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Simultaneous effects of age and territory quality on fecundity in Bonelli's Eagle *Hieraetus fasciatus*

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Several factors that interact with a bird's age are likely to affect breeding performance. Because of habitat heterogeneity, individuals of different subpopulations may experience different probabilities of breeding, depending on the habitat that they occupy. The aim of this work is to test the hypothesis that age and territory quality independently affect breeding performance. We analysed data on breeding biology and fecundity at 298 breeding sites of Bonelli's Eagle *Hieraetus fasciatus* in Andalusia from 1980 to 2000. Our data confirmed that age and territory quality simultaneously affect reproductive output. After controlling for the effect of year and age, breeding performance varied among territories. Independently of territory quality, the age of breeding birds affected the number of fledged young and variance in productivity.

Most bird species that have been studied appropriately exhibit age-specific patterns of breeding performance, with fecundity increasing with age (Sæther 1983, Forslund & Pärt 1995). Three main mechanisms may explain the relationship between age and fecundity (see reviews in Curio 1983, Forslund & Pärt 1995). The *constraint hypothesis* proposes that age-related changes in competence during a bird's lifetime may improve skills that are essential to high reproductive performance, whereas the *restraint hypothesis* suggests that younger birds abstain from or put less effort into reproduction, because at that age reproductive effort increases mortality risk. Both mechanisms may operate on the same individual, and it is difficult to distinguish between them. For this reason, they were recently encompassed within the *inadequate experience hypothesis* (see Espie *et al.* 2000). The third mechanism, the *differential mortality hypothesis*, proposes that individuals of different phenotypic quality differ in age of first reproduction or in survival probability, thereby leading to a progressive appearance or disappearance of phenotypes as a cohort ages.

Several factors are likely simultaneously to affect breeding performance, interacting with age-effects. Within the same population and in a relatively

limited geographical region, pairs may be found in a variety of habitats of different quality. Individuals of different subpopulations may experience different probabilities of survival and reproduction, depending on the habitat that they occupy (Weiss *et al.* 1988, Newton 1989, Kadmon 1993, Penteriani *et al.* 2002). In territorial species, the quality of the territory may determine reproductive success: territories of different quality require different levels of effort for successful reproduction (Catchpole & Phillips 1992, Ens *et al.* 1992, Siikamäki 1995, Panek 1997).

Although many studies have clearly demonstrated that fecundity increases with the age of mates (e.g. Newton 1989, Sæther 1983, Desrochers & Magrath 1993, Espie *et al.* 2000), several others have found no correlation between age, clutch size or fledging success (Davis 1976, Nol & Smith 1987, Boekelheide & Ainley 1989). Moreover, although several studies have attempted to determine the impact of landscape heterogeneity and age on animal reproductive performance and demography (e.g. Sæther 1983, Wunderle 1983, Danielson 1992, Dhondt *et al.* 1992, Kadmon 1993, Ferrer & Donazar 1996, Espie *et al.* 2000), few of them tested for a combined effect of both types of factors (see Newton 1991).

This paper tests the hypothesis that age and territory quality independently affect breeding performance. For this purpose, we analysed a long-term data set on the breeding parameters of Bonelli's Eagle

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Hieraetus fasciatus in Andalusia. The Bonelli's Eagle is an endangered bird of prey that has suffered a dramatic decline in most of its European range, including Spain (Real *et al.* 1996, Arroyo *et al.* 1998). The species is now mainly confined to the Iberian Peninsula and northern Africa (Real *et al.* 1996), and Andalusia is one of its remnant strongholds.

METHODS

Study area

We monitored the breeding population of the Baetic Mountains (36°44'N, 2°07'W), the main mountain system of the region, composed of the Penibaetic massif in the south, close to the Mediterranean Sea, and the Subbaetic massif in the north. Altitude ranged from 80 to 3482 m above sea-level, and the climate was Mediterranean and Subarid (Rivas-Martínez 1986), with mean annual rainfall ranging from 200 to 1500 mm. The landscape was characterized by a mosaic structure of forests (*Quercus suber*, *Q. rotundifolia* and *Pinus* spp.), matorral (*Quercus coccifera*, *Thymus vulgaris* and *Rosmarinus officinalis*), limestone karst topography, as well as pastures and fallow lands at lower altitudes.

Data collection

Data on breeding biology and fecundity of Bonelli's Eagle in Andalusia were collected from 1980 to 2000, during which potential nesting cliffs were surveyed three times per year. The term 'nesting cliff' is used to denote the cliff where a pair attempted to breed, irrespective of whether it was successful. Between January and early February, we checked for territory occupancy (e.g. territorial displays, nest material transfer) and recorded the age of the birds. An individual was considered to be adult when its wing feathers showed no pale bars ($> 3\frac{1}{2}$ years old; Cramp & Simmons 1980, Forsman 1999). To avoid bias associated with differential skills of fieldworkers in sexing eagles, data from the two sexes were pooled and only adult and subadult classes were considered. We defined an adult pair as one consisting only of adults, and a mixed-aged pair as having at least one subadult. A second check of nesting cliffs was made from late February to March to verify whether the pairs present on the territory had laid eggs, and the last visit occurred during April and May, to estimate the number of young fledged. The hatch date was calculated by backdating from the

age of nestlings on the basis of feather development, using personal observations at focal nests and data from Cramp and Simmons (1980) and Torres *et al.* (1981).

Trends in fecundity were analysed on a sample of 298 different breeding territories. Fecundity was expressed as the percentage of nests that fledged at least one chick, the mean number of young fledged per breeding pair (hereafter referred to as productivity) and the mean number of young fledged per successful pair. We used the nearest neighbour distance (NND) as an estimate of density (Newton *et al.* 1977).

Statistical analysis

To determine the trends in long-term fecundity, and relate them to territory quality and bird age, a successive stepwise procedure was employed.

We first compared (Mann–Whitney *U*-test) the productivity under different density conditions: low (sites with a NND higher than 7 km, the population mean NND) and high (sites with a NND lower than 7 km). This allowed us to detect whether our data were confounded by a density-dependent effect.

To test for the effect of territory quality on eagle fecundity, we first eliminated the year effect on productivity. Owing to the existing annual variation, we controlled for year effects by subtracting annual means from the raw data. The corrected data are referred to as relative productivity. For the number of fledglings, negative values indicate a poorer breeding performance than average, whereas positive values indicate a better one. Finally, in order to test for the variation in the relative productivity due to territory quality, we performed a univariate ANOVA (with the breeding site as a random factor to correct for pseudoreplication) considering only those territories occupied exclusively by adult pairs during the study period (to control for the age effect). In addition, we used a stepwise multiple regression analysis (Norusis 1993) to identify those landscape elements that determined the differences in breeding performance among territories. Again, to correct for a possible interference with the age effect, we only used those territories in which only adult pairs were recorded.

To test the effect of age on eagle fecundity, a Wilcoxon signed-ranks test was performed to detect any differences in the number of fledged young per breeding pair between adult and mixed-aged pairs within the same territory (thus controlling for territory

Table 1. Landscape characteristics within 3500 m of Bonelli's Eagle breeding sites (Andalusia, Spain) occupied by mixed pairs ($n = 19$) and adult pairs ($n = 46$). Variables marked by an asterisk (*) are the ones that entered a stepwise DFA discriminating the two groups.

Variable	Sites with mixed pairs ^a (mean \pm sd)	Sites with adult pairs ^b (mean \pm sd)
% woodland	6.1 \pm 7.4	7.0 \pm 10.7
% open areas	93.9 \pm 7.6	93.0 \pm 12.4
Distance to nearest woodland (m)*	1833.6 \pm 1720.9	2342.4 \pm 2629.4
Distance to nearest openland (m)*	2083.3 \pm 845.4	1913.2 \pm 1075.4
Distance to nearest source of human disturbance (m)*	2886.1 \pm 1517.1	3150.6 \pm 1656.4
Distance to nearest electric power line (m)	7508.2 \pm 6528.2	6205.9 \pm 6400.7
Nest-site elevation (m)*	537.8 \pm 398.3	764.0 \pm 390.2
Slope at the nesting cliff (%)	65.2 \pm 31.6	65.9 \pm 42.8

^aSite occupied at least once by a mixed pair (with at least one subadult).

^bSite always occupied by adult pairs.

quality). Non-parametric procedures were used successively to explore the association between the age of mates within a pair and productivity parameters (such as egg-laying date and number of fledged young), as well as between productivity and its coefficient of variation (Ferrer & Donazar 1996, Kruger & Lindström 2001).

Finally, we performed a discriminant function analysis (DFA) to test for differences in habitat structure and composition at the landscape level between nest-sites occupied by breeding pairs of adults and nest-sites occupied at least once by a mixed-aged pair. A chi-square analysis tested the significance of the site classification established by the DFA procedure (Sokal & Rohlf 1998). Landscape characteristics were analysed through a Geographic Information System (GIS; IDRISI program, Eastman 1997), using a landcover layer with a resolution of 50 m and a Digital Elevation Model (DEM) layer with a resolution of 20 m. We used eight variables to describe the landscape surrounding the nest-site (Table 1): the analysis of landscape features was based on circular plots centred on the active nest and extending to a radius of 3500 m around it, representing half the mean distance between neighbouring nest-sites (Liberatori & Penteriani 2001, Penteriani *et al.* 2001).

Several analyses were run on a subsample of breeding sites, for which data were available for all variables of interest (nesting habitat features, age and fecundity). When data were not normally distributed, they were \log_e , square-root or arcsine square-root transformed prior to parametric tests (Sokal & Rohlf 1998). When, in spite of the above transformations, the data did not approach normality, non-

parametric tests were employed (Siegel & Castellan 1988). All tests were two-tailed, and statistical significance was set at $P < 0.05$. We applied sequential Bonferroni's adjustment of α level (Rice 1989) each time that we tested a hypothesis with multiple statistical tests. Means are given with ± 1 sd. All tests were computed using SPSS 10.0.

RESULTS

Overall population fecundity

The mean number of fledged young per breeding pair was $1.38 \pm$ sd 0.71 ($n = 591$), and the mean number of fledged young per successful pair was $1.59 \pm$ sd 0.51 ($n = 518$). No differences were detected in the mean number of fledged young ($z = -1.045$, $P = 0.296$, $n = 30, 29$; Mann-Whitney U -test) or its coefficient of variation ($z = -0.106$, $P = 0.915$, $n = 30, 29$; Mann-Whitney U -test) between breeding sites in areas of low and high breeding pair density.

Effect of territory quality and age on productivity

After controlling for year and age effects, significant differences between territories were detected for productivity ($F_{44,214} = 2.044$, $P = 0.0001$). Distance to open land appeared to be the strongest parameter of landscape structure determining the variation in breeding output and quality of an adult eagle territory ($n = 37$). The number of fledged young ($R^2 = 0.15$) was negatively related to the distance to open areas ($\beta = -0.39$, $t = -2.45$, $P = 0.02$).

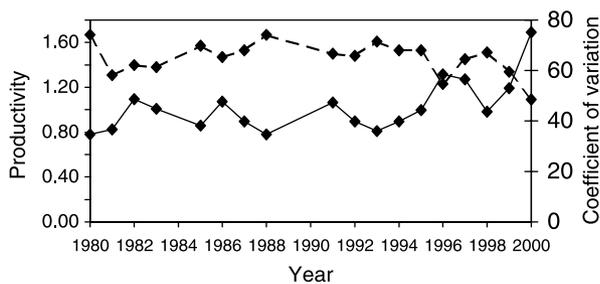


Figure 1. Variations in mean productivity (fledged young per breeding pair, broken line) and in coefficient of variation of productivity (solid line) for a population of Bonelli's Eagle (Andalusia, Spain, 1980–2000).

Within the same territory, relative productivity (again used to control for the year effect) was higher when it was occupied by an adult pair than when occupied by a mixed-age pair ($z = -2.103$, $P = 0.03$, $n = 9$; Wilcoxon signed-rank test). The average number of fledged young for mixed-age pairs was 0.9 ($sd = \pm 0.74$) compared with 1.3 ($sd = \pm 0.63$) for adult pairs. This result provides evidence for an age effect on productivity, while controlling for territory quality. Breeding by two adults did not affect laying date ($z = -0.287$, $P = 0.774$, $n = 6$, 82; Mann–Whitney U -test), but it positively affected the mean number of young fledged ($z = -6.439$, $P = 0.0001$, $n = 28$, 431; Mann–Whitney U -test). The coefficient of variation of productivity was inversely related to its mean ($r_s = -0.78$, $P = 0.0001$, $n = 18$; Fig. 1), and positively related to the percentage of subadults in a pair ($r_s = 0.685$, $P = 0.002$, $n = 18$).

Across territories, the highest mean number of fledged young produced per nesting attempt (1.7) was found in two territories never occupied by subadult eagles, whereas in the two territories with the poorest productivity at least one subadult was present in 16.7 and 33.3% of breeding attempts. Mean territory productivity was negatively correlated with the proportion of mixed pairs occupying these territories ($r_s = -0.33$, $P = 0.02$, $n = 46$).

Characteristics of adult vs. mixed-age pair territories

DFA differentiated the landscape characteristics of sites occupied by adult pairs ($n = 46$) from those of sites occupied at least once by a mixed-age pair ($n = 19$; Table 1). Four variables entered the stepwise analysis: distance to the nearest woodland (less in sites with subadults), distance to nearest openland

(greater in sites with subadults), elevation of the nesting cliff (lower in sites with subadults), and distance to the nearest source of potential human disturbance, such as built-up areas and roads (less in sites with subadults). The model correctly reclassified 13 (68.4%) of the sites with mixed pairs and 34 (73.9%) of the sites with adult pairs: 72.3% of the overall cases were correctly reclassified. This classification rate was higher than random ($\chi^2 = 11.36$, $P = 0.02$).

DISCUSSION

Our analyses showed independent effects of age and territory quality on reproductive output. After controlling for the effects of year and age, breeding performance varied among territories. Productivity was related to the ages of the mates of a pair: the presence of a subadult as a mate in a territory was associated with a reduced number of fledged young and greater variance in productivity.

Newton (1991) showed an interactive effect of territory quality and age of breeders on reproductive performance of Sparrowhawks *Accipiter nisus*: the variation in the breeding performances between nesting places was a function of the habitat and bird quality. Moreover, subadults were over-represented in low-quality territories. Several ecological factors, such as territory quality in our study, can explain intraspecific variation in reproductive traits. The latter are also influenced by variables related to the quality of the individual, such as its age and experience (Ryder 1981, Forslund & Larsson 1992). Generally, subadults seemed to settle in poorer sites than adults, closer to sources of human disturbance and with higher proportions of unsuitable foraging habitat such as woodlands. Distance from open areas was greater in territories with subadults and negatively affected productivity, probably because this type of habitat represented a high-quality foraging habitat. Open areas had higher densities of the main prey species such as rabbit *Oryctolagus cuniculus* and Red-legged Partridge *Alectoris rufa* (Balbontin *et al.* 2000), and had a vegetative structure allowing easier detection and pursuit of prey than closed-structure habitats, such as forests. More than 60% of the recorded causes of breeding failure were related to human presence and disturbance (J. Balbontin, V. Penteriani & M. Ferrer unpubl. data), so the choice of nesting sites near humans may affect the age-dependent low reproductive rate of subadults.

Subadults may occupy habitats of poor quality more frequently, not only because of inexperience (Sæther 1983) or lower competitive ability (Newton 1989, 1991), but also because these habitats are characterized by higher mortality or migration rates and thus offer more opportunities to find an unoccupied territory. An alternative process driving territory occupation by subadults could be a sudden increase in adult mortality. The number of territories occupied by unpaired adults in our population has increased since 1997 (Balbontín *et al.* in press). A similar phenomenon has been observed in Peregrines *Falco peregrinus* (Ratcliffe 1980) and Golden Eagles *Aquila chrysaetos* (Valverde 1960, Novelletto & Petretti 1980) when human persecution reduced the number of adults in the population. As in our study on Bonelli's Eagles, Steenhof *et al.* (1983), Sánchez-Zapata *et al.* (2000) and Pedrini and Sergio (2001) found that mixed-age pairs of Golden Eagles had a lower productivity than adult pairs. Moreover, Steenhof *et al.* (1983) reported that territories occupied by subadults were associated with higher levels of human disturbance. Improvement in productivity with age has also been found in Kestrels *Falco tinnunculus* (Cavé 1968) and Sparrowhawks (Newton 1976, Newton *et al.* 1979, 1981).

Ferrer and Donazar (1996) observed an increase in the fecundity variance of the Spanish Imperial Eagle *Aquila adalberti* under density-dependent pressures. In that species, a decline in mean productivity was attributed to an increasing number of new pairs using poorer territories, a result in accordance with the predictions of the habitat heterogeneity hypothesis (Dhondt *et al.* 1992, Kadmon 1993). This theory predicts that in low-density populations individuals select optimal habitat, and variance in fecundity among individuals is expected to be low (i.e. the habitats occupied should not differ greatly in quality). As density increases, proportionately more individuals are forced to occupy lower quality habitats and, consequently, mean population fecundity decreases and variance increases. Our results show that such effects on fecundity may be age- and territory-dependent, occurring when individuals of lower quality, such as subadults, replace adults in a low-quality territory. For this reason, we suggest that the habitat heterogeneity hypothesis, in which fecundity is depressed by habitat heterogeneity in a density-dependent manner (Ferrer & Donazar 1996), should be extended to age-dependent depression too, when subadults replace adults in the poorest breeding sites. Two different conditions (density

and age) can produce a similar effect (decreasing fecundity) in animal populations.

The interaction between habitat, age-structure of the population and productivity complicates any prediction of the effect of habitat alterations and human pressures on population viability. Alteration of good quality territories and human-induced higher mortality of adult-age classes can affect breeding performance: we may be unable correctly to identify threatened populations and situations at risk, if we monitor demographic parameters without simultaneously testing their interaction with habitat changes (Green & Hiron 1991). These interactive effects between age and habitat quality require caution when identifying factors affecting species at risk and when planning their management and conservation.

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