J. Avian Biol. 38: 335–346, 2007
doi: 10.1111/j.2007.0908-8857.03811.x

Received 5 October 2005, accepted 9 June 2006

Sex-biased juvenile survival in a bird with extreme size dimorphism, the great bustard *Otis tarda*

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We explored sex-biased mortality patterns in a species showing the most extreme sexual dimorphism among birds, the great bustard Otis tarda. Between 1991 and 2005 we studied juvenile and immature survival in a sample of 361 great bustards radio-tagged at two different populations in Spain, Villafáfila and Madrid. Mortality decreased with age, from high rates during the first year (0.70), to 0.10 in the second year. Using the known-fate model in program MARK we found that monthly survival increased throughout the first year. Offspring showing higher body mass at marking, i.e. those hatched earlier in the season and those with better body condition, survived in higher proportion. This was probably related to the earlier breeding dates of more experienced mothers, as well as to the observed decrease in food availability as the season progresses. Monthly survival estimates were higher in females than in males, which suggests that juvenile males are more vulnerable to reduced food availability and other factors due to their much faster growth rates. The proportion of non-natural deaths increased with age, and was higher in the Madrid population, where illegal hunting and collision with powerlines showed a high incidence. The male-biased mortality found in young birds in this study explains the female-biased population sex ratios observed in great bustard populations. The different degrees of incidence of human-induced causes of mortality found between both populations studied suggest that such differences may contribute to the variation observed in the adult sex ratio among populations.

The study of mortality rates and factors that influence survival of animal species is essential to understand their life history patterns and population dynamics. In the case of endangered species it is also important to design their conservation plans (Newton 1979, Verner 1992, Lebreton et al. 1993). Differences in individual characteristics and survival have been studied in a considerable number of birds and mammals. A number of these studies have paid special attention to sex bias in juvenile mortality (review in Clutton-Brock 1991). Sex-biased offspring survival is important because it could cause biased sex ratios before and during the adult stage and involve many ecological and evolutionary consequences (Trivers and Willard 1973, Promislow et al. 1992).

Body size can influence survival, and therefore sex-biased mortality is more likely in species with sexual size dimorphism rather than in monomorphic ones. Some studies have reported greater mortality in the smaller sex, and explained it as a consequence of sibling competition during the nestling stage (Breitwisch 1989, Mulvihill et al. 1992, Arroyo 2002). On the other hand, several studies have shown that the larger sex suffers greater mortality than the smaller, both in species where males are larger (Røskaft and Slagsvold 1985, Teather and Weatherhead 1989, Griffiths 1992, Milonoff et al. 1993), and smaller than females (Newton 1979, Torres and Drummond 1997). The usual explanation of such bias towards the larger sex in juvenile mortality argues that reduced food availability has a greater effect on the survival of the sex with higher nutritional requirements associated with its larger size and faster growth rates (Fiala and Congdon 1983, Clutton-Brock et al. 1985, Slagsvold et al. 1986, Teather and Weatherhead 1988, Weatherhead and Teather 1991, Anderson et al. 1993, Torres and Drummond 1997). Thus, biased sex ratios at the end of juvenile stage may probably result from the cost of sex dimorphism in size evolved through sexual selection. However, most studies on juvenile survival have been carried out during the nestling phase on species with altricial offspring. Data from precocial birds are remarkably scarce, and there are very few studies on bird species showing high sex dimorphism in size.

We investigated these relationships in a long-term study on survival patterns and mortality causes of a large sample of great bustards Otis tarda radio-tagged as offspring and tracked during their first two years of life, i.e. through their juvenile and immature phases. The use of radio telemetry represents a new, ideal method in survival studies, since it provides unbiased results through relatively long periods of an individual's life, both in altricial and precocial species, and during different age stages and specific seasons (McFadzen and Marzluff 1996, Rohner and Hunter 1996, Pace 2000, Combreau et al. 2002, Grant 2002, Spears et al. 2005, Sunde 2005). Great bustards are large, lekking birds that occur in cereal pseudo-steppe habitats mostly in the Iberian Peninsula, with much smaller and endangered populations in central Europe, Morocco and China (del Hoyo et al. 1996, BirdLife-International 2004). Females nest on the ground and rear alone their usually single precocial chick during 6 to >12 months (Alonso and Alonso 1992, Martín 1997, Alonso et al. 1998, Martín 2001, Morales and Martín 2002). Great bustards exhibit one of the highest sexual size dimorphisms among Vertebrates, with males showing 2.4 times the weight of females (Alonso et al. 2004). Male chicks grow much faster and are already heavier than female chicks at an age of three weeks, reaching double the weight of females at three months (Heinroth and Heinroth 1928, Radu 1969, Glutz et al. 1973). This species therefore represents an ideal study subject to investigate the influence of various potential factors on survival patterns, which might be expected to be sex-biased, in line with its marked sex dimorphism in size. Our aims were: (1) to determine mortality rates and their seasonal and interannual patterns, (2) to explore the influence of sex, hatching date and body condition on survival, (3) to identify the main mortality causes and their significance, and (4) to compare survival patterns between two populations subject to different degrees of human-induced negative environmental factors, in order to establish the possible influence of non-natural mortality on survival patterns of this endangered bird species. In addition, we also (5) assessed the possible impacts of catching and tagging on juvenile mortality.

Methods

Radio-tracking methods

Between 1991 and 2003 we marked 361 young great bustards in two different regions of Spain: 101 birds in 1991–93 at the Important Bird Area 039 'Villafáfila' (41°50′N 5°35′W, Zamora, 327 km^2, ~2 000 birds), in the north, and 260 birds in 1995–2003 in central Spain, mainly at the IBA 074 'Talamanca-Camarma' (40°40′N 3°25′W, Madrid and Guadalajara, 520 km^2, ~1 100 birds) but also at some other minor areas within Madrid province (Alonso et al. 1996, Viada 1998, Alonso et al. 2003a). We captured the birds in the second half of July, when they were 3–10 weeks old and still dependent on their mothers, by chasing them down. After one or two flights the young usually separated from its mother, lay down and remained motionless, hidden when possible in the ground vegetation, trying to go unnoticed. After a marking process lasting 10–15 minutes, we released the bird in the same spot where we had caught it to facilitate that it was rejoined by its mother as soon as possible. The average weight at capture was 2,131 g in males (n = 186) and 1,433 g in females (n = 175); birds weighing less than 1 kg were released unmarked. We marked the birds with patagial tags and radiotransmitters. The tags were of PVC (Gravoply), 70 × 65 mm large and 1.5 mm thick. Each tag had a different design using various colours and symbols, to allow visual identification with telescope. The tags were attached to the wing patagium using special pliers (Allflex). The total weight of tag plus rivet was ca. 12 g. The tags were covered with thin brown paper painted with black imitating the plumage design of the birds to reduce as much as possible the visibility of the tag to predators. The paper usually fell off after some days. The transmitters (Biotrack) were TW3 2 × 2/3AA 'poncho'-mounted or neck-lace units (30 g), which we used on many small females, or TW3 2 × AA backpack-mounted units (60 g), which we used to tag larger females and all males. We used elastic harness material to allow the harness to expand as the young grew. The total weight of transmitter plus harness did not exceed the recommended limit of 3–5% of the bird's weight (Kenward 2001). All marked birds were located at least once per month throughout their lives, using Telonics TR2-TS1 telemetry receivers. When the birds dispersed outside the range usually covered by ground tracking, we used E-24 Beechcraft aeroplanes from the Spanish

Air Forces to locate them from the air. The total flight time during this study exceeded 900 h.

To allow birds to adjust to tags we only included in our analyses those birds that survived the week immediately after marking (Table 1; Pollock et al. 1989, Kenward 2001, Warren and Baines 2002). In order to assess possible effects of marking, we compared survival of marked and unmarked young in the period of maximum mortality (from July to September), by counting the number of females and chicks in early summer (July in Madrid, early August in Villafáfila) and late summer (mid September). Surveys were made from four-wheel drive vehicles, using binoculars and telescopes 20–60 ×, with frequent stops at vantage points to carefully look for birds, covering the whole study areas (September) or most of them (July and August) (Alonso et al. 2003b). As female bustards are much more secretive during the early stages of chick-rearing and some females nest outside the study areas it was not possible to directly compare the number of chicks counted in July/August and September. Therefore we calculated the productivity (young/females) in early summer and applied this value to the total number of females counted in September to estimate the number of chicks in July/August. The proportions of tagged and untagged birds surviving from early to late summer were compared using χ^2 test.

Variables analyzed

Sex

We sexed 55% of all marked birds visually in September, when young males are larger than their mothers and young females still smaller. Young males are also distinguishable by their relatively longer tarsi, and a more conspicuous white band along the wing edge. Birds that died before September were sexed through genetic analysis ($n = 29$), or using discriminant functions based on body measurements that classified 96.5–100% of the birds correctly (Martín et al. 2000).

Table 1. Number of juvenile great bustards by sex and year used to estimate survival parameters in this study.

Year	Population	Males	Females	Total
1991	Villafáfila	26	12	38
1992	Villafáfila	3	8	11
1993	Villafáfila	25	19	44
1995	Madrid	13	6	19
1996	Madrid	14	23	37
1997	Madrid	24	17	41
1998	Madrid	16	26	42
1999	Madrid	21	14	35
2000	Madrid	6	4	10
2001	Madrid	9	5	14
2002	Madrid	3	4	7
2003	Madrid	9	21	30
Total		169	159	328

Body mass and hatching date

According to body mass at capture we divided our data set into three groups: large (≥ 1950 g), medium (< 1950 g, > 1500 g), and small (≤ 1500 g). We estimated their Julian hatching date using the growth curves based on body mass published by Heinroth and Heinroth (1928), and Radu (1969).

Body condition

We used Principal Component Analysis to obtain a body size index for each bird (Rising and Somers 1989, Freeman and Jackson 1990). We analyzed males and females separately, using the following linear measurements: wing arch, tail length, tarsus length, central toe length and head length (see Martín et al. 2000 for definition of these variables). The first principal component explained 90% of the body size variance in males, and 77% in females. The residuals of the regression of body mass (dependent variable) on the body size index were used as body condition estimators (Piersma and Davidson 1991, Brown 1996, Korpimäki et al. 2000).

Date of death

The date of death was estimated, whenever possible, through the degree of decomposition of the carcass. When we only found some remains such as feathers or bones, or just the transmitter, we assumed the date of death as the mean between the last time the bird had been controlled alive and the date when the remains were found. The interval between these two dates did not usually exceed 30 days (67% of the cases; mean: 13 days; range 0–30). We divided the juvenile mortality period into two phases, summer (July–September) and winter (October–June).

Hatching year

Twelve years (1991–93, and 1995–2003).

Population

Villafáfila and Madrid.

Number of siblings

When the young was captured (usually 0, sometimes 1).

Mortality causes

Whenever possible, we tried to determine the cause of mortality through a necropsy. In most cases, however, the degree of decomposition of the carcass due to the high summer temperatures in our study areas, or the few remains left by predators, did not allow a precise determination of the cause of death, and we classified it into the following classes after visual inspection of the remains.

Natural death without predation: the carcass was found complete without signs of injury by any predator. Transmitter and wingtags were usually found in place, without signs of human manipulation. Most birds included in this category probably died of starvation, or other natural causes such as growth alterations, or diseases, which might indeed have ultimately been determined by undernourishment, either with the influence of bad weather conditions, e.g. heavy rain, or not.

Predation: the carcass was found partly devoured, and usually the head and breast were missing. The most frequent predators were probably foxes and feral dogs. Some of these birds could have been scavenged after having died due to starvation or another cause included in the previous category.

Human-induced causes: (a) bird shot: we found pellets through radiography, or the holes of the shot were clearly visible in the body or wingtag; (b) other deaths due to hunting: the harness was found cut with a knife, most times without any remains of the bird; neither transmitter nor harness had a putrid smell, which indicated that they had been separated from the bird before rotting started, i.e. just after having been shot; (c) bird killed by a hunter's or shepherd's dog: the harness was found cut with a knife and the carcass usually bitten or partly eaten; the harness and transmitter showed signs of bites; (d) collision with powerlines: the carcass was found below a powerline and usually with broken bones, or neck or breast showing cuts or signs of feather abrasion caused by the cables; (e) bird disappeared: ten birds were never located after their transmitter's signal was heard last time; we assume these transmitters were destroyed deliberately by hunters; (f) other human-induced causes: birds killed by harvesters, knocked down by cars, etc.

We considered the first two causes above as natural mortality factors (although an undetermined, but small number in the second category could have been eaten by feral dogs), and the third one as non-natural mortality factors, i.e. birds died due to the direct or indirect influence of man.

Data analysis

Survival curves were estimated by the Kaplan-Meier or product-limit procedure (Kaplan and Meier 1958). According to this method the survival rate, the number of individuals at risk, dead, and censored (end of monitoring), were calculated for as many sampling intervals as events. To compare survival times of the different groups we used Gehan's generalized Wilcoxon test (Gehan 1965). The proportions of birds survived among groups were compared through χ^2 test.

We used program MARK to model the monthly survival of radio-tagged young and to explore several biological hypotheses (White and Burnham 1999). We used the known-fate model included in MARK, which is appropriate for data derived from radio-tracking studies, in which resighting probability is assumed to be $=1$. Survival estimates calculated by MARK using the known-fate model are analogous to those obtained using the Kaplan-Meier product-limit estimator. For the first year we used August as a starting date to estimate monthly survival and June of the next year as the last month, when young are one year old. For the second year we considered the July–June period. We tested a number of factors potentially affecting survival of young great bustards, including month, which in our design is a surrogate of age of the young, sex, population, number of siblings and year. Initially we also included three covariates (body mass, hatching date and body condition) but since they were correlated (body mass vs hatching date: $r = -0.68$, $n = 328$, $P < 0.01$; body mass vs body condition $r = 0.35$, $n = 318$, $P < 0.01$; hatching date vs body condition $r = -0.46$, $n = 318$, $P < 0.01$), and body mass was the variable we measured, whereas hatching date and body condition were inferred from it, we finally included only body mass as a covariate and assumed it was a proxy of both, hatching date and body condition. We used the Corrected Akaike's Information Criterion (AICc) of MARK to select the most parsimonious model from a set of candidate models (Cooch and White 2001). One model was selected above another when the difference between their AICc was >2 (Anderson and Burnham 1999). We corrected for overdispersion in the model set when the overdispersion parameter c of the global model was >1. In that case quasi-likelihood methods were used to derive QAICc (Anderson et al. 1994). The logit link function was used throughout the modelling procedure.

Results

Tagging effects

No significant differences in the survival of radio-tagged and untagged young between early and late summer were detected in any of the years (radio-tagged: 58% $n = 251$; untagged: 62% $n = 1043$; $\chi^2 = 1.85$, $df = 1$, $P = 0.174$). Furthermore, the body mass distribution of young that died during the week immediately after marking (large: 36.4%, medium: 24.2%, small: 39.4%) was not significantly different to that of birds who survived longer (large: 35.7%, medium: 32.9%, small: 31.4%; $\chi^2 = 1.304$, $df = 2$, $P = 0.521$),

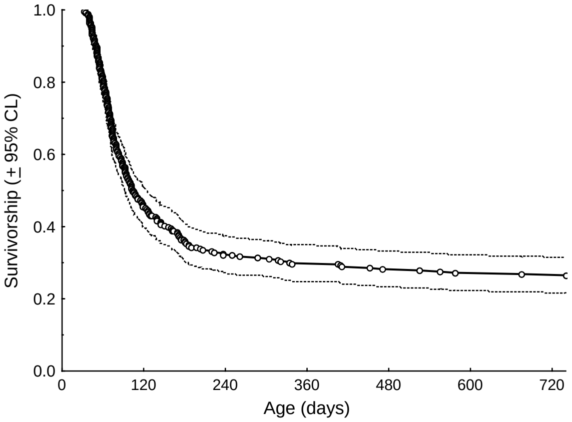

Fig. 1. Survivorship of 328 young great bustards between the date of marking and the end of their second year of life (estimates with 95% confidence limits, CL).

which suggests that the possible short-term effects of tagging were similar on the three body mass categories and did not affect more the smaller individuals.

To look for different effects of neck-lace and harness transmitter mounts on juvenile survival we compared first-year survival of females weighing $<1{,}500$ g marked with either method. We found no differences in survival between these two groups (neck-lace: 14.3%, harness: 15.1%; $\chi^2 = 0.095$, df = 1, $P = 0.922$; $P_{\text{Gehan's}} = 0.144$), suggesting that both transmitter fitting methods did not differ in their possible effects on survival.

Age-related mortality

Mortality was related to the age of the young, being very high during the first two months after marking and decreasing progressively throughout the rest of the first year (Fig. 1). Approximately half of all marked birds (54.6%) died before reaching the age of 120 days, 13.1% at an age of 120–240 d, and 2.4% between the age of 240 d and one year (Table 2). Only 29.9% of marked offspring survived after their first year (95% confidence limits: 24.9–34.8%). Mortality decreased to 9.8% in the second year, and later stabilized around this value (average for the 2nd–5th year = 9.1%; SE = 1.6).

Factors affecting survival

We found interannual differences in first year survival (0% in 2001, n = 11; 51.5% in 1993, n = 33). However, monthly differences were much more important than interannual differences (Table 3) and therefore we pooled all years together to test other factors potentially affecting survival. Of the 17 candidate models selected to examine the influence of all variables, the model including month, sex and body mass was the most parsimonious (model 1, Table 4). This model was 2.3 times better supported by the data than the second most parsimonious model (model 2). However the difference between their QAICc was <2 and therefore model 2 is also reasonably well supported by the data.

Model 1 showed that survival exhibited by juvenile great bustards was month-dependent, differed by sex and was influenced by body mass. Monthly survival estimates obtained by model 1 are illustrated in Fig. 2. The graph shows higher survival estimates for females from August to January and no differences between sexes from February to June. Both sexes show a progressive increase in the monthly survival estimate throughout the first year of life. Additionally, survival estimates increased in males and females with increasing body mass (Fig. 3).

Model 2 also showed that juvenile survival differed between populations, being lower in Villafáfila. Exploring these differences by season, we found that during summer the survival was lower in the Villafáfila population (Villafáfila 38%, n = 93; Madrid 54%, n = 235; $\chi^2 = 7.18$, df = 1, $P = 0.007$), while during winter survival was lower in Madrid (Villafáfila 91%, n = 35; Madrid 52%, n = 127; $\chi^2 = 17.88$, df = 1, $P < 0.001$).

None of the factors analyzed affected survival during the second year of life of the birds. Model 18, the reduced or no effects model, was selected as the most parsimonious one (Table 5). Models including the effect of body mass, population and sex (models 19, 20 and 21 respectively) were also well supported by the data, although they cannot be considered different from the reduced model (ΔQAICc <2).

Table 2. Life table of young great bustards. P_x = probability of survival up to the following age class.

Age range (d)	Dead	Alive	% Alive	P_x	% total deaths
Capture-120	179	149	45.4	0.638	77.8
120–240	43	106	71.1	0.768	18.7
240–365	8	98	92.5	0.925	3.5

Table 3. Models testing the effect of month, year and their interaction on first year survival. Models are ranked according to QAICc (see Methods); w_i is the model weight and K is the number of parameters.

Model	QAICc	ΔQAICc	w_i	K	QDeviance
S_{month}	141.22	0.00	1.00	12	117.05
S_{year}	160.39	19.17	0.00	12	136.22
$S_{\text{month} \times \text{year}}$	406.45	265.23	0.00	142	98.98

Mortality causes

Eleven out of 241 deaths (4.6%) recorded during the first two years of life of the radio-tagged birds could not be assigned to any of the three categories defined and therefore were excluded from the analysis of mortality causes. Non-natural mortality causes increased between the first summer and the second year (Table 6), and tended to affect male offspring more than female offspring (Fig. 4a), although sex differences did not reach significance (Fisher exact test, one tailed: first summer 32% vs 27%, $P = 0.312$; first winter 55% vs 49%, $P = 0.392$; second year 100% vs 67%, $P = 0.273$; whole period 40% vs 36%, $P = 0.311$).

These non-natural causes were also more important in the Madrid population in all three periods considered (Fig. 4b, Fisher exact test, one tailed: first summer 37% vs 13%, $P = 0.002$; first winter 52% vs 33%, $P = 0.476$; second year 88% vs 67%, $P = 0.491$; whole period 45% vs 17%, $P < 0.001$). Because data were collected from each of the two populations over a different, non-overlapping range of years (Villafáfila: 1991–93, Madrid: 1995–2003), the effects of year and population are confounded. To assess whether it was likely to be a year effect, rather than a population effect, we tested the differences between both populations splitting the sample by years. The annual proportions of first-year human-induced mortality were consistently higher in Madrid (mean = 48.0, range 20.8–75.0%) than in Villafáfila (mean = 10.5, range 0 and 19.0%; Student's t-test: $t = -3.46$, $df = 10$, $P = 0.006$).

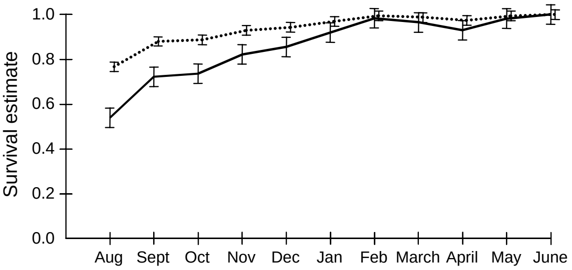

Fig. 2. Young great bustard monthly survival probabilities for first year. Survival estimates were generated from model 1, Table 4. Solid line = males; dotted line = females; vertical bars represent SE.

Discussion

Tagging effects

We did not find evidence of adverse effects of the marking method on the survival of our radio-marked birds. Thus, we assumed that our marking method did not negatively affect the birds, as has been also shown or assumed for similar radio-tagging methods with other species (Rohner and Hunter 1996, Combreau et al. 2001, Grant 2002). Handling and tagging short-term effects did not differ by young body mass, which suggests that marking did not affect lighter individuals

Table 4. Summary of model selection results for first year monthly survival of juvenile great bustards. The factors considered were month, sex, population, number of siblings and body mass. Models are ranked according to QAICc (see Methods); w_i is the model weight and K is the number of parameters. Pop = population (Villafáfila, Madrid). Sib = number of siblings.

Model	QAICc	ΔQAICc	w_i	K	QDeviance
1. $S_{\text{month+sex+body mass}}$	316.60	0.00	0.56	12	292.40
2. $S_{\text{month+sex+pop+body mass}}$	318.25	1.65	0.25	14	289.98
3. $S_{\text{month+sex+sib+body mass}}$	320.47	3.86	0.08	14	292.19
4. $S_{\text{month+body mass}}$	321.70	5.09	0.04	11	299.52
5. $S_{\text{month+pop+body mass}}$	323.59	6.99	0.02	12	299.38
6. $S_{\text{month+sib+body mass}}$	323.64	7.04	0.02	12	299.44
7. $S_{\text{month+sex+pop+sib+body mass}}$	325.04	8.44	0.01	18	288.59
8. $S_{\text{month+sex}}$	325.78	9.17	0.01	11	303.60
9. $S_{\text{month+sib}}$	326.09	9.49	0.00	11	303.92
10. $S_{\text{month+pop}}$	326.11	9.51	0.00	11	303.93
11. S_{month}	326.12	9.52	0.00	11	303.95
12. $S_{\text{month+pop+sib+body mass}}$	326.56	9.96	0.00	14	298.29
13. $S_{\text{body mass}}$	364.04	47.44	0.00	2	360.04
14. $S_{(.)}$	369.72	53.12	0.00	1	367.72
15. S_{sex}	371.10	54.50	0.00	2	367.10
16. S_{sib}	371.68	55.08	0.00	2	367.67
17. S_{pop}	371.72	55.12	0.00	2	367.72

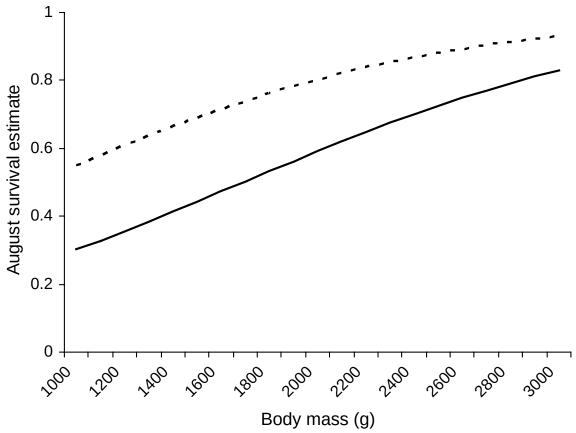

Fig. 3. Predicted increase in August survival probabilities of young great bustards with increasing body mass, which is a proxy of hatching date and body condition. Survival estimates were generated from model 1, Table 4. Same pattern was observed in all months. Solid line = males; dotted line = females.

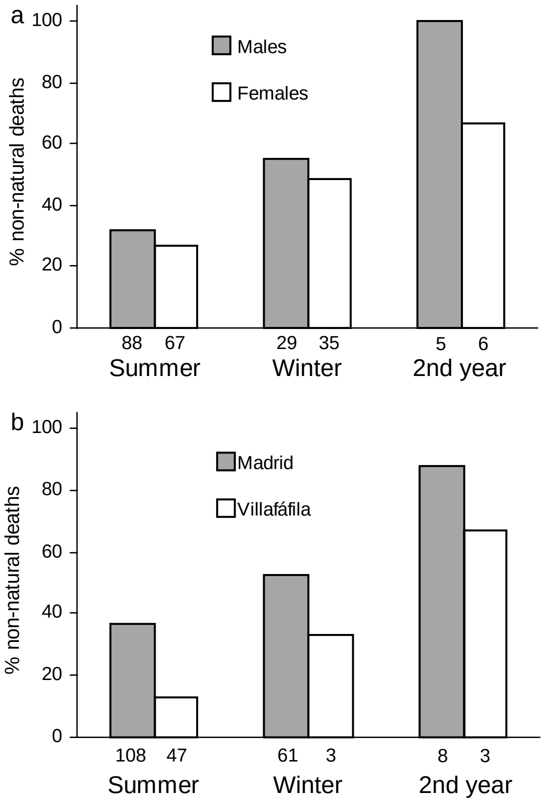

Fig. 4. Proportion of non-natural deaths during first summer, first winter and second year of life of marked great bustards (sample sizes are given below bars). a) Comparison between sexes. b) Comparison between populations.

disproportionately. We neither found differences in juvenile survival between both transmitter fitting methods used, back-pack or 'poncho'-mount, which allowed us to analyze birds marked with both fitting methods together.

Seasonal pattern of survival

The results of this study showed a clear inverse relationship between offspring age and mortality, following the usual pattern found in other bird species (Lack 1954). The very high mortality affecting young great bustards during their first months of life decreased steeply throughout the first year. The first-year survival (0.30) was particularly low between marking and the end of the summer, and may be in part explained by the high nutritional requirements of young birds, as a consequence of their fast growth rates at that age. In addition, the disappearance of the shelter caused by harvesting of cereal fields in July might determine an increase in the vulnerability to predators, as has been suggested for other bird species inhabiting similar agricultural environments (Whitmore 1979, Rodenhouse and Best 1983).

Little is known about survival rates of young great bustards during their first weeks of life, that is, between hatching and the age when we radio-marked them (3 to 10 weeks old). Ena et al. (1987), in a one-year study at Villafáfila based on survey data without marked birds, estimated a survival rate of 43% form hatching to August, when chicks are approximately two months old. Preliminary results based on the tracking of 50 radio-tagged adult females during the breeding seasons 1998–2003 in Madrid indicate a survival rate of 27% from hatching in May–June to the age of marking in late July (Magaña et al. 2007). Combining these data with the results obtained in this study, first year survival would be ca. 10%.

Our results showed that body mass at marking was an important predictor of juvenile mortality in great bustards. Since body mass was correlated with hatching date and body condition, we conclude that offspring hatched later in the season and those that had not acquired a good body condition during the first weeks of life had lower survival rates. The strong inverse relationship found between hatching date and body condition suggest they were influenced by the same causal factors, which may be related to the high selective value of breeding as early as possible. First, studies with marked females revealed that older females lay eggs earlier than younger ones (Magaña et al. 2007), and are more successful breeders (Morales et al. 2002). A decline in offspring survival rate as the season progresses has also been observed in other bird species (Guyn and Clark 1999, Arroyo 2002, Blums et al. 2002, Reed

Table 5. Summary of model selection results for second year monthly survival of immature great bustards. The factors considered were month, sex, population and body mass. Models are ranked according to QAICc (see Methods); w_i is the model weight and K is the number of parameters. Pop = population (Villafáfila, Madrid).

Model	QAICc	ΔQAICc	w_i	K	QDeviance
18. $S_{(.)}$	99.00	0.00	0.38	1	97.00
19. $S_{body\ mass}$	99.66	0.66	0.27	2	95.65
20. S_{pop}	100.88	1.88	0.15	2	96.87
21. S_{sex}	100.97	1.97	0.14	2	96.96
22. $S_{month+body\ mass}$	105.26	6.26	0.02	9	87.09
23. $S_{month+pop}$	106.40	7.40	0.01	9	88.24
24. $S_{month+sex}$	106.50	7.50	0.01	9	88.33
25. $S_{month+sex+body\ mass}$	106.53	7.53	0.01	10	86.33
26. $S_{month+pop+body\ mass}$	107.12	8.12	0.01	10	86.92
27. $S_{month+sex+pop+body\ mass}$	110.44	11.45	0.00	12	86.16
28. S_{month}	112.65	13.65	0.00	12	88.36

et al. 2003). To explain this finding most authors have argued that older and more experienced females probably reach earlier the physiological conditions necessary to start breeding (Korpimäki 1990, Arnold et al. 2004). Second, offspring hatching late in the season may usually face poorer environmental conditions (Lepage et al. 1999). In our study area the abundance of arthropods, the main food of young bustards during summer, decreases through this season (Lane et al. 1999). The poorer development and lower reserves of late-hatched offspring may represent important handicaps, making them less competitive when families integrate in flocks in early autumn, and more susceptible to possible food shortages during winter. In addition to starvation risk, the poorer health status and the associated decrease in resistance against parasites and infectious diseases has been cited as a cause of a decline in survival as the season progresses (Dubiec and Cichon 2001). On the other hand, late-hatched offspring obviously have a lower flying ability to escape from predators, especially when the shelter provided by cereal fields disappears after harvesting in July (see Götmark 2002).

Table 6. Relative importance (%) of mortality causes during first summer, first winter and second year of life of marked great bustards.

Mortality causes	Summer	Winter	Second year
Natural deaths:			
Predation	44.5	15.6	9.1
Natural death without predation	25.8	32.8	9.1
Non-natural deaths:			
Related to hunting	24.5	34.4	9.1
Birds disappeared	0.0	12.5	18.2
Collision with powerlines	3.2	4.7	54.5
Harvester	1.9	0.0	0.0
n	155	64	11

The fact that the number of siblings was not included in the most parsimonious survival models supports the idea that the experience of the mother is a very important factor determining juvenile survival. Sibling offspring are indeed mostly reared by older females (Morales et al. 2002), and they did not show different survival rates than single chicks.

Sex and mortality

First-year survival was lower in males than in females when controlling for body mass. Sex-biased juvenile mortality has been reported for several bird and mammal species, and associated with the faster growth rates and increased nutritional requirements of the larger sex (Clutton-Brock et al. 1985, Slagsvold et al. 1986, Clutton-Brock 1991, Weatherhead and Teather 1991, Anderson et al. 1993, Bennett et al. 1995, Torres and Drummond 1997). Quaisser et al. (1998) showed that ten-days-old male great bustard chick requirements are 16% higher than those of females (540 vs 465 kJ/day), and that this difference increases with age. In the highly dimorphic capercaillie Tetrao urogallus chicks, heavier male offspring may have an inferior ability to escape from predators due to their disproportionately small breast muscles, which may contribute to the sex biased survival observed (Milonoff and Linden 1989). Finally, human-induced mortality causes may be involved in the lower survival of juvenile great bustard males, as discussed in the next section.

The higher mortality of male offspring may also be related to the experience of the mothers. Young bustards are dependent on their mothers during their first 5–17 months of age (Alonso et al. 1998, Martín 2001). They obtain most of their food by pecking at food items themselves, but receive complementary feedings from their mother, at a rate decreasing throughout the dependence period. Probably more experienced mothers are able to satisfy both male and female offspring requirements while less experience ones are sometimes incapable to cope with young males' demands. In an earlier study we suggested that male offspring hatched early probably have a strong selective advantage over those hatched late. We showed that young males feeding at higher rates, i.e. obtaining quickly a good body condition, became independent from their mothers earlier and also settled as breeding adults earlier. These relationships were not found in young females (Alonso et al. 1998). Thus, natural selection has probably favoured a rapid body growth in males but not in females, and penalized male offspring hatched late in the season. This has led to an early development of the marked sex dimorphism in size found in this species, probably the most extreme among birds. The weight of adult males is 2.4 times that of the females, and the mean weight of chicks captured during this study showed already marked sex differences (males = 2,131 g, females = 1,433 g).

Sex-biased offspring mortality has important implications for the population sex ratio. The sex biases observed in the adult populations studied were 1.7 females per male in Villafáfila (Alonso et al. 1996) and 2.4 females per male in Madrid (Alonso et al. 2003a). Although sex ratio at hatching seems to be 1:1 (H. Litzbarski, pers. comm., based on a sample of 531 eggs collected for artificial breeding at Buckow Station, Germany, 1979–1998), it was already biased when we captured the young in July (1.24 females per male, average for 1995–2003). This suggests that differential mortality starts very early after hatching, and continues probably until adulthood, when males are still more susceptible than females to various mortality causes (Martín et al. unpubl. data). An alternative explanation would be that more males are produced early in the breeding season and more females later, as has been shown for a few bird species (Andersson et al. 2003, Genovart et al. 2003). Our sample of captured young indeed shows more males than females among young hatched early, and more females than males among those hatched late, but we cannot be sure if this is due to females rearing more males early and more females late in the season, or to male-biased mortality having operated before we caught the birds.

Influence of human-induced mortality

Finally, we found significant survival differences between both populations studied. Summer survival rates were lower in Villafáfila (38% vs 54%), where mortality due to predation was also significantly higher (Villafáfila 70%, n = 47; Madrid 33%, n = 108; Fisher exact test, two-tailed, $P < 0.001$). This suggests that offspring are subject to a higher predation pressure in this area, although there are no predator density estimates to support this. In contrast, during the first winter juvenile great bustards suffered much higher mortality rates in Madrid (48%) than in Villafáfila (9%). The higher incidence of non-natural mortality in Madrid as compared to Villafáfila (52% vs 33%) suggests that human-induced causes, mainly deaths related to hunting activities, may be the main factors responsible of the difference in winter mortality observed between both populations. In Madrid hunting is a common winter activity, allowed between early October and late January, whereas in Villafáfila hunting is restricted to some areas and only a limited number of days through the winter.

The proportion of deaths brought about by non-natural causes increased with the age of the birds. During the first summer 70% of the birds died by starvation, predation and other natural causes. During the first winter, half the deaths were caused by human-induced causes, and during the second year 82% of the birds died due to non-natural causes, with a particularly high incidence of collision with powerlines, which caused a 55% of the deaths. Collision with powerlines has been identified as the main mortality cause also in adult great bustards (Martín et al. unpubl. data).

Males were apparently more susceptible than females to non-natural mortality causes, although differences did not reach significance. This could contribute to the higher female-biased sex ratio found in the adult population in Madrid (2.4 females per male) as compared to Villafáfila (1.7 females per male). Other great bustard populations subject to human-induced negative pressures show even more female-biased sex ratios (Alonso et al. 2005a,b).

Acknowledgements – We thank all farmers of Villafáfila Reserve and bustard areas in Madrid and surrounding provinces for allowing us to work on their properties. E. Martín and M. B. Morales collaborated during fieldwork. Additional help was provided by L. M. Bautista, H. Bustami, C. Caldero, A. Correas, S. J. Lane, I. Martín, C. Martínez, R. Muñoz, M. A. Naveso, P. E. Osborne, E. Izquierdo, E. Fernández, I. de la Hera and R. Manzanedo. We thank the 42 Group of the Spanish Air Forces for their generous collaboration in locating radio-tagged birds. The field work was financed by the Dirección General de Investigación (projects PB91-0081, PB94-0068, PB97-1252 and BOS2002-01543), and the Instituto Nacional para la Conservación de la Naturaleza, with contributions from the Dirección General de Medio Natural of Madrid Community, and the Junta de Castilla y León. We thank two anonymous referees for improving the quality of an earlier version of the manuscript with their valuable comments.

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