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Population size, breeding performance and territory quality of Bonelli's Eagle *Hieraaetus fasciatus* in eastern Spain

PASCUAL LÓPEZ-LÓPEZ[1]*, CLARA GARCÍA-RIPOLLÉS[2] and VICENTE URIOS[1]

[1]*Estación Biológica Terra Natura (CIBIO – Fundación Terra Natura), Universidad de Alicante, Apdo. 99 E–03080, Alicante, Spain and* [2]*Pza. Jesús de Medinaceli 6, 3º-14, 46024 Valencia, Spain*

Capsule A five-year monitoring study is described of overall population stability and differential reproductive success in relation to habitat heterogeneity.

Aims To assess the effect of the altitude and orientation on laying date and breeding performance, and analyse the effect of territory quality as a likely factor that could be regulating the population.

Methods We monitored a population of 28–33 pairs, from 2002 to 2006, counting a total of 131 breeding attempts.

Results Territories located at lower altitude showed higher mean fecundity than those located at higher altitude. The mean laying date was February 18 ± 16 days. Laying date was positively correlated with nest altitude, the coastal pairs laying earlier than those in mountainous regions. Pairs located at lower altitudes showed higher mean fecundity than those located at higher altitudes. There was no preference in mean orientation either in breeding performance or in relationship to nest altitude. We did not find a difference in breeding performance between territories classed as being at high density and those classed as being at low density.

Conclusion The population has remained stable since the first national census was conducted 17 years ago. Our results could be explained in the light of the Habitat Heterogeneity Hypothesis. We suggest a differential reproductive success in relation to habitat heterogeneity.

Bonelli's Eagles *Hieraaetus fasciatus* are distributed from the European Mediterranean region to southeast Asia (Cramp & Simmons 1980, Del Hoyo *et al.* 1994, Hagemeijer & Blair 1997). The species experienced a period of decline in the mid-1980s in the Iberian Peninsula (Arroyo & Garza 1995, Real & Mañosa 1997, Real 2004), and is currently considered as endangered in Spain (Real 2004). Today the population size remains stable or is increasing slightly in its strongholds, although it is experiencing a slight decline in some small local populations located at the northern and western extremes of the distribution range (Del Moral 2006).

The Iberian Peninsula holds approximately 80% of the European population and therefore most of the studies focusing on the species have been performed in this area. The first papers focused on local breeding performance (Leshem 1976, Cheylan 1981, Alamany *et al.* 1984, Del Junco 1984), population trends (Gil-Sánchez *et al.* 1994, 2004), and competition with other raptors (mainly Golden Eagle *Aquila chrysaetos* and Peregrine Falcon *Falco peregrinus*) (Jordano 1981, Carrete *et al.* 2002, 2005). More recent studies have focused on conservation (Real & Mañosa 1997, Mañosa *et al.* 1998, Real *et al.* 2001, Carrete *et al.* 2002, Balbontin *et al.* 2003, Ontiveros *et al.* 2004), habitat selection (Ontiveros 1999, Balbontin 2005, López-López *et al.* 2006), juvenile dispersal (Real *et al.* 1998, Real & Mañosa 2001, Angulo 2002, Cadahía *et al.* 2005, Cadahía *et al.* in press), genetics (Cadahía *et al.* 2007) and ecological factors regulating breeding performance (Ontiveros & Pleguezuelos 2000, Penteriani *et al.* 2003, Balbontin & Ferrer 2005, Carrete *et al.* 2005, 2006).

Although preliminary results on distribution pattern (López-López *et al.* 2004) and habitat selection (López-

*Correspondence author. Present address: Cavanilles Institute of Biodiversity and Evolutionary Biology, Terrestrial Vertebrates Group, University of Valencia, Apartado Oficial 22085, E-46071 Valencia, Spain.
Email: Pascual.Lopez@uv.es, lopez.pascual@gmail.com

López *et al.* 2006) of the species in the study area have been reported previously, a thorough report on population status and an analysis of factors influencing breeding performance and population regulation of Bonelli's Eagle in the eastern Iberian Peninsula is lacking. This paper reports on a five-year monitoring programme of population size and breeding performance of Bonelli's Eagles in this area. We also assess the effect of altitude and orientation on laying date and breeding performance. Finally, we analyse the effect of territory quality as a likely factor that could be regulating the population under the Habitat Heterogeneity Hypothesis proposed by Fretwell & Lucas (1970) and developed for raptors by Ferrer & Donázar (1996). This hypothesis states that 'as density raises an increasing proportion of individuals is relegated to lower quality habitats, as a result of which mean population fecundity declines' (Brown 1969, Ferrer *et al.* 2006).

STUDY AREA AND METHODS

Study area

The study area was located in eastern Spain and included the entire Castellón province and the neighbouring municipalities of Gátova, Marines, Serra and Estivella in the Valencia province (40°47′N, 39°42′S, 0°51′W, 0°32′E, Fig. 1). The area covers 7090 km^2 and ranges from 0 to 1814 m asl. The climate is Mediterranean, with annual mean temperatures varying from 17°C along the coast to 8°C in the inner highlands. Further details on description of the study area can be found in López-López *et al.* (2004, 2006).

Census and reproductive parameters

We monitored the Bonelli's Eagle population from 2002 to 2006. During each breeding season all known and potential territories were visited at least three times. Observations were made 300 m away from cliff nest sites with a 20–60 × Leica Televid 77 telescope during clear days to avoid disturbance to eagles. A territory was considered occupied if we observed nests with green branches, typical pair behaviour, courtship, brood rearing activity or young (Newton 1979, Steenhof & Kochert 1982). During the study period many pairs moved from one nest to another in the same territory (in some cases just a few metres away on the same cliff); the nest used the most was considered for calculations.

The reproductive parameters were calculated as follows: fecundity = fledged chicks/occupied territory (i.e. a breeding site where there is evidence of a mated pair, e.g. pair of birds seen, repaired or new nest present, mating behaviour observed); productivity = fledged chicks/pairs initiating reproduction (i.e. pairs that had laid eggs); breeding success = successful pairs/pairs initiating reproduction; flight rate = fledged chicks/successful pairs (i.e. pair that raised at least one chick to fledging age) (Steenhof 1987).

Laying date

Laying date was estimated from nestling age, which was estimated from feather development by accurate observations with a field telescope according to the figures given by Torres *et al.* (1981) and Gil-Sánchez (2000). This method has an error of ± 5 days, and gives the laying date by adding 39 days to the estimated

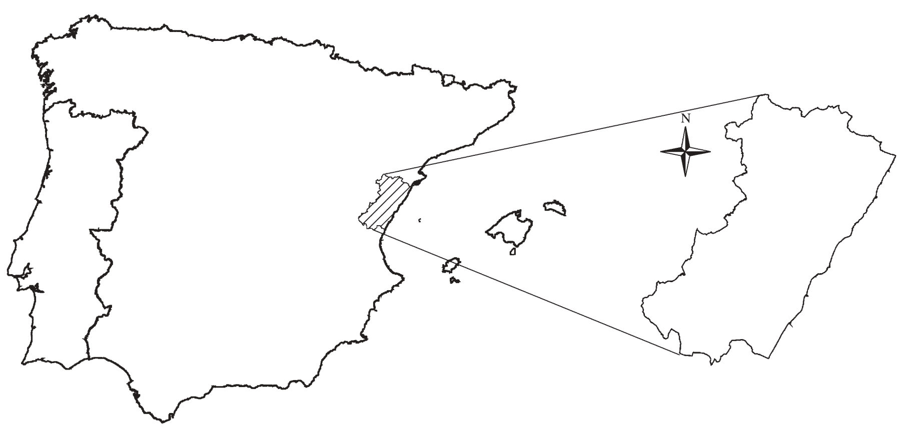

Figure 1. Study area: Castellón province in the Iberian Peninsula (left, shaded area, and right, enlarged).

nestling age (the mean incubation period for the species)(Arroyo *et al.* 1995). A chick was considered to have fledged when it reached 80% of the fledging age (more than 50 days old) at the last visit, provided that at this age nestlings were fully feathered and ready to fly (Carrete *et al.* 2002, Gil-Sánchez *et al.* 2004).

Effects of altitude on fecundity and laying date

We compared territories located at high altitude (those higher than the mean altitude of Bonelli's Eagle territories in the study area) with territories located at low altitude (territories below the mean altitude), in relation to the mean fecundity of each territory for the entire study period, with a *t*-test. In addition, a correlation analysis between fecundity, coefficient of variation (CV) of fecundity and altitude was performed.

To test the effects of altitude on laying date, we first performed a univariate ANOVA to compare the laying date between years (considering the territory as a random factor to avoid pseudo-replication), followed by correlation analyses between altitude and laying date, considering each year separately, and finally the complete data pool considering all territories once.

Effects of nest orientation on fecundity

We calculated mean nest orientation with circular statistics (Fisher 1995) to check for the existence of a preferred orientation in the study area. For calculations, we used the mean orientation of each cliff hosting the nest (or nests) of each pair once, to avoid pseudo-replication. We tested for uniformity in nest orientations by means of the Rayleigh uniformity test. We compared the mean fecundity between pairs nesting on north- (from 315° to 25°), east- (from 26° to 134°), south- (from 135° to 225°) and west- (from 226° to 314°) facing nests by a Kruskal–Wallis test (Gil-Sánchez *et al.* 2004). In addition, we compared differences in mean orientation between pairs located at high altitude and pairs located at low altitude with the circular statistic Watson–Williams test for two samples (Zar 1984).

Territory quality

We compared fecundity under different density conditions (low-density sites versus high-density sites), in order to detect whether data were influenced by a density-dependent effect, with a Mann–Whitney *U*-test (Penteriani *et al.* 2003). High-density sites were those with a nearest-neighbour distance (NND) lower than the average in the study area, and low-density ones those with a NND higher than this average distance.

To analyse the effect of territory quality, we tested first differences in fecundity between years by means of a univariate ANOVA (with year as a random factor to avoid pseudo-replication) to check whether annual differences might confound our results (a year effect) (Penteriani *et al.* 2003). We then performed a Kruskal–Wallis test to test the variation in fecundity between territories.

Following the Habitat Heterogeneity Hypothesis (Ferrer *et al.* 2006) we checked the fit of the fecundity and its CV to a normal distribution, followed by a correlation analysis between mean fecundity and its CV. We also analysed the relationship between mean fecundity and skewness following Ferrer *et al.* (2006) rationale.

RESULTS

We found between 28 and 33 pairs, and counted a total of 131 breeding attempts for the five-year monitoring period (2002–06). Mean (± sd) values for reproductive parameters were: fecundity = 0.968 ± 0.178 fledged chicks/occupied territory (CV = 18.44%, n = 155), productivity = 1.145 ± 0.152 fledged chicks/laying pair (CV = 13.28%, n = 131), breeding success = 0.824 ± 0.077 successful pairs/laying pair (CV = 9.34%, n = 131), and fledging rate = 1.389 ± 0.114 fledged chicks/successful pair (CV = 8.24%, n = 108). Detailed annual reproductive parameters are given in Table 1.

The average altitude of Bonelli's Eagle territories in the study area was 508 ± 151 m. Territories located at lower altitudes showed higher mean fecundity than those located at higher altitudes ($mean_{HA}$ = 1.03 chicks/year, $mean_{LA}$ = 1.34 chicks/year, t = 2.84, P = 0.008) (Fig. 2). A negative relationship exists between altitude and mean fecundity (r = –0.433, P = 0.012), but not between altitude and CV of fecundity (r = 0.087, P = 0.630).

We estimated laying date for the period 2004–06. The mean laying date in the study area was 18 February ± 16 days, with a range from 27 January to 28 March (n = 35). We were able to estimate the age of 57 chicks belonging to 20 pairs. No inter-annual differences were found in laying date (ANOVA, $F_{2,32}$ = 0.089, P = 0.915). This was positively correlated with nest altitude considering all data (r = 0.370, P = 0.014, n = 35) (Fig. 3), and when considering only the years 2004 (r =

Table 1. Annual reproductive parameters of Bonelli's Eagle in the eastern Iberian Peninsula.

	2002	2003	2004	2005	2006
Hatched chicks	37	45	27	32	26
Fledged chicks	32	38	24	31	25
Monitored pairs	28	33	30	32	32
Laying pairs	27	32	27	24	21
Successful pairs	22	28	19	20	19
Pairs with 0 fledgling	5	4	8	4	2
Pairs with 1 fledgling	12	18	14	9	13
Pairs with 2 fledglings	10	10	5	11	6
Fecundity	1.143	1.152	0.800	0.969	0.781
Productivity	1.185	1.188	0.889	1.292	1.190
Breeding success	0.815	0.875	0.704	0.833	0.905
Fledging rate	1.455	1.357	1.263	1.550	1.316

0.531, P = 0.047, n = 11) and 2005 (r = 0.571, P = 0.026, n = 12), but not 2006 (r = –0.025, P = 0.470, n = 12). We did not find a relationship between laying date and fecundity (r = –0.008, P = 0.974, n = 20).

The mean nest orientation in the study area was 20.19° ± 74.86°, and nests were not orientated preferably to any direction (Rayleigh test, r = 0.302, P = 0.496, n = 33). There was no relationship between nest orientation (categorically considered) and fecundity (Kruskal–Wallis test, $H_{3,33}$ = 4.764, P = 0.190). Also,

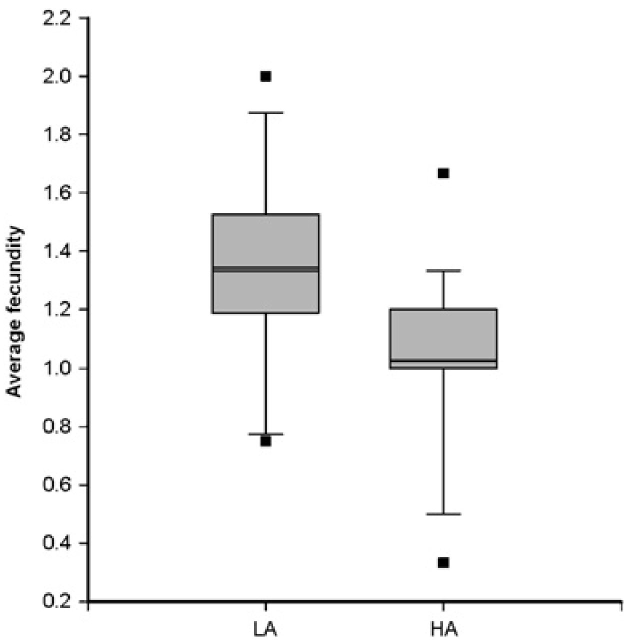

Figure 2. Comparison between territories sited at higher altitudes (HA) than the mean altitude of Bonelli's Eagle territories in the study area versus territories located at altitudes below the mean (LA) in relation to average fecundity, in eastern Spain. The median, 10th, 25th, 75th and 90th percentiles are plotted as boxes with error bars. Outliers are marked with black dots.

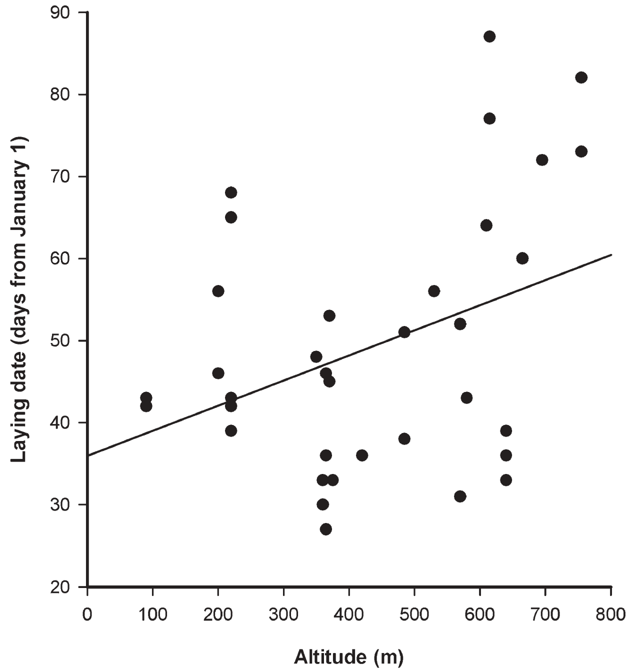

Figure 3. Laying date of Bonelli's Eagle in eastern Spain during 2004–06, in relation to nest altitude.

when comparing nests located at high and low altitude, we did not find differences in mean orientation (Watson–Williams test for two samples, $W_{19,14}$ = 0.0372, P > 0.10) and there was no preference in mean orientation (Rayleigh test, R_{high} = 0.397, P = 0.839, n = 19, R_{low} = 0.216, P = 0.527, n = 14).

The average NND in the study area was 8328 ± 6156 m. No differences were found between breeding sites in areas of low and high breeding pair density, either in the mean number of fledged young (Mann–Whitney U-test, z = 0.637, P = 0.524, n = 25, 8) or its coefficient of variation (Mann–Whitney U-test, z = 1.370, P = 0.171, n = 25, 8).

In relation to territory quality, no differences were detected in fecundity between years (univariate ANOVA, $F_{4,125}$ = 1.320, P = 0.266), and no differences were found in fecundity between territories (Kruskal–Wallis test, $H_{32,130}$ = 36.663, P = 0.261). However, the overall fecundity and its coefficient of variation were normally distributed (Kolmogorov–Smirnov test, z = 0.855, P = 0.458, and z = 0.581, P = 0.889, respectively) and there was a strong negative relationship between them (Pearson correlation, r_p = –0.889, P = 0.044, n = 5). In addition, mean fecundity was inversely related to skewness of fecundity (linear regression, r^2 = 0.7824, P = 0.0463).

Only one territory produced two fledged young every year during the study period, and only one territory produced an average of less than 0.5 young per reproductive attempt. In relation to the timing of failure, 24 pairs did not initiate reproduction (15.48% of the monitored pairs), whereas 23 pairs failed during the laying period or brood rearing (14.84% of the monitored pairs). The causes for not beginning reproduction or failure were unknown. It was not possible to determine whether the failure occurred during the laying period or when young were a few days old. We observed that 17 chicks did not reach fledging age; the causes for failure remain unknown, but are likely to be predation, trichomoniasis, inadequate parental care, lack of food supply or extreme climate conditions.

DISCUSSION

In this paper we have shown the results of a monitoring scheme of the Bonelli's Eagle population in an area where a healthy population still remains in the eastern Iberian Peninsula. Our results show that the population has remained stable since the first national census was conducted 17 years ago, when 32 pairs were reported (Arroyo *et al.* 1995). The reproductive parameters were similar to those reported in other study areas (Table 2), and the breeding success was higher than the national mean. The productivity and flight rate were lower than those reported for southern regions of Spain and Morocco, but higher than those reported for northern regions of France and Catalonia (Spain), thus suggesting a positive clinal variation in these parameters from north to south in the distribution area. This variation has been explained by climatic factors that could be limiting the species' breeding performance (Ontiveros & Pleguezuelos 2003b). It is important to note that for Bonelli's Eagle the Mediterranean region is at the extreme of its distribution range, and it is usual for ecological constraints to be strong at the boundaries of the distribution area (Cox & Moore 2000).

The effect of latitude is similar to the effect of altitude (Blondel 1995). In the study area, laying date was positively correlated with nest altitude, with the coastal pairs laying earlier than those located in mountainous regions. Pairs located at lower altitudes showed higher mean fecundity than those at higher altitudes, suggesting physiological limitations as altitude increases. However, although we found a negative relationship between laying date and fecundity, we did not find a significant relationship between them. Similar results have been found in regions such as Granada (Gil-Sánchez 2000), and a negative effect of prey availability as altitude increases has been proposed as a causative factor of this relationship. The advance in laying date in relation to territory quality (in terms of prey availability) has been reported in other raptors, where a better physiological status caused by higher prey availability will result in the advance of reproduction (Newton 1979, Dijkstra *et al.* 1982, Korpimäki 1987, Steenhof *et al.* 1997).

Unlike other studies, we did not find a preference in mean nest orientation towards favourable thermal conditions (Ontiveros & Pleguezuelos 2000), either in breeding performance or in relation to nest altitude. The relative proximity of all territories to the coastline (in some cases less than 10 km away) could be causing a smoothing effect; a temperate climate is found far from climatic extremes like those found in more inland areas, which show greater variations in temperatures.

The average NND in the study area was lower than the national mean of 11.9 km reported in Arroyo *et al.* (1995). We did not find a difference in breeding performance between territories classed as being at high density and those classed as being at low density, either in the mean number of fledged young or its coefficient of variation. Although no differences were detected in fecundity between years when comparing all territories, a negative relationship between fecundity and its coefficient of variation, and a negative relationship between mean fecundity and the skewness of fecundity were found. This could suggest differential reproductive success in relation to habitat heterogeneity (Ferrer *et al.* 2006). Our results could be explained in the light of the Habitat Heterogeneity Hypothesis (Fretwell & Lucas 1970, Ferrer & Donázar 1996). A prediction of this hypothesis is an increase in fecundity variance with density (because at high densities more poor sites are occupied) and lower fecundity is detected. Ferrer *et al.* (2006) propose that it is a critical test to demonstrate a negative relationship between mean fecundity and its coefficient of variation, and our results match this prediction. Research is being conducted to address this issue and to test this hypothesis with additional criteria, including density-independent territory fecundity, territory turnover rates and territory variability, as suggested by Ferrer *et al.* (2006).

Future research for the species will involve determining the causes of breeding failure in our study area. This issue is especially difficult to assess properly, as very accurate and continued monitoring of each territorial pair is needed. The data currently recorded

Table 2. Summary of breeding parameters recorded for Bonelli's Eagle around the world and particularly in other regions of the Iberian Peninsula.

Source	Study area	Breeding success	Productivity	Fledging rate	Study period	Pairs (*n*)
Del Hoyo *et al.* (1994)	World	1.0–1.5 chicks/ clutch	–	1.4–1.6 chicks/ breeding attempt	–	–
Rico *et al.* (1990)	Alicante (E Spain)	–	1.21 chicks/pr/yr	–	1988–90	24
Alamany *et al.* (1984)	Catalonia (NE Spain)	1.24 chicks/pr/yr	1.12 chicks/pr/yr	1.50 chicks/pr/yr	1970–83	32
Jordano (1981)	Sierra Morena (S Spain)	–	0.8–1.8 chicks/pr/yr	1.5–2.0 chicks/ laying pair	1975–78	10
Del Junco (1984)	Baetic Mountains (S Spain)	–	1.27 chicks/pr/yr	–	1981–82	30
Baguena *et al.* (1987)	Valencia (E Spain)	–	0.66 chicks/pr/yr	–	1984	–
Martínez *et al.* (1988)	SE Albacete (SE Spain)	–	1.5 chicks/pr/yr	–	1984–87	3
Perennou (1989)	Provence and Languedoc (S France)	0.71 chicks/ laying pair	0.89 chicks/pair	–	1989	19
Gil-Sánchez *et al.* (1994)	Granada (SE Spain)	100% successful breeding pairs	1.50 chicks/pair	1.61 chicks/ successful pair	1994	14
Gil-Sánchez *et al.* (2004)	Granada (SE Spain)	86.6 ± 6.4 successful breeding pairs	1.43 ± 0.11 chicks/ pr/yr	1.66 ± 0.04 chicks/successful pr/yr	1994–2002	18–33
Penteriani *et al.* (2003)	Baetic Mountains (S Spain)	–	1.38 ± 0.71 chicks/ pair (*n* = 591)	1.59 ± 0.51 chicks/successful pair (*n* = 518)	1980–2000	–
Cheylan (1981)	Provence (S France)	75% successful breeding pairs	1.17 chicks/pr/yr (*n* = 104)	–	1956–80	26
Ontiveros & Pleguezuelos (2003a)	Granada (SE Spain)	77.3% successful breeding pairs (*n* = 150)	1.34 ± 0.76 (*n* = 150)	–	1994–2001	16–22
Carrete *et al.* (2002)	Murcia (SE, Spain)	1.35 ± 0.70 chicks/ laying pair (*n* = 171)	1.13 ± 0.81 chicks/ pr/yr (*n* = 218)	–	1983–97	17–35
Rico *et al.* (1999)	Valencia (E Spain)	–	–	1.64 chicks/ successful pair	1996–98	36
Ontiveros & Pleguezuelos (2000)	Granada (SE, Spain)	–	1.42 ± 0.38 (*n* = 19)	–	1994–98	19
Real & Mañosa (1997)	Spain (review) and Provence (France)	–	0.36–1.24 chicks/ pr/yr	–	1980–1994	–
Bergier & Naurois (1985)	Atlas Mountains (Morocco)	–	1.50 chicks/pr/yr	–	–	25
Leshem (1976)	Israel	–	0.90 chicks/pr/yr	–	1974–76	20–23
Arroyo *et al.* (1995)	Spain (review)	54.0% successful breeding pairs (*n* = 198)	0.82 chicks/pair (*n* = 198)	1.56 chicks/ successful pair (*n* = 172)	1990	198
Present study	Castellón (E Spain)	0.82 ± 0.08 successful breeding pairs (*n* = 131)	1.15 ± 0.15 chicks/ pr/yr (*n* = 131)	1.39 ± 0.11 chicks/successful pair (*n* = 108)	2002–06	28–33

Breeding parameters are expressed as appeared in the original papers and in some cases the calculations do not correspond with those used in this paper. For further details on breeding parameter estimation it is necessary to consult the original reference. Chicks/pr/yr, Chicks per pair per year. –, No data.

on adult and subadult mortality are not sufficient to develop a consistent predictor of population and demographic trends, but we suspect that in the future it might be possible to find a territory-specific mortality association that could determine whether there is a habitat heterogeneity framework similar to that found in southern Spain (Carrete *et al.* 2006).

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