

SEASONAL AND INTERANNUAL POPULATION DYNAMICS OF THE GREAT BUSTARD (*Otis tarda*) AT VILLAFÁFILA RESERVE, NW SPAIN

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SUMMARY.-Seasonal and interannual population dynamics of the Great Bustard at Villafafila Reserve, NW Spain. The seasonal and interannual trends of the Great Bustard (*Otis tarda*) population at Villafáfila Reserve between 1987 and 1995 were analysed, based on 42 censuses and radiotracking results. The numbers of birds changed between a minimum of 1000-1300 during summer (May-September) and a maximum of 1700-2000 birds during winter (October-April), with an absolute maximum of 2013 birds in January 1995. These numbers show that the Reserve holds the world's densest population of the species. Peak numbers of males occur in March, when they gather at display sites, after which over half of them abandon the Reserve before summer. About 20-30% of males return to it in autumn, while the remaining will only come back next spring to try mating again. The number of females breeding in the Reserve is 600-700, increasing during October-April to 1000-1100 birds. In contrast to the main mating target of males arriving in spring, all females arrive in autumn, being probably more attracted by food abundance, and their winter distribution may in part determine the lek distribution. Given these seasonal movements of up to 25 linear km, any conservation effort within the Reserve may be fruitless if areas surrounding it are not adequately managed. The population has remained stable throughout the eight years covered by our study, with a slight but not significant trend to increase.

Key words: Great Bustard, population trends, Villafáfila.

RESUMEN.-Dinámica estacional e interanual de la población de avutardas de la reserva de Villafáfila. Se analizan las tendencias estacionales e interanuales de la población de Avutardas (*Otis tarda*) de la Reserva de Villafáfila entre 1987 y 1995, con base en 42 censos y en resultados de radioseguimiento. Las cantidades oscilaron entre mínimos de 1000-1300 aves durante mayo-septiembre y máximos de 1700-2000 durante octubre-abril, con un máximo absoluto de 2013 censado en enero de 1995. Con ello, la Reserva es la zona de mayor densidad de Avutardas del mundo. Los machos alcanzan máximos en marzo, cuando se reúnen en lugares de exhibición, abandonando la zona a continuación, antes del verano, más de la mitad de la población. Un 20-30% regresan en otoño, pero el resto no lo hacen hasta la siguiente primavera, para intentar de nuevo reproducirse. Las hembras que crían en la Reserva son 600-700, aumentando a 1000-1100 durante octubre-abril. En contraste con los machos que sólo acuden en primavera, la llegada de todas las hembras en otoño sugiere una clara atracción por el alimento, y su distribución invernal podría determinar cómo se distribuirán los leks en primavera. Considerando los movimientos descritos, de hasta 25 km lineales, los esfuerzos de conservación en la Reserva pueden resultar infructuosos sin gestión adecuada de las zonas aledañas. La población ha permanecido estable a lo largo de los ocho años del estudio, con una ligera, aunque no significativa, tendencia al aumento.

Palabras clave: Avutarda, tendencias poblacionales, Villafáfila

INTRODUCTION

The first reliable published data on the numbers of Great Bustards (*Otis tarda*) at the Reserve of Villafáfila, NW Spain, stated that the population fluctuates seasonally between

ca. 1000 and 1800 birds (Alonso *et al.*, 1990a). Figures published prior to that study were confusing (ICONA, 1982; Otero *et al.*, 1982; Ena & Martínez, 1988, Grimmet & Jones, 1989) and consistently underestimated the real size of the population due to metho-

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dological deficiencies during censuses (see Alonso *et al.*, 1990b; Alonso & Alonso, 1995). Some of these technical flaws also invalidate most of the censuses that the staff of the Reserve has begun to carry out only three years ago.

In the present paper we summarize our census data recorded during a study carried out continuously at the Reserve since 1987, and discuss the interannual and seasonal population trends in the light of both census results and radiotracking of some birds. Since there is no other report covering several years of census data of this remarkable population, the present report should be useful as a groundwork for further studies on it, as well as to adequately plan present and future management and conservation measures for this population.

STUDY AREA AND METHODS

The Wildlife Reserve of Villafila (39°55', 41°50', about 700 m a.s.l.) extends over 32682 ha of dry farmland around a group of small and shallow endorheic lagoons which cover ca. 400 ha in the province of Zamora, NW Spain. The land is almost entirely cultivated with cereal (mostly wheat and barley, covering over 80% of the surface), and alfalfa (ca. 8%). There are also some sunflower, rape and vineyards. The rest (about 9%) is natural grassland used for sheep grazing. The area is almost treeless and gently undulated, with a hilly zone of about 200 ha in its center, southwards of the lagoons, where the ground level reaches maximum heights of about 50 m above the lagoon basin.

Between January 1987 and April 1995 we carried out 49 complete censuses of the Reserve, distributed more or less regularly throughout the study period. Each census was made by four people in two cars during two consecutive days, following pre-determined itineraries to cover the whole study area. The itinerary was 384 km long and both teams spent a total of ca. 20 hours to cover it. Counting was interrupted during midday hours (between 10:00-11:00 and 15:00-16:00 GMT), when the birds are usually inactive and thus less detectable. Since the maximum distance between tracks used during censuses

was ca. 1 km, and due to the large size of the birds and excellent visibility conditions, we assumed that the error of our counts was negligible (Alonso *et al.*, 1990b). An exception to this were the numbers of females counted between early May and late July, when most are incubating and hardly visible due to the height of the cereal. During these months we assumed that female numbers in the Reserve were the same as those counted in early September, when breeding was over and the cereal already harvested. This assumption was based on our observations of marked females (both successful and unsuccessful breeders), which remained approximately at the same areas during late spring and summer. Throughout most of the paper we refer to birds older than one year to avoid irregular variations in number of birds produced by the variable breeding success from year to year, and by high mortality during the first two-three months of life of the young. These first-year or juvenile birds usually disperse at an age of 7-12 months. Females return in general to their natal sites after a short dispersal period, while males stay away longer, some of them never returning (see Alonso & Alonso, 1992; Alonso *et al.*, 1995). So, the number of males used throughout the paper is equal to the number of total males minus the number of first-year males, which can be recognized in the field at least until they are one year old. Although two- and three-year birds sometimes also move quite considerable distances and do not show such a site fidelity as adults (Alonso & Alonso, 1992; and unpublished data), their numbers were very low as compared to the total number of true adults. Moreover, other males of that age behaved in a similar way as older males with regard to seasonal movements. Therefore, including them together as males older than one year would not affect the conclusions of this paper. Regarding the females, since first-year birds are only recognizable in the field until late September, we assumed that the number of juvenile females counted on that month remained unchanged until the next June, so that we subtraced it from each monthly total of females counted between October and June. This is the closest possible approximation to the real number of females older than

one year, since it seems that after September only a negligible percentage of females disperse outside the Reserve or die during their first year (own unpublished data). To simplify data analysis, the few birds which could not be sexed during censuses (2% on average, and only 0.17% in the last 25 censuses) were considered as females: females double males in number and are more difficult to sex in the field, so that the probability that an unsexed bird was a female is much higher than 50%. In September, when juveniles of both sexes are similar in size and appearance to adult females, birds of undetermined sex and age were distributed among females and juveniles of both sexes in proportion to numbers counted of each class (see Alonso *et al.*, 1990b for a detailed discussion).

In addition to the censuses, each year between 1983 and 1993, 6-40 young Great Bustards were marked with patagial tags during July and August, when they were still dependent on their mothers and weighed 1-3.5 kg. One hundred were also provided with radiotransmitters. The ca. 2500 resightings

recorded up to now of these marked birds (on different day each), and the almost 300 resightings of another 10 males captured as adults in 1992-93 and radiotracked since then, have allowed us to study their dispersive and seasonal movements (see details in Alonso *et al.*, 1995). This information provided independent evidence to evaluate the trends deduced from census data.

RESULTS AND DISCUSSION

Seasonal changes in numbers

The numbers of Great Bustards in the Reserve changed throughout the year between a maximum of 1700-2000 birds during winter (October-April) and a minimum of 1000-1300 during summer (May-September) (all differences between winter and summer monthly means based on ≥ 3 censuses were statistically significant, $P < 0.05$, see Table 1). Excluding December, with only one census, all other October-April monthly samples showed maximum counts exceeding 1700 birds,

TABLE 1

Mean and maximum (in parenthesis) monthly numbers of Great Bustards censused at Villafila Reserve between January 1987 and April 1995. The significance of the differences mentioned in the text between pairs of monthly means was tested with the LSD-test of an ANOVA of all monthly means based on ≥ 3 censuses.

[Variación estacional en las cantidades medias y máximas (entre paréntesis) mensuales de *Avotardas* censadas en la Reserva de Villafila (periódico enero 1987 - abril 1995). La significación de las diferencias mencionadas en el texto entre medias mensuales se comprobó mediante el test LSD de un ANOVA con medias basadas en ≥ 3 censos.]

Month	no. of censuses	Total no. of birds	males	females
Jan	3	1701 (2013)	445 (526)	1114 (1272)
Feb	5	1670 (1907)	500 (666)	1064 (1255)
Mar	3	1855 (2008)	635 (692)	1086 (1122)
Apr	6	1603 (1793)	548 (606)	929 (1138)
May	4	1115 (1346)	382 (493)	634 (717)
Jun	3	1016 (1070)	291 (315)	616 (717)
Jul	1	1020 (1020)	219 (219)	611 (611)
Aug	3	1222 (1355)	290 (360)	722 (775)
Sep	8	1101 (1293)	295 (406)	700 (775)
Oct	2	1535 (1714)	463 (527)	963 (991)
Nov	3	1571 (1728)	436 (523)	963 (1003)
Dec	1	1492 (1492)	375 (375)	1091 (1091)

TABLE 2

ges in the sex ratio (females/males). Number of censuses as in Table 1. The values in March, re significantly lower (LSD-test, see Table 1) than those in other months. *La proporción de sexos (hembras/machos) a lo largo del año. Las cantidades de censos para de la Tabla 1. Los valores de marzo, abril y mayo son significativamente menores que los de .SD, véase Tabla 1).*

Monthly means including birds < 1 year		Monthly means only birds > 1 year	
mean	standard error	mean	standard error
2.41	0.15	2.57	0.21
2.20	0.26	2.21	0.28
1.64	0.07	1.72	0.07
1.68	0.10	1.72	0.12
1.77	0.20	1.70	0.11
2.22	0.20	2.17	0.38
2.70	0.00	2.79	0.00
2.24	0.25	2.57	0.33
2.37	0.24	2.55	0.30
2.07	0.26	2.11	0.23
2.15	0.28	2.31	0.37
2.87	0.00	2.91	0.00

These trends deduced from censuses were confirmed by data from individually marked birds. Out of 12 adult males radiotracked in detail in 1994-95, 8 spent all the year round in the Reserve, 1 spent the summer outside it, and 3 only arrived at Villafáfila to display and mate (Alonso *et al.*, 1995 and pers. obs.). Moreover, radiotracking data showed that the distances between display sites of males and the areas where they spend the summer or the whole nonbreeding season were of 20-25 km (Fig. 1; for further details see Alonso *et al.*, 1995).

Concerning the females, the pattern is slightly different. The number of breeding females (with or without success) in the Reserve was 600-700 birds (May counts, Table 1). These females remained in the Reserve all the year round, independently of their breeding success (e.g. females A, B, C and E in Fig. 2). They may perform seasonal displacements of variable magnitude, although usually within the limits of the Reserve (see e.g. females D and E in Fig. 2). The number of females present in May remained stable

lute maximum of 2013 birds in 5. The month with the highest of birds was March, with the and minimum (1713 birds) figure numbers almost equal to count. From these numbers we t the Reserve of Villafáfila holds world's densest Great Bustard

s, however, sex differences in the term described above. Excluding ar birds to avoid variations due to n annual productivity, maximum males were observed in March, gather at display sites to attract ble 1; all differences between other months were significant, ith April, $P < 0.05$). In mid April, in copulating period is over, more e males progressively abandoned ; where numbers decreased to a uring summer (differences between months -June to September- are significant, $P < 0.05$). About 20-

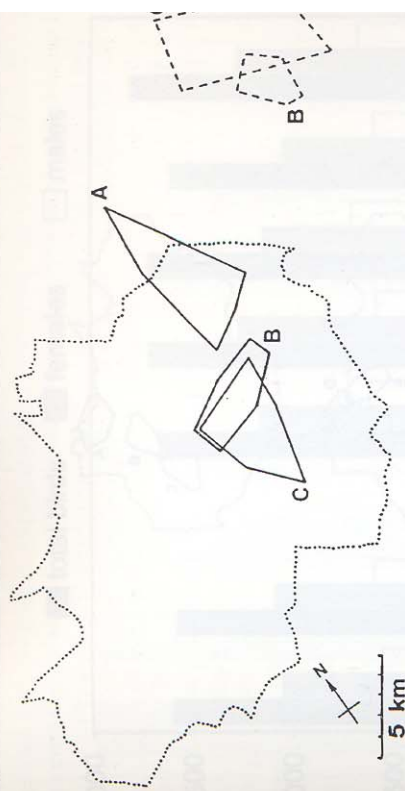


Fig. 1.- Sketch map of the home range of 3 male Great Bustards as determined by radiotracking line shows the Reserve limits. The solid lines refer to periods spent in the Reserve, varying from all the (e.g. male A) to only the mating period (e.g. male C). The dashed lines refer to periods spent outside. 40-50% of all males usually remain in the Reserve more or less in the same area throughout the year (e.g. male A), the rest abandon the Reserve once the mating period is over, and ca. 20-30% of them Reserve in autumn (e.g. male B was in the Reserve from October to May), or do it only to try mating next spring (e.g. male C was in the Reserve only from February to June). The numbers of sightings days) were: 52 of male A (March 1993-August 1995), 37 of male B (February 1994-August 1995), at C (March 1994-August 1995).

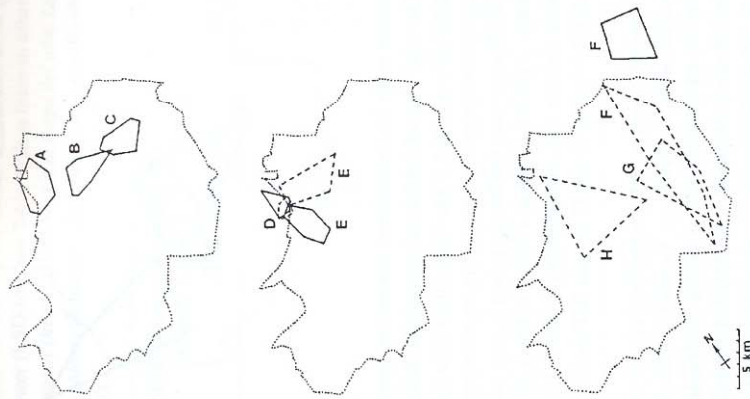
[Mapa esquemático de las áreas de campeo de 3 machos de Avutarda, según resultados de seguimiento por radio. La línea punteada muestra los límites de la Reserva. La línea continua representa los periodos de la Reserva, que varían entre todo el año (macho A) a sólo el periodo de cópulas (macho C), y la línea representativa los periodos fuera de la Reserva. Mientras el 40-50% de los machos suelen permanecer en estables en un área a lo largo de todo el año (por ej., el macho A), el resto abandonan la Reserva al inicio del periodo de cópulas, regresando alrededor del 20-30% en otoño (p. ej., macho B, que estuvo octubre y mayo), o bien permaneciendo fuera hasta la primavera siguiente (p. ej., macho C, dentro el junio). Los contactos (en días distintos) fueron: 52 del macho A (marzo 1993-agosto 1995), 37 del B (a agosto 1995) y 32 del C (marzo 1994 a agosto 1995).]

September and October the female population increased significantly due to the arrival of many unsuccessfully breeding females, together with some females with young, coming from outside. Maximum female numbers (1000-1100 birds) were observed in December and remained unchanged until March-early April, when the new mating period takes place. Examples of this arrival of females that breed outside the Reserve are females F, G and H in Fig. 2.

Females arriving in autumn could probably be more attracted by the better foraging conditions in the Reserve (particularly, by the higher abundance of alfalfa fields) as compared

trasts with the 20-30% males that the Reserve to display and copulate way to explain changes in female would be to consider that, since wintering and mating in the Reserve have not enough space to breed must disperse after mating. Since we few data on marked females that the Reserve in winter and breed elsewhere cannot evaluate the extent of tl ments, but we guess they may at milar, not far away from those of

The sex differences in seasonal described above make it difficult a unique value for sex-ratio repres



etch map of the home range of 8 marked female Great Bustards at Villafañila Reserve (dotted line), and C represent the typical sedentary females living all the year round in a relatively small area. move between a 'wintering' area (October-April, dashed line) and a 'breeding' area (May-June, dotted line) which were close together or even overlapped, the latter being either within the limits of the reserve (e.g. female D). Finally, about 40% of the females wintering in the Reserve move outside it. Examples of this pattern were females F (October-April in the Reserve, May-June outside), and G and H (only January-April in the Reserve, rest outside, but at unknown locations since they were g-tagged only). The numbers of sightings were respectively, 44 (July 1985-April 1995), 30 (July 1985-April 1995), 50 (July 1993-August 1995), 23 (July 1989-April 1992), 25 (July 1985-April 1992), and 3 (July 1989-April 1992).

quemático de las áreas de campeo de 8 hembras marcadas de Avutarda en la Reserva de Villafañila. Las hembras A, B y C representan las típicas hembras sedentarias, que permanecen fijas a una zona pequeña durante todo el año. Otras hembras se desplazan entre zonas de 'invernada' (octubre-abril) y de 'cría' (mayo-septiembre, trazo continuo) cercanas o solapadas, estando la zona de cría dentro de la Reserva (hembra E), bien fuera (D). Por último, alrededor del 40% de las hembras que pasan el verano fuera de la Reserva nidifican y pasan el invierno fuera de la misma. Ejemplos de este patrón son las hembras F, G y H (vistas en la Reserva sólo entre enero y abril, área de cría fuera de la misma, aunque no localizada al estar estas hembras marcadas sólo con placas alares, no con anillos). Los contactos respectivos fueron 44 (julio 1985-abril 1995), 30 (julio 1984-julio 1991), 42 (julio 1993-agosto 1995), 23 (julio 1989-abril 1992), 25 (julio 1993-julio 1995), 10 (julio 1985-abril 1992), y 3 (julio 1989-abril 1992).

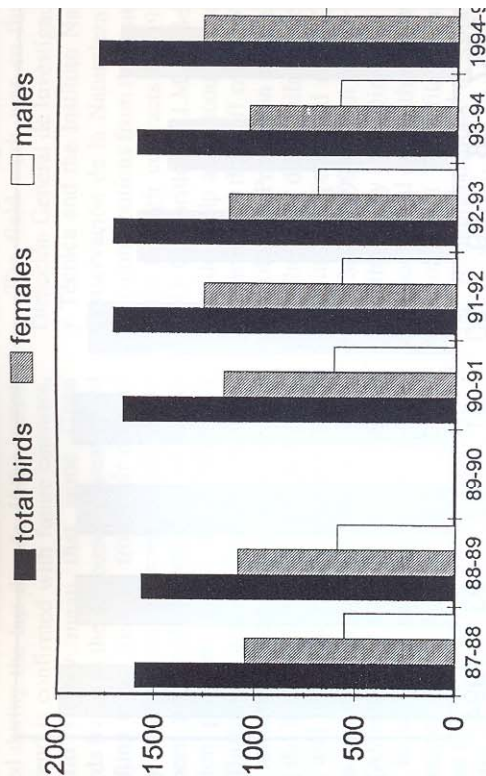


Fig. 3.- Changes in maximum numbers of Great Bustards >1 year old counted during each winter season (between 1st October and 15th April) of the next year. The slight increasing trends in total numbers of birds, females and males were not significant, as shown by the significance value of the Spearman's rank correlation test, $r_s=0.60$, $P=0.14$; $r_s=0.68$, $P=0.096$, and $r_s=0.36$, $P=0.38$. First-year birds have been the influence of annual changes in breeding success, and juvenile dispersal and mortality.

[Variaciones en las cantidades máximas de Avutardas >1 año de edad censadas durante la temporada de cría en la Reserva de Villafañila entre 1987 y 1995 (cada temporada invernal incluye desde el 1 de octubre hasta el 15 de abril del año siguiente). La tendencia al aumento insustancial en el número total de aves, de las hembras y de los machos no fue significativa, según indican los valores de significación de los coeficientes de correlación de Spearman: $r_s=0.60$, $P=0.14$; $r_s=0.68$, $P=0.096$, y $r_s=0.36$, $P=0.38$. Se han omitido las aves menores de un año por la influencia de las variaciones interanuales en el éxito reproductivo, y dispersión y mortalidad.

sex-ratio is biased towards females in all months. The values in March, April and May (ca. 1.7 females per male) are significantly lower than those in other months, when it increases to 2-2.5 females per male ($P<0.05$). This is because a significant number of males come to the Reserve just to display and try mating in March-April, as stated above. The sex-ratio recorded during mating (1.7 females per male) would thus be the closest to the operational sex ratio (proportion of fertilizable females in relation to sexually active males) for this population. However, the number of females that actually succeed in mating is much lower than those present (own unpublished data), while almost all females two or more years old may be fertilized. Therefore,

more biased towards females than mentioned figure of 1.7 females per male. The preceding description of the dynamics of a Great Bustard population may be useful to explain changes observed in areas where both adequate series of counts and data on the movements of birds are lacking, thus preventing from reaching a reliable interpretation. From a biological perspective, the information discussed above are useful to understand the peculiar mating system of the Great Bustard, which clearly reflect its lekking reproductive behaviour, but our data on sex difference in the use of the Reserve may also be useful in giving support to the hypothesis of

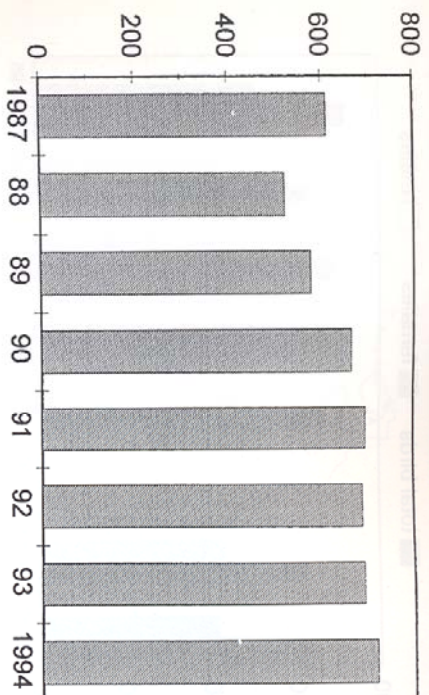


Fig. 4. Numbers of breeding females counted in the Reserve between 1987 and 1995 (females ≥ 2 years old censused in early September). The increasing trend was significant ($r_s=0.86$, $P=0.02$).
(Cantidad de hembras reproductoras censuadas entre 1987 y 1995 (hembras de ≥ 2 años de edad censuadas a primeros de septiembre). La tendencia al aumento fue significativa ($r_s=0.86$, $P=0.02$)).

Flocks of females occupy from the beginning of the autumn certain sites offering favourable feeding conditions, such distribution pattern could to a certain extent determine the males' spring distribution pattern. We are currently studying the behaviour of individually marked males at leks to investigate this and other aspects of this species' unique mating system.

Finally, as an important applied conclusion from our study, we should advise that any conservation effort within the Reserve, as well as within any other protected zone, may be fruitless, or at least it will fail to reach optimal rewards, if wide areas surrounding them are not adequately managed. Our results show how large the area used by the Great Bustards of Villafraña is (see Alonso *et al.*, 1995), and thus provide the basic information to support and encourage large-scale conservation policies, which in fact are still to be adequately implemented. Most areas of the Tierra de Campos, the large region surrounding and including Villafraña Reserve, are indeed still poorly managed in this sense, and disappearance of suitable habitat at distant areas could seriously threaten local Great Bustard popula-

tions but also indirectly affect the population of Villafraña. Up to now, conservation of Great Bustards in this and other regions of Spain has depended more on the farmers' will to voluntarily maintain traditional land uses than on the little, if any, true management measures by regional authorities, apart from mere prohibition of hunting.

Interannual trends

The Great Bustard population living in the Reserve between autumn and early spring has remained stable throughout the eight years covered by our study, with a slight but not significant trend to increase (Fig. 3). This was also true for each sex separately, although the increasing trend was marginally significant for males ($r_s=0.67$, $P=0.09$). On the other hand, the number of females breeding in the Reserve also seems to have increased slightly throughout the study period, from about 600 birds during the mid-eighties to the current ca. 700 birds ($r_s=0.86$, $P=0.02$; Fig. 4).

Although our series of censuses is still too small to be sure of the insinuated increase, at

least it shows that no evident decrease has occurred during the last decade. If the increasing trend is confirmed with future censuses, it could simply mean that some Great Bustards living in the surrounding areas could be shifting to the Reserve from their original display and wintering areas, which might have been subjected to some kind of habitat reduction pressure. Since the numbers of Great Bustards at a national scale have apparently remained more or less stable at least during the last decade (see Alonso & Alonso, 1996), and given the capacity shown by the species to move between relatively distant areas (Alonso *et al.*, 1995; Hellmich, 1991) it would be advisable to monitor not only the main nuclei used for wintering and mating, but also several marginal groups and particularly also isolated populations in order to prevent an excessive concentration of birds in the future.

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The Junta de Castilla y León gave us the permits to capture and mark Great Bustards until March 1994, when further captures were prohibited by the Dirección General del Medio Natural due to the negative attitude of the director of Villafraña Reserve, in spite of the recommendations to continue research from the Spanish Council for Scientific Research (CSIC), the Spanish Institute for Nature Conservation (ICONA) and the Complutense University, (ICNA) and the express wish of local people, who also supported the continuation of our radiotracking activities in a letter to the head of the regional Department of Environment. Discontinuation of individual marking is seriously damaging the progress of our long-term research program on the biology of Great Bustards at Villafraña and shows that regional authorities do not understand that a deep scientific knowledge is necessary to adequately manage and conserve our natural resources.

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