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Annual productivity and individual female reproductive success in a Great Bustard *Otis tarda* population

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The reproductive success of Great Bustards *Otis tarda* in north-western Spain was studied between 1987 and 1998, both at the population (*c.* 700 adult females breeding in our study area) and the individual level (sample of 32 marked females). Overall productivity was low, with a population mean of only 0.14 chicks reared per adult female, and an average breeding success of 0.15 chicks per year in the sample of marked females, but interannual variability was high (0.04–0.29). Population productivity was positively correlated with winter (October–March) precipitation prior to each breeding season, and negatively correlated with the number of days of rain during the hatching period. High annual productivity resulted from a high proportion of females rearing two chicks. Reproductive success was higher in females older than 6 years than in younger birds. The proportion of females in the marked sample that failed in breeding after having bred successfully the previous season was significantly higher than the proportion of those that did not. Finally, females with a higher than average breeding success tended to breed successfully in years of both low and high population productivity, whereas those with lower than average breeding success did so only in years of high productivity.

The Great Bustard *Otis tarda* is a globally threatened (Alonso & Alonso 1996, Heredia *et al.* 1996), steppe-living, sexually dimorphic, lekking bird in which parental care is exclusively undertaken by females (Gewalt 1959, Johnsgard 1991, Alonso *et al.* 1998). Chick growth rates are highest in the first 3 months of life, when their diet is based on insects (Litzbarski & Litzbarski 1996a). Probably due to the high nutritional needs of the offspring at this time, the home range of families then reaches its largest size (*c.* 3 km average diameter, Martín 1997), which results in a decrease of the carrying capacity of the breeding habitat. Chick mortality is highest during this phase, 60–70% in our study area (Martín 1997). Although female reproductive performance has been identified as a critical parameter in the survival of Great Bustard populations (Streich *et al.* 1996), it has been poorly studied. Ena *et al.* (1987) studied the breeding success in a single population during one breeding season, and a few other studies have provided productivity values for different populations in single years (Alonso & Alonso 1990). However, no study has so far analysed annual productivity and individual variation in reproductive success in a wild population and over a reasonably long series of years (reviews in Johnsgard 1991, Del Hoyo *et al.* 1996). Consequently, data on mean breeding success and its interannual and individual variation in the Great Bustard should provide valuable information for population modelling as a basis for conservation management.

This paper presents the results of an 11-year study of several aspects of female Great Bustard breeding success. From a population perspective, we studied the influence of different weather variables on annual productivity, particularly those acting at critical times of the year, like rainfall during the winter prior to each breeding season, and rainfall and temperature during the last days of incubation and first days

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after hatching, which have been shown to be a determinant of breeding success in many species of birds (e.g. Slagsvold & Grasaas 1979, Lucio 1990, Carrascal *et al.* 1993, Potts & Aebischer 1995, Bealey *et al.* 1999, Puigcerver *et al.* 1999). At the individual level, we studied the relationship between the age of a sample of marked females and their breeding success, as well as the effect of maternal effort on the ability of females to breed successfully in the following attempt. In a wide variety of bird species, reproductive success has proved to be lower during the early years of maturity and senescence (see reviews in Clutton-Brock 1988, Newton 1998). We finally explore the differences between marked females of varying quality as breeders in years of high and low population productivity.

METHODS

Study area

Our study was carried out in the Wildlife Reserve of Villafáfila (41°50′N, 5°35′W, about 700 m asl), which extends over 32 682 ha of dry, treeless and gently undulating farmland in the Province of Zamora, NW Spain. The land is almost entirely cultivated with wheat and barley. The remaining surface (about 9%) is occupied by natural grassland used for sheep grazing. The Reserve holds the world's densest population of Great Bustards, with more than 2000 birds at mating time in spring, and 650–750 adult females breeding in summer (Alonso *et al.* 1995a,b).

Estimation of annual productivity and average brood size

Annual productivity was defined as the total number of yearlings divided by the number of adult females (≥ 2 years old) in September, when the period of highest juvenile mortality during summer is over (Martín 1997). Average brood size was the number of chicks reared per successful female in September. By this time of the year, practically all of the families in the Reserve were detected, due to the lack of vegetation cover for them to hide after harvesting (see details of census methodology in Alonso *et al.* 1990). In September 1996 and 1997 an abnormally high cover of sunflower fields (still not harvested) was found for the first time in the study area. The number of families was therefore underestimated in those years because of the high probability of missing birds hidden in the sunflower fields, so productivity estimates have not been considered for those years.

Breeding success of individual females

Females used in this study come from a sample of birds, wing-tagged or radio-tagged as juveniles in each summer between 1983 and 1993, after they had become established as breeding adults in the study area, normally at about 2 years of age (Alonso *et al.* 1998). We determined their breeding success during monthly censuses of the Reserve (June–September, see Alonso *et al.* 1996, Alonso *et al.* 2000, Morales 1999, for details). Individual breeding success (reproductive success index) was measured as the number of young successfully raised by each female averaged over all breeding attempts recorded for that female. A female was considered to have successfully bred if it was seen followed by a chick or chicks in September, once the 60–70% juvenile summer mortality peak was over.

Juvenile mortality from September on and up to the moment of independence from the mother by the onset of the next breeding season, the following March–April, was less than 10% in a sample of 101 chicks marked and radio-tracked in the Reserve between 1991 and 1993, thus being comparable to adult mortality rates (Martín 1997). Therefore, the juvenile survival rate by mid-September can be considered as a reasonable estimate of the annual recruitment of young birds into the population. From October onwards, families join large flocks, and identification of female yearlings becomes practically impossible (Alonso *et al.* 1990). Records of successful or failed breeding attempts were obtained for a total sample of 32 marked females between 1987 and 1997.

Statistical analyses

Weather variables were obtained at the only weather station in the Reserve, located at 41°51′20″N, 5°29′47″W, 691 m asl. We used multiple regression analysis to study the relationship between annual productivity and weather during the two critical periods considered (see Introduction): winter and hatching period. Since the series of years was relatively small (1987–95), after exploratory regression analyses of a larger set of variables including mean monthly rainfall, monthly number of rain days, and mean, maximum and minimum monthly temperatures, we selected the following independent variables: mean monthly rainfall from October to March prior to each breeding season (winter rainfall), and the number of rain days during the hatching phase (last week of May and the first week of June in our study area, see Martín 1997).

The frequency of families with two chicks was used to estimate population breeding success, and to compare productivity between years. Years in which the number of yearlings counted in September was higher than the average for the whole study period were considered 'good years', and other years as 'bad years'. Differences in frequency of two-chick families between high and low productivity years were analysed using a Mann–Whitney *U*-test.

To analyse the influence of age on breeding success we divided marked females into two categories: females up to 6 years old, and females older than 6 years. This was the minimum age at which age seemed to have an important effect on the individual reproductive success index. Breeding success differences between these age classes were analysed using a two-factor ANOVA in which the random factor 'individual' was nested in the 'age' factor, after square-root transformation of the data. Birds with breeding attempts in both age levels were removed from the analysis.

The influence of maternal effort on a female's ability to breed successfully in two consecutive years was investigated by considering the probability that a given female breeds successfully in two consecutive years as a binomial variable (success or failure in second consecutive year). In total, seven females were used for which records of two consecutive breeding attempts existed. To account for a possible across-year effect, we tested the independence between first-year quality (good or bad) and successful and failed attempts in either good or bad second consecutive year by means of a 2×4 contingency table. No female contributed more than once to either the binomial test or the contingency table.

In order to study the relationship between female long-term reproductive performance and year quality in terms of population productivity, marked females were classified as good breeders if their reproductive success index was higher than the mean value of the reproductive success index of those females that reared at least one chick during the study period ($n = 11$), or bad breeders if their individual reproductive success index was lower than that value. The association of these two classifications was analysed by means of a Chi-square test.

RESULTS

Mean annual productivity of the population

Table 1 shows the productivity and weather values for each of the study years. Overall productivity was low, only 0.14 chicks reared per female, and showed high interannual variability (0.04–0.29). In the multiple regression analysis, the only significant weather variable was winter precipitation. Annual productivity was positively correlated with average rainfall during the previous winter (Fig. 1). Dry winters thus resulted in low annual productivities. In the multivariate analysis, this relationship could mask the effect of rain during hatching, in the likely event that many females decided not to breed, or reduced their clutch size, after extremely dry winters. Absence of rain during hatching would not result in any productivity increase for those females. Therefore, we performed a new regression analysis excluding 1992 and 1995, which

Table 1. Reproductive parameters of female Great Bustards and weather variables in the Reserve of Villafáfila between 1987 and 1995. Productivity is expressed as number of chicks survived to September per adult female ≥ 2 years old. See Methods for definition of other variables.

Year	No. of chicks in September	Overall productivity (chicks/females)	No. of chicks per family	Winter rainfall (mm)	No. of rainy days during winter	No. of rainy days during hatching	Min. temperature during hatching (°C)
1987	198	0.29	1.33	40.48	47	2	–
1988	69	0.11	1.22	28.55	70	3	–
1989	65	0.10	1.13	27.76	35	4	8.61
1990	115	0.17	1.22	56.85	76	2	10.42
1991	69	0.09	1.07	36.50	62	5	10.35
1992	27	0.04	1.08	12.52	28	9	10.17
1993	102	0.14	1.11	28.74	45	6	8.68
1994	209	0.27	1.16	33.47	64	1	9.29
1995	36	0.04	1.12	25.30	57	0	10.1
Mean ± sd	99 ± 65	0.14 ± 0.09	1.16 ± 0.08	32.24 ± 12.13	53.7 ± 16.2	3.6 ± 2.8	9.66 ± 0.79

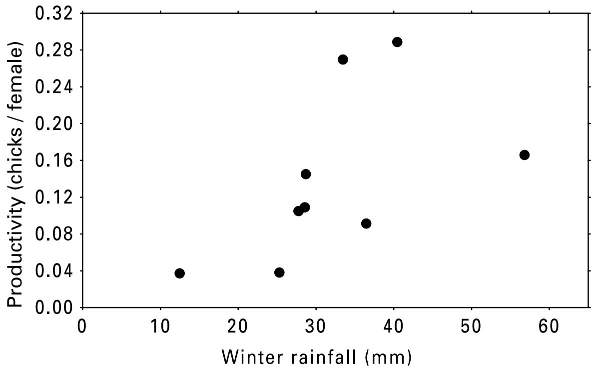

Figure 1. Relationship between Great Bustard productivity (no. of chicks counted in September per adult female – older than 2 years – in the population) and winter precipitation between 1987 and 1995. The correlation was significant in a multiple regression analysis ($r = 0.64$, $P = 0.04$).

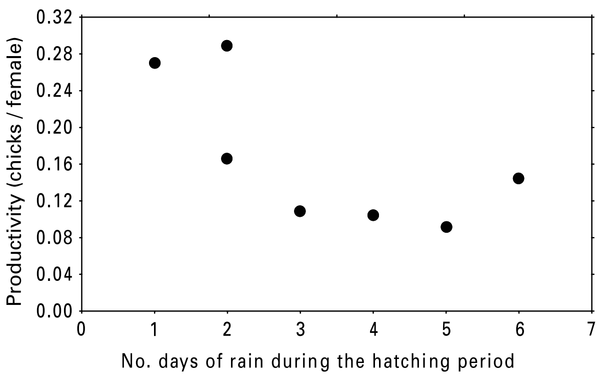

Figure 2. Relationship between Great Bustard productivity and number of days of rain during the hatching phase (last week of May and first week of June) over the period of study, excluding the dry years 1992 and 1995 (see text for explanation, and values in Table 1). The correlation was significant in a multiple regression analysis ($r = -0.80$, $P = 0.03$).

had the driest winters and springs during the study period, and consequently the lowest annual productivities (see Table 1). After removing both years, productivity and number of rain days during hatching showed a significant negative correlation (Fig. 2).

The mean number of chicks raised by a successful female was 1.16 (Table 1). This variable was positively correlated with overall productivity ($r = 0.70$, $P = 0.03$). The number of families with two young was significantly higher in years with higher than average productivity than in years with lower than average productivity (Mann–Whitney U-test = 2.0, $P = 0.02$, $n = 5$ and 6, respectively). Finally, winter precipitation was also significant ($P = 0.04$) in a multiple regression analysis using brood size as the dependent variable.

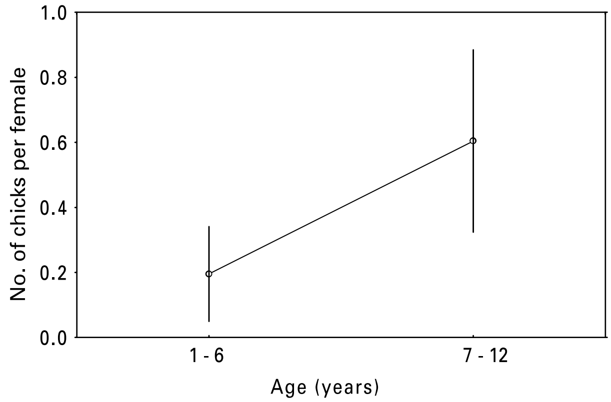

Figure 3. Differences in individual breeding success with age of marked females: variation of the mean number (± 95% confidence intervals) of successfully bred chicks per female and year in the two age classes considered ($F_{1,20} = 11.77$, $P = 0.004$).

Individual reproductive success of females

Reproductive success increased significantly from 0.20 chicks per year in females ≤ 6 years to 0.40 chicks in older ones (Fig. 3). Age class was highly significant in the two-factor ANOVA that analysed the mean number of young reared per female ($F_1 = 11.77$, $P = 0.004$), while the factor 'individual' was not ($F_{20} = 0.60$, $P = 0.90$). The mean age of first successful breeding, i.e. chicks surviving until September, was 4.20 years (sd = ±1.48, $n = 10$ marked individuals with complete data series). However, females may already attempt to breed when less than 2 years old, as shown by a 24-month-old marked female observed in the company of a recently hatched chick in June, which died later in the season.

The proportion of females that bred successfully in a given season and failed in the following one was significantly higher than that of females that bred successfully in two consecutive years (86% and 14%, respectively, binomial $z = 0.35$, $P = 0.05$, $n = 7$) irrespective of yearly overall productivity (2 × 4 Chi-square contingency table, $P = 0.45$, see Table 2). No significant association was found between the number of good breeders and the quality of the year in terms of overall productivity (Chi-square, $P = 0.42$). However, females with a high reproductive success index tended to maintain a good reproductive performance in years of low overall productivity, while no female with a value lower than the average was successful in years of low overall productivity (Table 3). The mean value of the reproductive success index for the total sample of marked females was

Table 2. Distribution of females succeeding or failing in their second consecutive reproduction in relation to the quality of first (Year *t*) and second years (Year *t* + 1). The second column of the table was not computed in the Chi-square test.

	Year *t* + 1 'good', success	Year *t* + 1 'bad', success	Year *t* + 1 'good', failure	Year *t* + 1 'bad', failure
Year *t* 'good'	1	0	1	4
Year *t* 'bad'	0	0	1	0

Table 3. Long-term performance, year quality and number of successful reproductions in 'bad' years corresponding to marked female with at least one recorded successful breeding attempt.

Female	Long-term reproductive performance	Successful reproductions in 'bad' years
a	good	1
b	good	2
c	good	1
d	good	0
e	good	1
f	good	1
g	bad	0
h	bad	0
i	bad	0
j	bad	0

0.15 chicks reared per breeding attempt and female (sd = ±0.25, n = 32). This value was almost identical to that of the mean overall productivity (Table 1), supporting the view that our sample of marked individuals was representative.

DISCUSSION

Influence of weather on productivity

The only weather factor that seemed to have an important effect on the annual breeding success of female Great Bustards was rainfall during the winter before each breeding season. The influence of winter rainfall seemed to be especially important during the driest years 1992 and 1995, which were also the ones of lowest productivity (see Table 1). Winter precipitation may have two main effects on the breeding performance of females. First, it is probably the major factor determining the productivity of annual plants during the following spring (Mooney & Munerow 1981) and therefore the availability of arthropods during the period of maximum growth rate of Great Bustard chicks in early summer (see, e.g. Litzbarski *et al.* 1987, Miller *et al.* 1994). The significantly higher number of females with two chicks in high productivity years, i.e. years of greater winter rainfall and therefore greater food abundance, reflects the importance of winter rain in the ability of females to increase their brood size. The diet of young birds is based on orthopterans (Lane *et al.* 1999), whose abundance depends directly on grass productivity (Litzbarski & Litzbarski 1996a). Secondly, early spring development of herbaceous vegetation also contributes to the good physiological condition of females, which also influences the percentage of females attempting to breed, and clutch size and viability (Lack 1968, Clutton-Brock 1988, Newton 1989). The analysis of winter and early spring diet of adult female Great Bustards has indeed shown a high presence of wild annual plants such as Poppy *Papaver rhoeas* and Bugloss *Echium* spp. (Lane *et al.* 1999).

Although it was not possible to determine the relative importance of both effects described above, a decrease in the number of females breeding, as well as in the mean clutch size, after extremely dry winters could mask the negative effect of a rainy hatching period on chick survival. The lack of precipitation during hatching would indeed have little beneficial effect if the previous winter was already extremely dry, inducing a number of females not to breed. Consequently, a rainy hatching period would only act as an enhancing factor of the negative effect of winter drought, whereas its absence would hardly contribute to increase the benefits yielded by a wet winter. This explains why the removal of the two driest years 1992 and 1995 gave a significant negative correlation between productivity and rain during the hatching period.

Frequent precipitation during the days following hatching probably increased mortality among small chicks due to lowered thermoregulation capacity, in spite of temperature stability in our study area. In another Great Bustard population in central Spain, May–June 2000 was the wettest hatching season of the last 50 years, and productivity in this year was by far the lowest recorded during the last 5 years (Alonso *et al.* unpubl. data). Litzbarski and Litzbarski (1996b) suggested that Great Bustard chick mortality could increase because of rain during hatching in the

German population. Similar effects have been described in other species, both altricial and precocial. Slagsvold and Grasaas (1979), for example, found a negative correlation between number of rain days and precipitation levels during the first days of life of Capercaillie *Tetrao urogallus* chicks in southern Norway, and the density of young during the following autumn in the same area. Similarly, Carrascal *et al.* (1993) found a negative correlation between breeding success of White Storks *Ciconia ciconia* in a region in central Spain characterized by its mild temperatures, and the number of rain days after hatching.

Productivity and quality of females

Only one out of eight breeding females in the population was successful in rearing young. There are no published long-term studies of reproductive success in other Great Bustard populations, although our preliminary results obtained in central Spain yielded similar values (own unpubl. data). Major juvenile mortality causes in this species are egg destruction by corvids and chick predation by foxes and dogs (Ena *et al.* 1987, pers. obs.), but starvation also plays an important role due to the high energetic demands of young during their phase of fastest growth (Litzbarski & Litzbarski 1996b, Quaisser *et al.* 1998). A similar effect has been described in a long-term study of British Grey Partridge *Perdix perdix* population dynamics (Potts & Aebischer 1995).

Another factor that might determine the low reproductive success is the high energy cost for females incurred by a successful breeding attempt, as can be inferred from the small percentage of marked females that bred successfully in two or more consecutive years. Once families aggregate in winter flocks, chicks still depend on their mothers up to the beginning of the next breeding season (Alonso *et al.* 1998). During that period mothers continue feeding them and, in some extreme cases, females were observed feeding juveniles even after the following breeding season (Martín 1997, pers. obs. on radio-tagged families). It is thus reasonable that after such maternal effort females will have a high probability of failing in their next reproductive attempt. This has also been described in several species of mammals with prolonged periods of maternal care (Clutton-Brock *et al.* 1982, Clutton-Brock & Godfray 1991).

Our data showed an increase in breeding success with age. Only two of the 10 females in which it was possible to verify their first breeding attempt were successful in that attempt. Gewalt (1959) reported the usual desertion of nests by first breeding, captive-raised Great Bustard females, and Glutz *et al.* (1973) found that in a wild population in Germany the frequency of one-egg clutches was significantly higher among females making their first breeding attempt. The lack of association between performance of bad or good breeders and year quality further reinforces the role of age as a determinant of individual reproductive success, given its independence from inter-annual oscillations in any population parameter affected by environmental factors such as weather or food availability. Differences in breeding success with age may result from different physiological conditions being associated with different ages, accumulated experience, or the combination of both. Although physiological condition may indeed limit clutch size as a consequence of immaturity, the high egg losses by young females as reported by Gewalt (1959) and Glutz *et al.* (1973) should be attributed to lack of experience.

In spite of this low reproductive success, the Great Bustard population of the Reserve of Villafáfila remained stable between 1987 and 1996, with a slight tendency to increase (Alonso *et al.* 1995a, 1996). However, as argued in those studies, the latter tendency may reflect a concentration of breeding females from neighbouring populations as a consequence of habitat loss, rather than intrinsic population growth in the study area. Low reproductive rates can be regarded as part of the Great Bustard life strategy, in which population viability depends on the survival of long-lived adults rather than on a high recruitment rate. However, a decrease in breeding success below the average productivity recorded in this study might be critical to population viability, as suggested by recent computer simulations (Streich *et al.* 1996, Lane & Alonso 2001). In the latter study, annual productivity was the most sensitive demographic parameter, reducing the probability of extinction of small leks from 88% to 11% within ranges of 0.14–0.26 chicks per female. Low productivity due to lack of arthropods in intensively cultivated farmland has been identified as one of the main causes of the sharp decline of the German Great Bustard population from 1200 birds in 1960 to fewer than 100 today (Litzbarski & Litzbarski 1996b, pers. comm.). The Spanish population studied here, probably the one with highest breeding density in the world, had lower productivity values than other Iberian populations (Alonso & Alonso 1990, own unpubl. data), which suggests that it could be close to its carrying capacity.

The results presented here are important for the conservation of Great Bustards. First, they represent the first long-term data on breeding success of this threatened species, providing mean and variability values of demographic parameters needed in population viability modelling. Secondly, they may help the species' managers to predict the effect of winter drought on Great Bustard population productivity. Given that food scarcity after dry winters seems to be a major cause of low productivity, provision of drought-resistant crops (e.g. alfalfa and other legumes) could improve female condition over the winter leading to enhanced productivity the following year. Such measures might be particularly important in small populations with very low productivity. Finally, the relationship found between population breeding success and the proportion of families with two chicks can be used by managers to evaluate yearly overall population productivity in the Great Bustard.

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