0.2% by a polyandrous trio; in 21.8% of the cases we were unable to assess the breeding status, age or sex of the individuals involved.

In 270 breeding attempts (15%), the pair was composed of at least one non-adult individual: 62 cases of non-adult male x non-adult female (3.5%

of the breeding attempts), 46 cases of adult male x non-adult female (2.6%), and 162 cases of non-adult male x adult female (9%).

The average percentage of non-adult pairs differed significantly between the four areas considered (Kruskal-Wallis, $H_3 = 14.51$, $P = 0.002$): $2.88 \pm 4.17\%$ in the western, $3.48 \pm 5.04\%$ in the central, $7.08 \pm 7.70\%$ in the southern, and $9.68 \pm 6.02\%$ in the northern (Table 1).

The average percentage of non-adult pairs increased significantly over the years ($r_s = 0.86$, $P = 0.0001$), being 5.4% in 1981–93, 8.8% in 1994–99 and 13.2% in 2000–04. These values show significant differences between periods (Kruskal-Wallis, $H_3 = 8.92$, $P = 0.012$, Fig. 2). This ten-

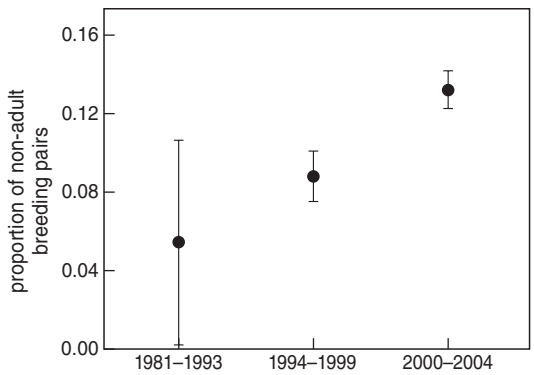


Figure 2. Variation of the proportion of non-adult pairs in the different periods of population growth considered in this study. Values as means \pm SD.

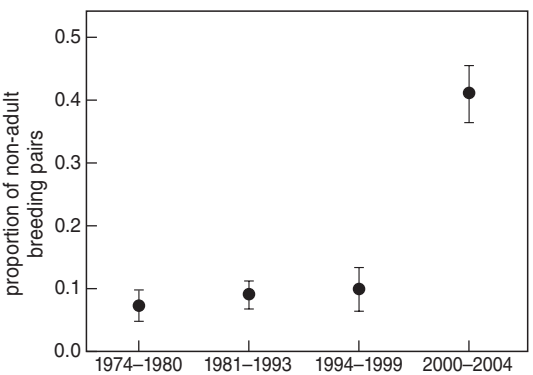


Figure 3. Variation of the proportion of non-adult pairs in the territories during 2000–2004 according to the year of their establishment. Values as means \pm SD.

Table 1. Average proportions of non-adult pairs in the different subpopulations and periods studied. Due to small sample sizes, data from the following years and subpopulations are not considered in the calculations: central 1990 and 1991, western 1990 and 1991. For each subpopulation, different superscripts indicate significant differences between periods (Mann-Whitney U-test, $P < 0.01$).

	1981 - 1993	1994 - 1999	2000 - 2004	Kruskal-Wallis	
				H	P
Central	0.00 \pm 0.00 (n = 9) ^a	0.03 \pm 0.01 (n = 6) ^a	0.10 \pm 0.02 (n = 5) ^b	14.42	0.001
Western	0.00 \pm 0.00 (n = 10) ^a	0.03 \pm 0.01 (n = 6) ^b	0.08 \pm 0.02 (n = 5) ^b	11.01	0.004
Northern	0.05 \pm 0.01 (n = 13) ^a	0.13 \pm 0.01 (n = 6) ^b	0.17 \pm 0.01 (n = 5) ^c	16.10	0.0001
Southern	0.00 \pm 0.00 (n = 9) ^a	0.10 \pm 0.02 (n = 6) ^b	0.16 \pm 0.02 (n = 5) ^b	16.49	0.0001

dency of increase was evident in each of the areas considered, with statistically significant differences for periods in each population (Table 1).

The proportion of non-adult pairs in each territory during the period 2000–04 was significantly higher in territories established in 2000–2004 in comparison to territories established in earlier periods (Kruskal-Wallis, $H_3 = 11.82$, $P = 0.008$, Fig. 3).

Reproductive output and age

The percentage of pairs laying eggs was higher in adult-adult pairs than in non-adult pairs (Table 2), notably when comparing adult-adult pairs with non-adult pairs (Tukey, $P = 0.017$) and pairs consisting of an adult female and a non-adult male (Tukey, $P = 0.023$). No such difference was found between adult pairs and pairs composed of an adult male and a non-adult female (Tukey, $P = 0.17$). Likewise, adult pairs produced significantly more chicks than partly non-adult pairs, and these produced more chicks than pairs in which both individuals were non-adult (Kruskal-Wallis $H_3 = 18.43$, $P = 0.0001$, Table 2). The lowest productivity was found in pairs in which the male was non-adult. Clutch size and brood size were significantly larger in adult pairs in comparison with non-adult pairs (Table 2), but fledging rate did not show statistically significant differences between pairs of various age composition (Kruskal-Wallis $H_3 = 1.90$, $P = 0.128$).

We found significant differences in productivity between adult pairs (1.24 ± 0.69) and non-adult pairs (0.92 ± 0.97) present in the same territory (Wilcoxon's signed-rank test, $Z = -3.18$, $P = 0.0001$). Considering the whole period, from 1981 to 2004, there was no relationship between the proportion of non-adult pairs and productivity ($r_s = -0.02$, $P = 0.92$).

DISCUSSION

From a temporal perspective, the proportion of non-adult breeders has increased considerably in all the studied subpopulations of Spanish Imperial Eagle since the early 1980s, in parallel with the growth in numbers of this population. In addition, the current proportion of non-adult pairs remains lower in territories that have been occupied for the longest period of time, and is in particular high in the more recently occupied territories. This indicates that the increasing participation of non-adults in the breeding population is not related to an overall increase in adult mortality, as is the case in the Doñana population (Ferrer *et al.* 2003). Instead, our observations suggest that the increase of non-adult birds in the breeding population is related to the population increase itself, possibly due to increased resource availability (nest sites or food supply), which can boost the numbers of non-adult breeders (Wyllie & Newton 1991,

Table 2. Average values of the breeding parameters considered for the different age combinations of breeding pairs (M: male; F: female). Sample sizes given in brackets.

	Non-adult pair			Adult pair	Kruskal-Wallis	
	M non-adult/ F non-adult	M adult/ F non-adult	M non-adult/ F adult		H	P
Proportion of pairs laying	0.51 ± 0.32 (17)	0.58 ± 0.35 (13)	0.54 ± 0.30 (20)	0.77 ± 0.08 (24)	4.25	0.008
Fledging rate	1.94 ± 0.73 (18)	1.89 ± 0.68 (18)	1.62 ± 0.76 (73)	1.82 ± 0.77 (937)	1.90	0.128
Productivity	0.74 ± 1.05 (47)	0.92 ± 1.06 (37)	0.80 ± 0.97 (147)	1.35 ± 1.03 (1261)	18.43	0.0001
Brood size	1.79 ± 0.71 (19)	1.84 ± 0.69 (19)	1.72 ± 0.80 (82)	2.05 ± 0.77 (769)	5.52	0.010
Clutch size	1.80 ± 0.45 (5)	1.00 ± 0.00 (3)	2.19 ± 0.74 (27)	2.27 ± 0.80 (199)	3.07	0.029

Brommer *et al.* 1998). This idea is supported by further evidence. First, since the 1990s, the proportion of non-adults has been higher during periods of population growth and low adult mortality, and lower during periods of population stability and higher adult mortality (González *et al.* 2007, Ortega *et al.* in press). Secondly, the occupation of new territories was mostly by non-adult birds (González *et al.* 2006).

However, from a spatial perspective, the variation observed in the proportion of non-adult breeders could also reflect differential adult survival rates between populations. In the northern and southern subpopulations, a high frequency of non-adult breeders coincided with the lowest adult survival rates (Ortega *et al.* in press). Previous studies have shown that the recruitment of non-adults into the breeding population of the Spanish Imperial Eagle took place mainly after mate loss in the northern and western subpopulations (those increasing the least), whereas in the subpopulations that grew the most (southern and central) this occurred more frequently as a result of new settlements (González *et al.* 2006). Protection and conservation management in the latter subpopulations reduced pre-adult mortality (González & Oria 2004, González *et al.* 2007), probably facilitating the occupation of territories by floating non-adults.

Changes in the age structure of a population can lead to changes in productivity if the latter is related to age. In the case of the Spanish Imperial Eagle, breeding success and productivity are significantly higher in adult pairs than in pairs in which one or both participants are non-adult, in accordance with previous studies (González 1991, Ferrer & Bisson 2003, Margalida *et al.* 2007a); productivity was particularly poor when the male was non-adult. The presence of an experienced adult male may result in a higher provisioning rate at the nest, and, therefore, in an increase in productivity in pairs with an adult male. In Spanish Imperial Eagles, the contribution of males in food provisioning during incubation and chick-rearing is much larger than that of females (Margalida *et al.* 2007b), and their hunting capacity is therefore likely to have a large impact on productivity.

In sum, our results support the idea that the proportion of non-adult birds within the breeding population may reflect a variety of processes and that this parameter should be viewed against the population trend (stable, declining, or increasing) before it can be correctly interpreted in terms of demographic health.

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SAMENVATTING

De Spaanse Keizerarend *Aquila adalberti* komt alleen op het Iberische Schiereiland voor. De wereldpopulatie werd in 2004 op 200 paren geschat. Van de vijf onderscheiden deelpopulaties valt in dit onderzoek die van Doñana buiten de boot, omdat deze al uitvoerig is beschreven. In de overige deelpopulaties is sprake van een toename van de aantallen. In dit onderzoek is het belang van onvolwassen arenden (in de leeftijd van 1 tot 5,5 jaar, dus inclusief subadulte vogels) in de populatieontwikkeling nagegaan. De meerderheid van de paren was samengesteld uit volwassen vogels (85%). Wanneer onvolwassen arenden tot broeden kwamen, ging het meestal om de combinatie onvolwassen man en volwassen vrouw. In 62 gevallen waren zelfs beide ouders onvolwassen. Het aandeel (deels) onvolwassen paren varieerde per deelgebied en nam significant toe in het tijdvak 1983–2004, gelijkopgaande met de groei van de onderzochte deelpopulaties. Recent bezette territoria hadden een hoger aandeel paren waarvan één of beide partners onvolwassen waren;

omgekeerd waren de langdurig bezette territoria meestal in handen van volwassen vogels. Paren waarvan beide partners volwassen waren, deden vaker een broedpoging, hadden een groter legsel en brachten meer jongen tot uitvliegen dan paren waarvan één of beide partners onvolwassen waren (in het bijzonder wanneer dat het mannetje was). Wanneer rekening gehouden werd met de kwaliteit van het territorium, bleek het effect van leeftijd op reproductie significant te zijn. Ondanks de mindere broedprestaties van onvolwassen Keizerarenden maakt hun toetreding tot de broedpopulatie, onder de huidige omstandigheden, een snelle groei mogelijk. Een hoog aandeel onvolwassen nestelende broedvogels kan dus zowel een gunstig teken zijn (groei van de populatie), als een ongunstig teken (afname, veroorzaakt door hoge mortaliteit van volwassen vogels, welke vestiging van onvolwassen vogels mogelijk maakt). (RGB)

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