

SEASONAL POPULATION DYNAMICS, NEST SITE SELECTION, SEX-RATIO AND CLUTCH SIZE OF THE GREAT BUSTARD *OTIS TARDA* IN TWO ADJACENT LEKKING AREAS

Rui MORGADO* & Francisco MOREIRA**

SUMMARY.—*Seasonal population dynamics, nest site selection, sex-ratio and clutch size of the Great Bustard Otis tarda in two adjacent lekking areas.* This paper describes the seasonal variation in Great Bustard *Otis tarda* numbers in two adjacent lekking areas within Castro Verde, the most important site for this species in Portugal. Furthermore, the first data on the breeding biology of the species in the region are presented. The pattern of flock size variation was similar to the one observed in other areas of the Iberian Peninsula, with larger flocks occurring during winter. The use of the two lekking areas was distinct, with one area having more birds during the breeding season (more important as display ground) and another during winter (more important as feeding ground). Cereal fields were the most important nesting habitat for Great Bustards, followed by first year fallow fields. Mean clutch size was 2.6 eggs/nest.

Key words: Great Bustard, lekking areas, nesting habitat, Portugal.

RESUMEN.—*Dinámica estacional, selección del lugar de nidificación, razón de sexos y tamaño de puesta en la Avutarda Común Otis tarda en dos áreas de apareamiento adyacentes.* Este trabajo describe la variación estacional del tamaño de la población de Avutardas Comunes *Otis tarda* presente en dos áreas adyacentes de apareamiento (*leks*) situadas en Castro Verde, la zona más importante para esta especie en Portugal. Se presentan además los primeros datos sobre la biología reproductora de la especie en esta zona. Los patrones de variación estacional del tamaño de bando fueron similares a los observados en otras zonas de la Península Ibérica, con los bandos mayores observados en invierno. El uso de las dos zonas de apareamiento adyacentes fue diferente, de manera que una de las áreas presentó más aves durante la época de cría y fue más importante como terreno de exhibición de los machos, mientras que la otra fue más importante durante el invierno como terreno de alimentación. Los campos de cereal fueron los sustratos más importantes para la nidificación de las Avutardas Comunes, seguidos por las rastrojeras de primer año. El tamaño medio de puesta fue de 2,6 huevos/nido.

Palabras clave: Avutarda Común, áreas de apareamiento (*leks*), hábitat de nidificación, Portugal.

INTRODUCTION

The Great Bustard *Otis tarda* is a globally threatened species with fragmented and largely declining populations in Europe (Tucker & Heath, 1994). Most of the world population of Great Bustards is concentrated in the Iberian Peninsula, with Portugal having the third largest population within Europe (500-700 birds; Tucker & Heath, 1994). The majority of this population is largely concentrated in the region of Castro Verde (Southern Portugal), a plain of ca. 70.000 ha on which the extensive cultivation of cereals created a landscape mosaic dominated by cereal fields, ploughed fields and fallow land. This area currently holds probably

more than 90% of the Portuguese population of Great Bustards (Rocha & Moreira, 1999). In spite of the importance of the region, no published data exist on the biology and habitat requirements of the species there. In this paper, we present the first data on seasonal population dynamics and several aspects (namely nest site selection, sex-ratios and clutch size) of the breeding biology of Great Bustards at two main lekking areas within the region and discuss some implications of these findings for the conservation of this population.

Other studies in the Iberian Peninsula have focused on seasonal movements in Great Bustards, based on counts (e.g. Hidalgo de Trucios & Carranza, 1990; Hellmich, 1991) or

* Liga para a Protecção da Natureza, Estrada do Calhariz de Benfica, 187, P-1500 Lisboa, Portugal. Current address: Centro de Ecologia Aplicada "Prof. Baeta Neves", Instituto Superior de Agronomia, Tapada da Ajuda, P-1349-017 Lisboa, Portugal.

** Centro de Ecologia Aplicada "Prof. Baeta Neve", Instituto Superior de Agronomia, Tapada da Ajuda, P-1349-017 Lisboa, Portugal.

using marked individuals (e.g. Alonso *et al.*, 1995; 1996; 2000; Morales *et al.*, 2000). These have shown a general pattern of seasonally changing numbers between a maximum during winter or early spring and a minimum during summer. Studies on the breeding biology of Great Bustards are scarce (see e.g. Cramp & Simmons, 1980; Ena *et al.*, 1987) and have not specifically addressed nesting habitat.

METHODS

Study areas

This study was carried out within the cereal steppe of Castro Verde (ca. 37°43' N, 7°57' W; Figure 1). The traditional agricultural system of this area has been described by Delgado & Moreira (1999) and creates a landscape mosaic of cereal fields, ploughed fields and fallow land (frequently used as pasture for sheep). Two study areas (Entradas, 3086 ha and São Marcos, 4616 ha), known to include important lekking areas for Great Bustards in the region, were defined. They were located at ca. 6 km of each other, the majority of the land use between them consisting of unsuitable habitat for the species (shrublands, woodlands and a river valley). The agricultural use of each area is slightly different, with Entradas having more productive soils and a larger area with cereal cultivation and São Marcos having poorer soils and a larger percentage of fallow land. During the study period, the approximate percentage of total area sown with cereals was 50% and 20% for Entradas and São Marcos, respectively.

Population and flock size-type dynamics

Data were collected from November 1996 to October 1997. Population censuses were done according to Hidalgo de Trucios & Carranza (1990). The study areas were covered by car along a fixed route (38 km in Entradas and 57 km in São Marcos), at a speed of 10–30 km/h, assuring that the entire area was searched. Along the route, stops were made at strategic observation points from which the adjacent area was scanned. Counts started just before sunrise. During spring and summer they were interrupted during the middle of the day,

when the greater heat causes a significant decrease in bustard activity and detectability (Hellmich, 1991; Alonso *et al.*, 1996). Both areas were censused on two consecutive days. Counts were usually made twice a month with the exception of September to November, when (due to logistic reasons) only one count was made. Additionally, from March to May the number of censuses increased to 3–4 per month, in order to obtain more detailed data during the breeding period. When a flock was found, flock size and its age and sex composition (only during the breeding season) were recorded. Following Martínez (1988), a flock was defined as any aggregation of individuals, including solitary birds, which occupies an area with a diameter smaller than the distance to the closest flock. The similar behavioural response of individuals was also taken into account. During the breeding season four types of flocks were identified: adult male, female, mixed flocks (composed exclusively of adult males plus females) and families (females with chicks). Other mixed flock types including immature males were not included in the analyses. Outside the breeding season we were not confident in our age and sex assessments for a significant proportion of the observed birds, so we did not consider these different flock types for data analysis.

Nest site selection and breeding biology

During the breeding season, a particular effort was devoted to nest finding. This included inquiries to farmers, shepherds and intensive searches in areas where females occurred regularly. The main goal of this procedure was to identify nesting habitat rather than exact nest locations. Nesting habitat availability was determined by identifying land use in both study areas in April 1997 (the beginning of the breeding season) with the help of aerial photographs and field checks. Four habitat types were considered: (i) cereal fields, (ii) recent fallow fields (which had cereal in the previous spring), (iii) old fallow fields (left fallow for more than one year) and (iv) ploughed land. Other land use types, such as leguminous crops and olive groves, were not included in the analysis as they were very scarce (less than 2.5% of the area) and no Great Bustard nest

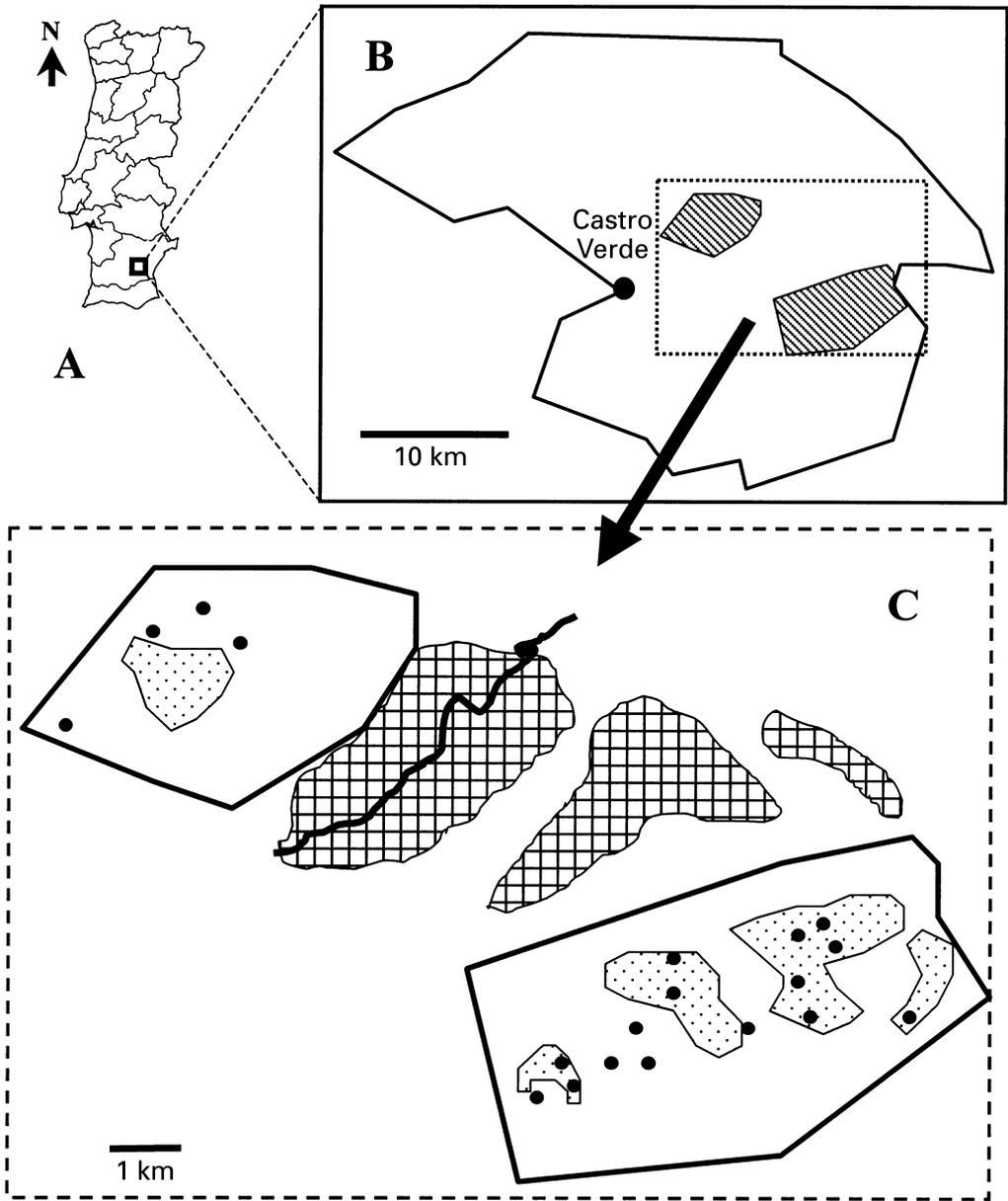


FIG. 1.—A) Location of Castro Verde region, the main area of Great Bustard occurrence in Portugal; B) location of the two study areas (stippled polygons) within each study area, the approximate location of nests found (black dots) and of unsuitable habitats (shrublands, forests, river valley; crossed patches) between study areas. Northwestern area: Entradas; Southeastern area: São Marcos.

[A] Situación geográfica de la región de Castro Verde, la principal área de cría e invernada de Avutardas Comunes en Portugal; B) situación de las dos áreas de estudio (polígonos rayados); y C) mapa detallado de las áreas de estudio mostrando las zonas de apareamiento (leks; polígonos punteados) dentro de cada área y las ubicaciones aproximadas de los nidos localizados (puntos negros) y de los hábitats desfavorables (matorrales, bosques, valle fluvial; manchas cruzadas) entre las dos áreas. Área noroccidental: Entradas; área sudoriental: São Marcos.]

was ever found in those habitats. The area covered by each land use type was measured with a planimeter. Data analysis was based on the comparison of available and used habitat, using resource selection functions (Manly *et al.*, 1993). Selection ratios and associated chi-square statistics to test the null hypothesis that selection was random were estimated for each habitat type. The standardized selection ratio represents the estimated probability of finding a Great Bustard nest if all habitats were equally available (Manly *et al.*, 1993). The best approximation to the operational sex ratio (Emlen & Oring, 1977) was estimated as the ratio between the maximum numbers of females and adult males observed in each study area during the period of highest display occurrence (between March and early April).

RESULTS

Population and flock size dynamics

The results of Great Bustard counts for each area (Figure 2) showed that in São Marcos population size attained its maximum value at the end of March (252 birds). In Entradas, the highest numbers of individuals were observed during the winter, with a maximum of 92 birds in December. During the breeding season the observed fluctuations could be attributed mainly to the variation in the number of females, which showed a similar pattern across areas ($r_s = 0.84$; $P < 0.01$; $n = 13$) with a peak at the end of March and first week of April. Chicks first started to be observed in the first week of May and family groups from the middle of May until September (when family groups merge into larger flocks).

The pattern observed for the monthly variation in flock size was similar in both areas (Spearman $r_s = 0.72$; $P < 0.05$; $n = 12$), with larger flocks (median size between 5 and 20 birds) occurring between October and January (Figure 3). The largest flock observed had 73 birds. There were no significant differences in flock size between areas for each month (Mann-Whitney tests with Bonferroni correction for the number of tests, $P > 0.05$). During the breeding season, size variation for each flock type is shown in Figure 4. The size of male flocks was greatly reduced since the beginning of March,

increasing again at the end of April. In contrast, female flock size showed less variation, the lowest values being observed at the end of the breeding season. Mixed flocks were observed between February and May. The more frequent mixed flock composition was 1 male and 2-10 females (representing ca. 45% of the total number of flocks), but flocks with 2-10 males plus females were also frequent (30% of the flocks).

Nest site selection and breeding biology

Nineteen nest locations (15 in São Marcos, 4 in Entradas; Figure 1) were recorded during the study period, out of which 15 were located in cereal fields. The rank preference of nest site habitat selection was cereal fields, first year fallows, older fallows and ploughed land, with standardized selection ratios of, respectively, 0.642, 0.296, 0.062 and 0.000. Chi-square tests yielded significant results only for cereal fields, which were used more often than was expected from the availability of this habitat. Nevertheless, these results should be interpreted with caution because of the small sample size. Mean clutch size was 2.6 eggs/nest, with a modal value of 3 eggs/nest (range = 2 – 3, $n = 16$). The sex-ratio (maximum number of females / maximum number of males) was estimated as, respectively, 1.10:1 and 1.41:1 for Entradas and S. Marcos (both areas pooled: 1.26:1). The composition of family groups ($n = 97$) was one female plus 1-3 chicks, and it varied throughout the breeding season (Table 1).

DISCUSSION

A major assumption of this single year study is that it correctly characterised the annual pattern of seasonal population dynamics in both study areas. The agricultural differences between areas (more cereal in Entradas relative to São Marcos) have been observed every year in the last 5-6 years (personal observations). Even so, climatic variations change crop options taken every year by farmers, and these will be reflected mainly in the amount of cereal fields available. Studies made in a much wider geographical area in Castro Verde and including more years (Rocha & Moreira, unpublished data) suggest that the described patterns are re-

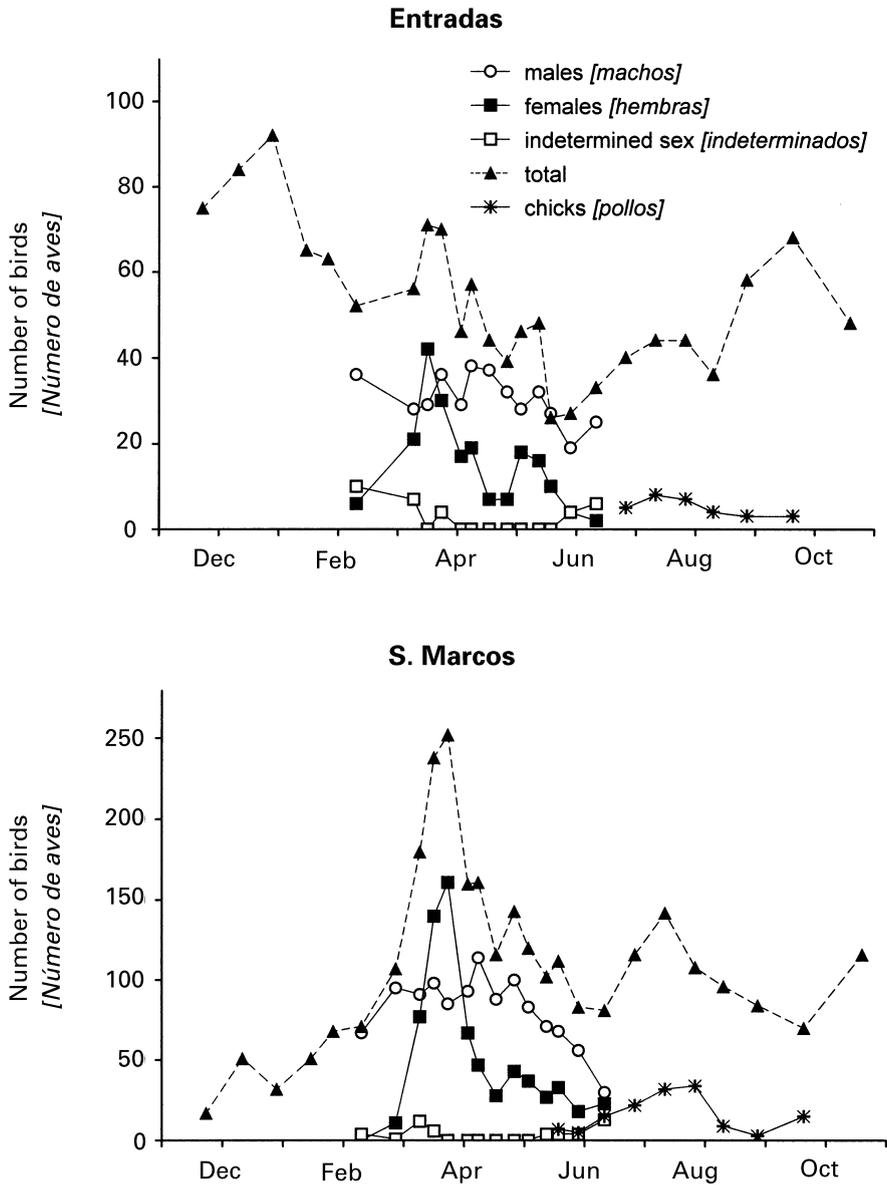


FIG. 2.—Variation of Great Bustard *Otis tarda* numbers in the two lekking areas (Entradas and São Marcos) in Castro Verde during 1996-1997. Sex determination was done only during the breeding season.
 [Variación en el número de Avutardas Comunes en dos zonas de apareamiento (Entradas y São Marcos) de la región de Castro Verde en el periodo 1996-1997. La determinación del sexo de las aves se realizó únicamente en la época de cría.]

gularly observed, but longer-term studies would be desirable to evaluate inter-annual variability in population dynamics, both within Castro

Verde and between Castro Verde and other regions of Great Bustard occurrence both in Portugal and in Spain.

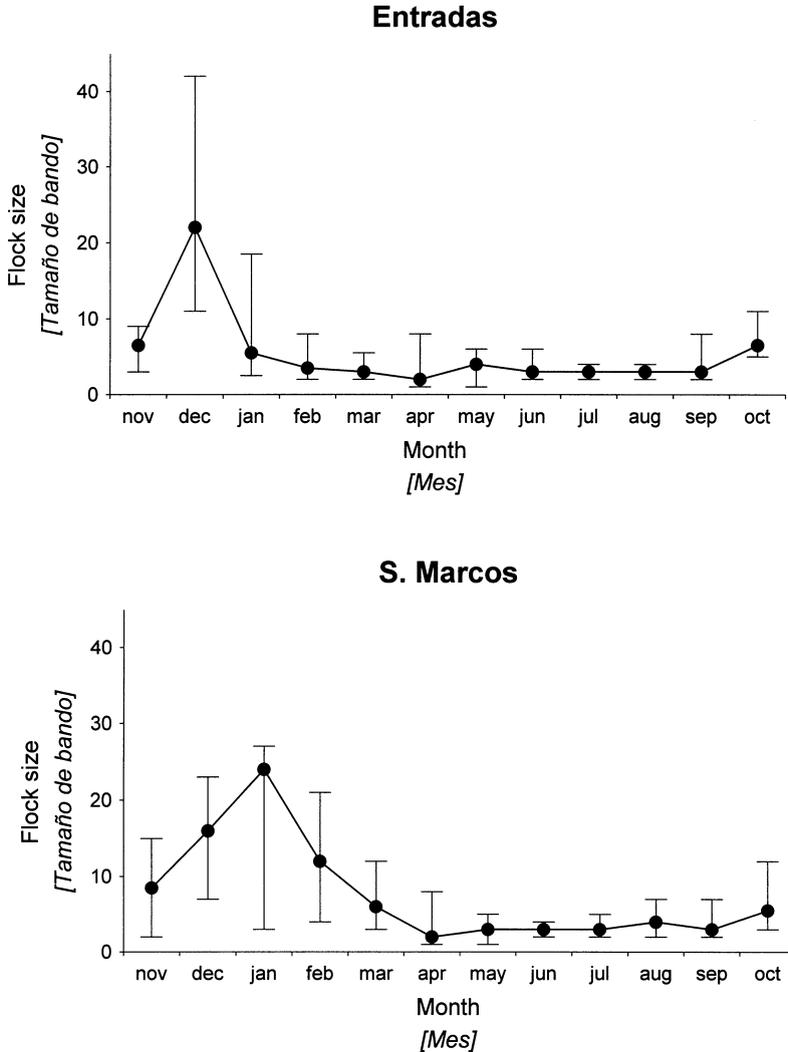


FIG. 3.—Median flock size and inter-quartile range of Great Bustard flocks in Entradas and São Marcos. [Mediana y rango entre cuartiles del tamaño de bando de Avutardas Comunes en Entradas y en São Marcos.]

Population dynamics differed between the two lekking areas. São Marcos was the main breeding area, with maximum population size occurring at the peak of breeding displays. Entradas had more birds during winter, which might be related to the higher availability of cereal fields, an important food source during this season (e.g. Hidalgo de Trucios & Carranza, 1990; Martínez, 1991b). As observed in other areas of the Iberian Peninsula, Bustards gathered in larger flocks during winter, probably to

exploit feeding opportunities and reduce predation risk (e.g. Martínez, 1988; Hidalgo de Trucios & Carranza, 1990). As the breeding season approached, birds started to disperse. Agonistic interactions between males including threats, chases and physical aggression were observed between December and March (*pers. obs.*). Male flock size was greatly reduced since March, when breeding displays began to be performed. Male flocks increased again in size at the beginning of May, coinciding with the end

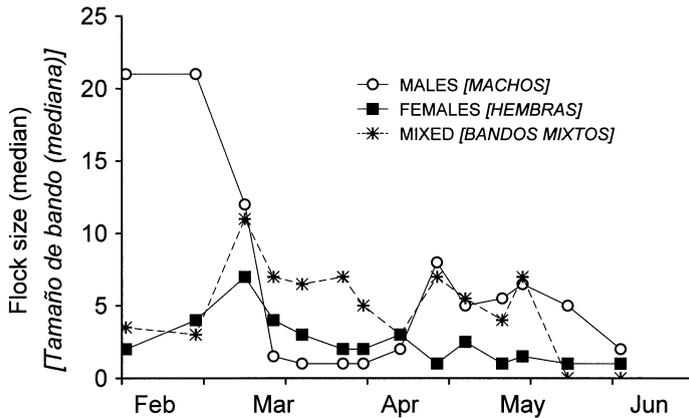


FIG. 4.—Variation in male, female and mixed flock sizes during the 1997 breeding season in Castro Verde. Data for São Marcos and Entradas were pooled because of small sample size.

[Variación en el tamaño de bando de machos, hembras y bandos mixtos durante la época de cría de 1997 en Castro Verde. Los datos para las dos áreas de estudio (Entradas y São Marcos) se han agrupado debido a los bajos tamaños de muestra obtenidos para algunas categorías.]

TABLE 1

Number of chicks in Great Bustard families in Castro Verde during the 1997 breeding season. Values are the % of females with 1, 2 and 3 chicks. *n*: sample size.

[Número de pollos por familia en la población de Avutardas Comunes de Castro Verde durante la época de cría de 1997. Los valores mostrados son los porcentajes de hembras con 1, 2 y 3 pollos. *n*: tamaño de muestra.]

Month [Mes]	<i>n</i>	1 chick [1 pollo]	2 chicks [2 pollos]	3 chicks [3 pollos]
May	7	14.3	71.4	14.3
June	21	19.0	66.6	14.3
July	47	40.4	46.8	12.8
August	11	36.4	54.5	9.1
September	11	45.5	45.5	9.0

of the main copulation period. In agreement with this, full-displays (see Hidalgo de Trucios & Carranza, 1991) were observed from March up to the middle of May (*pers. obs.*). Female numbers during the breeding season attained a maximum at the peak of the copulation period, after which females dispersed and became less visible during the incubation period. That is probably why lower flock sizes occurred at the end of the breeding period. Mixed flocks are probably temporary associations formed when females visit display grounds (e.g. Alonso *et al.*, 1996). The comparative analysis of the pattern of variation in population size across areas suggests that movements of birds between En-

tradas and S. Marcos, between winter and the breeding season, are possible, but studies of individually marked birds are necessary to confirm this possibility. Other studies in the Iberian Peninsula have confirmed the occurrence of movements between winter and breeding areas (e.g. Alonso *et al.*, 2000; Morales *et al.*, 2000).

The Great Bustard has a quite variable mating system (Cramp & Simmons, 1980; Morales *et al.*, 1996). The data collected in this study suggest that the more likely mating system in Castro Verde could be the exploded lek (Emlen & Oring, 1977), although the occurrence of resource-based polygyny should not be ruled out. Nevertheless, the mating system might vary

among populations and years (Carranza *et al.*, 1989), thus a longer term study is necessary to characterize the mating system in the region.

In spite of several studies on Great Bustard habitat selection (e.g. Hidalgo de Trucios & Carranza, 1990; Hellmich, 1991; Martínez, 1991a, b), few have focussed on the selection of nesting habitat. In Castro Verde, cereal fields were the preferred nesting habitat, probably providing adequate cover and tranquility. Most nests were located in the main lekking area (São Marcos), in spite of having fewer cereal fields than Entradas. The pattern observed for females also suggests that there is a preference for the selection of nesting sites near to the main lekking area (see Figure 1). This was observed in Villafáfila, where females normally attend the lek closest to their nesting areas (Alonso *et al.*, 2000). Thus, the lekking areas with the greatest number of birds should also have a high nest density in the vicinity, which was confirmed in the present study. This strongly suggests a exploded or resource based lek mating system, rather than a classical lek scenario (e.g. Ligon, 1999). The apparent preference for recent fallow land as nesting habitat, compared with older fallows, might be explained by the fact that a large percentage of recent fallows represented land set-aside, without agricultural use or sheep grazing until the following summer. Mean clutch size is similar to the ones reported in other studies (e.g. Cramp & Simmons, 1980; Ena *et al.*, 1987). The temporal increase, across the breeding season, in the proportion of families with only one chick is probably due to the high mortality rate of young Great Bustards during the first months of life (Ena *et al.*, 1987; Alonso *et al.*, 2000).

The present study highlighted the importance of extensive cultivation of cereals for the conservation of this Great Bustard population. This low profit farming practice is being abandoned throughout the Iberian Peninsula (Suárez *et al.*, 1997), and in Castro Verde the application of an agri-environmental programme has been essential for the maintenance of cereal fields. Furthermore, results suggest that set-aside land might be an important nesting habitat alternative to cereal fields. Unfortunately, in the last years the amount of land to be obligatorily set-aside decreased from 15% to 0%. Alternatively, the promotion of decreased sheep densities (at least in part of the farms) through

agri-environmental regulation (EC reg. 2078/92), to avoid overgrazing, could improve nesting habitat in fallow land and pastures. More studies on habitat use of this species in Castro Verde are necessary to correctly evaluate the impacts of changing agricultural practices on its population.

ACKNOWLEDGEMENTS. — This study was financed by the European Commission (LIFE project BA-3200/95/510), the Liga para a Protecção da Natureza (LPN) and Fundação Luso-Americana para o Desenvolvimento (FLAD). Thanks are due to Juan Alonso and Rui Borralho for their comments on an early version of the manuscript. Particular thanks are due to Manuel Morales for providing detailed comments on the last versions of the manuscript. F. Moreira was partly funded by the post-doctoral grant Praxis XXI/BPD/22102/99.

BIBLIOGRAPHY

- ALONSO, J. C., ALONSO, J. A., MORALES, M. & MARTÍN, E. 1995. Range and patterns of great bustard movements at Villafáfila, NW Spain. *Ardeola*, 42: 69-76.
- ALONSO, J. C., ALONSO, J. A., MORALES, M. & MARTÍN, E. 1996. Seasonal and interannual population dynamics of the great bustard (*Otis tarda*) at Villafáfila Reserve, NW Spain. In, J. P. Fernández, & J. Sanz-Zuasti (Eds): *Conservación de las aves esteparias y sus hábitats*, pp. 191-200. Junta de Castilla y León. Valladolid.
- ALONSO, J. C., MORALES, M. B. & ALONSO, J. A. 2000. Partial migration, and lek and nesting area fidelity in female great bustards. *Condor*, 102: 127-136.
- CARRANZA, J., HIDALGO, S. J. & ENA, V. 1989. Mating system flexibility in the great bustard: a comparative study. *Bird Study*, 36: 192-198.
- CRAMP, S. & SIMMONS, K. E. L. (Eds.) 1980. *The birds of Western Palearctic, Vol. 2*. Oxford University Press. Oxford.
- DELGADO, A. & MOREIRA, F. 1999. Bird assemblages of an Iberian cereal steppe. *Agriculture, Ecosystems and Environment*, 78: 65-76.
- EMLEN, S. T. & ORING, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science*, 197: 215-223.
- ENA, V., MARTÍNEZ, A. & THOMAS, D. H. 1987. Breeding success of the Great Bustard *Otis tarda* in Zamora province, Spain, in 1984. *Ibis*, 129: 363-370.
- HELLMICH, J. 1991. *La avutarda en Extremadura*. Monografías Alytes 2. ADENEX. Mérida.
- HIDALGO DE TRUCIOS, S. J. & CARRANZA, J. 1990. *Ecología y comportamiento de la avutarda (Otis*

- tarda* L.). Servicio de Publicaciones, Universidad de Extremadura. Cáceres.
- HIDALGO DE TRUCIOS, S. J. & CARRANZA, J. 1991. Timing, structure and functions of the courtship display in male great bustard. *Ornis Scandinavica*, 22: 360-366.
- LIGON, J. D. 1999. *The evolution of avian breeding systems*. Oxford University Press. Oxford.
- MANLY, B., MCDONALD, L. & THOMAS, D. 1993. *Resource selection by animals. Statistical design and analysis for field studies*. Chapman & Hall. London.
- MARTÍNEZ, C. 1988. Size and sex composition of great bustard (*Otis tarda*) flocks in Villafáfila, Northwest Spain. *Ardeola*, 35: 125-133.
- MARTÍNEZ, C. 1991a. Relaciones espaciales en una población de avutarda (*Otis tarda*) del noroeste de España. *Ardeola*, 38: 265-276.
- MARTÍNEZ, C. 1991b. Selección de microhábitat en una población de avutarda (*Otis tarda*) de un medio agrícola. *Doñana, Acta Vertebrata*, 18: 173-185.
- MORALES, M. B., ALONSO, J. C., MARTÍN, E. & ALONSO, J. A. 1996. Mating system in the great bustard: a review of published work in light of recent radiotracking results. In, J. Fernández, & J. Sanz-Zuasti, J. (Eds.): *Conservación de las aves esteparias y su hábitat*, pp. 287-291. Junta de Castilla y León. Valladolid.
- MORALES, M. B., ALONSO, J. C., ALONSO, J. A. & MARTÍN, E. 2000. Migration patterns in male great bustards (*Otis tarda*). *Auk*, 117: 493-498.
- ROCHA, P. & MOREIRA, F. 1999. Censo da abetarda no Campo Branco no período Fevereiro 97 - Março 99. In, P. Beja, P. Catry & F. Moreira (Eds.): *Actas do II Congresso de Ornitologia da Sociedade Portuguesa para o Estudo das Aves*, pp. 93-95. SPEA. Lisboa.
- SUÁREZ, F., NAVESO, M. A. & DE JUANA, E. 1997. Farming in the drylands of Spain: birds of the pseudosteppes. In, D. Pain & M. W. Pienkowski (Eds.): *Farming and birds in Europe. The Common Agricultural Policy and its implications for bird conservation*, pp. 297-330. Academic Press. San Diego.
- TUCKER, M. G. & HEATH, M. F. 1994. *Birds in Europe: their conservation status*. BirdLife Conservation Series n.º 3, Cambridge. UK.

[Recibido: 4-5-00]
[Aceptado: 28-9-00]

