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RANGE AND PATTERNS OF GREAT BUSTARD MOVEMENTS AT VILLAFAFILA, NW SPAIN

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SUMMARY.—*Range and patterns of Great Bustard* (Otis tarda) *movements in Villafáfila, NW Spain.* We studied the range of juvenile dispersal and adult seasonal movements in the Great Bustard *(Otis tarda)* population of Villafáfila Reserve, NW Spain, using data from censuses and individual marking between 1983 and 1994. Thirty birds (22 males, 8 females) of those marked as young were seen during their juvenile dispersal outside the Reserve, at distances of up to 63 km, preferentially northeastwards, over an area of ca. 2800 km^2. All males and 40 % of females abandoned the Reserve during their juvenile dispersal. About half the males born in the Reserve never returned to it as breeding adults, while all females returned. With respect to seasonal movements of adults, about 40 % of females wintering in the Reserve abandoned it during the spring-summer to nest, most of them returning in October. A 20-30 % of the males present at the display arenas in early spring only entered the Reserve during the exhibition and copulatory phase. About half the males present at that time abandoned the Reserve once the peak copulation period was over, remaining at up to 20 km of the display arenas during the summer. The observed dispersal patterns are discussed in relation to current conservation policy of the species in the region of study.

Key words: dispersal, Great Bustard, movements.

RESUMEN.—*Extensión y patrones de movimientos de las Avutardas* (Otis tarda) *de Villafáfila.* Se estudiaron la amplitud y los patrones de movimientos de las Avutardas *(Otis tarda)* de la Reserva de Villafáfila, a partir de datos de censos y marcaje individual durante 1983-94. Treinta individuos (22 machos, 8 hembras) de los marcados como pollos fueron vistos durante su dispersión juvenil fuera de la Reserva, a distancias de hasta 63 km, preferentemente hacia noreste, siendo la superficie cubierta por dichos contactos de unos 2800 km^2. Todos los machos y el 40 % de las hembras abandonaron la Reserva durante su dispersión juvenil, regresando posteriormente alrededor de la mitad de los machos y todas las hembras. En cuanto a los movimientos estacionales de los adultos, aproximadamente un 40 % de las hembras que pasan el invierno en la Reserva la abandonan para nidificar, volviendo a ella en su mayoría en octubre. Un 20-30 % de los machos presentes en las zonas de exhibición y cópula durante la primavera temprana viven fuera de la Reserva durante el resto del año. Alrededor de la mitad de los machos la abandonaron al concluir el período de cópulas, estableciéndose a distancias de hasta 20 km durante el verano. Se discuten los patrones de dispersión observados en relación con el estado de conservación actual de la población de Avutardas de la Tierra de Campos.

Palabras clave: Avutarda, dispersión, movimientos.

INTRODUCTION

Great bustards *Otis tarda* are reported as sedentary in the western and southern, and migratory in the northern and eastern parts of their distribution range (Gewalt, 1959; Glutz *et al.*, 1973; Cramp & Simmons, 1980; Hidalgo & Carranza, 1990). However, current information on movements of this species is purely speculative, since it is based on indirect data such as population counts and circumstancial evidences like isolated observations of flying flocks.

Since 1983, a wing-tagging program of Great Bustard young has been carried out uninterruptedly at the Wildlife Reserve of Villafáfila, Spain. More recently, we have also radio-tracked juvenile birds and adult males, as part of a long-term study of this species. In a previous paper (Alonso & Alonso, 1992) we showed that juvenile dispersal was male-biased using data obtained from wing-tagged

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birds inside the Reserve, and discussed the possible evolution of such sex bias in relation to the reproductive strategy of the species, emphasizing some theoretical aspects of causes and consequences of dispersal. In the present paper, using mainly data from radio-tracked birds, we describe with more detail the extent and patterns of juvenile dispersal and seasonal movements of adults outside the Reserve. Our main objective here, in contrast to the previous paper, is to identify the spatial requirements of the population breeding in the Reserve evaluating their zone of influence onto the surrounding areas. The study of individual home ranges and space use patterns in this endangered species is important not only to increase our knowledge of its biology, but also to provide a basis for improved management measures.

STUDY AREA AND METHODS

The study was carried out at the Lagunas de Villafáfila National Wildlife Reserve (32682 ha) in northwestern Spain and its surroundings. The Reserve, which holds probably the world's densest Great Bustard population, is almost entirely cultivated, mainly with cereal (more than 80 %). Alfalfa fields occupy ca. 8 % of the surface, and natural grasslands, which are used for sheep grazing, ca. 9 %. The treeless, gently undulated cereal and alfalfa fields represent an appropriate habitat for the great bustards, closely resembling the natural steppes once occupied by this species (see Alonso & Alonso, 1990 for a more detailed description of the study area). Each year between 1983 and 1993, 6-40 young great bustards were marked with patagial wing-tags during July and August. They were still dependent on their mothers when captured, weighing between 1 and over 3 kg. Marked birds were sexed by means of a biometrical index that discriminates almost 100 % of the cases at that age (Alonso *et al.*, 1995).

Throughout the study period we periodically searched the Reserve for marked birds, while censusing the bustard population. The frequency of such transects varied between one per week and one every 2-3 months, but all parts of the Reserve were searched with equal intensity, to avoid biases in the probability of contact with individual birds. Adjacent areas were also searched, but less intensively. In 1991-1993, 91 young bustards were radio-tagged and later located each month at least once until they died or the transmitter ran out. During the first three months of life of the young there is a high juvenile mortality (pers. obs.). Also, a small percentage of birds lost their wing-tags or transmitters. Therefore, the sample used in this paper was 107 juvenile birds that survived and conserved their tags after their first summer, with a total of over 2300 sightings on different days. Radio-tagged birds were located with hand-held yagi antennas from cars or, when necessary, with the aid of aircraft of the Spanish Air Forces. On these occasions one of us located the birds from the aircraft, while the others did the control by car. In February-March 1992 and 1993 we also captured adult males and provided them with backpack harnesses with radio-transmitters. Since some birds also lost the harness or dispersed because they were still immatures, the sample used in this study was finally reduced to 10 adult males, with 232 sightings on different days. These were also located from cars or aircraft at least once monthly during one (9 birds) or two (1 bird) years after capture.

In addition to the data on seasonal movements of adults obtained from individually marked birds, censuses of the number of birds in the Reserve also provided indirect information on such displacements. Between January 1987 and December 1994 we carried out 41 complete censuses of the Reserve. 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 ca. 360 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. An exception to this were the numbers of females counted bet-

ween 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) remaining approximately at the same sites during late spring and summer. For the purposes of this paper (seasonal movements of adult birds, see Fig. 2) we consider as 'adults' those birds older than one year. So, the number of 'adult' males in the Reserve was 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 might not be true adults (see Gewalt, 1959; Glutz *et al.*, 1973; Cramp & Simmons, 1980), their number is very low compared to the total number of true adults. Moreover, several individually marked two- and three-year males behaved in a similar way as older males with regard to seasonal movements. Therefore, including them as adults does not affect the conclusions of this paper. Since female first-year birds are only recognizable in the field until October, to estimate an equivalent number of 'adult' females we subtracted, from the total number of females counted in October and later, the number of juvenile females censused in the previous September. This is the closest possible approximation to the real number of females older than one year, since we know that after September only a negligible percentage of females disperse outside the Reserve or die during their first year (pers. obs.).

Throughout the paper, we refer our observations as in or outside the Reserve of Villafáfila. Although the limits of the Reserve may be somewhat artificial, they were useful for our main purpose, i.e. studying the area of influence of birds from it onto the surrounding areas, and trying to identify the spatial requirements of the adult population resident in the Reserve. In addition, the Reserve is immediately surrounded by areas of much lower Great Bustard density (Alonso *et al.*, 1990b), supporting our view of the birds in the Reserve as a populational unit.

RESULTS

Dispersal of juveniles

Thirty of a total of 107 marked young great bustards surviving the summer mortality period and conserving their wing-tags or radio-transmitters were later seen during their juvenile dispersal at variable distances from the Reserve (Fig. 1). Eight were females and 22 males. Nine of these male birds never returned to the Reserve after their second year, while all females returned after their juvenile dispersal. The farthest juvenile dispersal distance recorded was 63 km.

Since many of the birds were only wing-tagged but did not carry a radio-transmitter, the probability of resighting them outside the Reserve was very small. Therefore, the proportion of individuals dispersing as juveniles shown in Fig. 1 (30 birds of a total initial sample of 107) represents an underestimation of true dispersal. We calculated more realistic proportions of juveniles dispersing from the Reserve using only the sample of radio-tagged birds, with the result that all 13 males and only 8 of 20 females were seen outside the Reserve during their juvenile dispersal

Seasonal movements of adults

The numbers of great bustards in the Reserve change between a maximum in winter and a minimum in summer (Fig. 2). The seasonal patterns are slightly different in both sexes. Adult male numbers increase significantly in March with respect to winter numbers (all monthly differences were $P<0.05$ except March vs. October, ANOVA LSD-test). After April male numbers decrease again to minimum values during summer (all monthly differences between March or April and June to September were $P<0.05$). Adult female numbers are significantly lower between May and September than during the rest of the year (all monthly differences were $P<0.05$).

Three of 10 adult males captured in the Reserve in February-March and radiotracked with sufficient detail during one year spent the summer months outside it, returning respectively in early October, late October and February. Another male was only

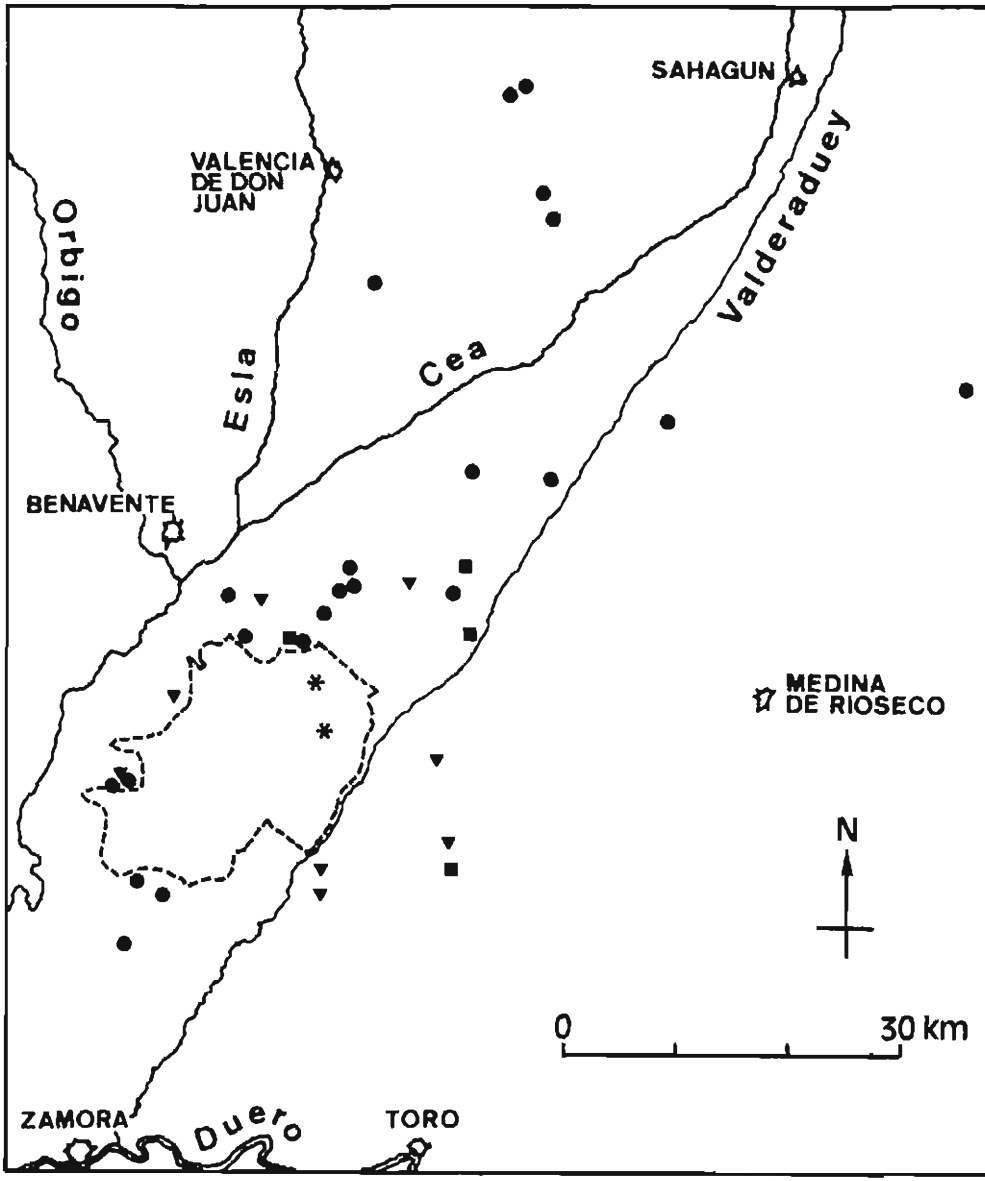

FIG. 1.—Map of the study area showing the farthest sites where great bustards marked individually in the Reserve of Villafáfila during 1983-93 were sighted until December 1994. Each dot represents a different individual: males (circles) or females (triangles) of various ages marked as young in the Reserve, and males marked as adults (squares) in two display sites (asterisks) in early spring. The dashed line represents the limits of the Reserve. The main cities (capital letters) and rivers (lower case) are shown.
[Mapa del área de estudio en el que se muestran los contactos más lejanos habidos hasta diciembre de 1994 con avutardas marcadas individualmente en 1983-93 en la Reserva de Villafáfila. Cada símbolo representa un individuo distinto: machos (círculos) o hembras (triángulos) de diferentes edades, todos ellos marcados de pollos en la Reserva, y machos marcados de adultos (cuadrados) en dos zonas de exhibición (asteriscos) al comienzo de la primavera. La línea discontinua señala los límites de la Reserva. Se indican los principales ríos (minúsculas) y poblaciones más importantes (mayúsculas).]

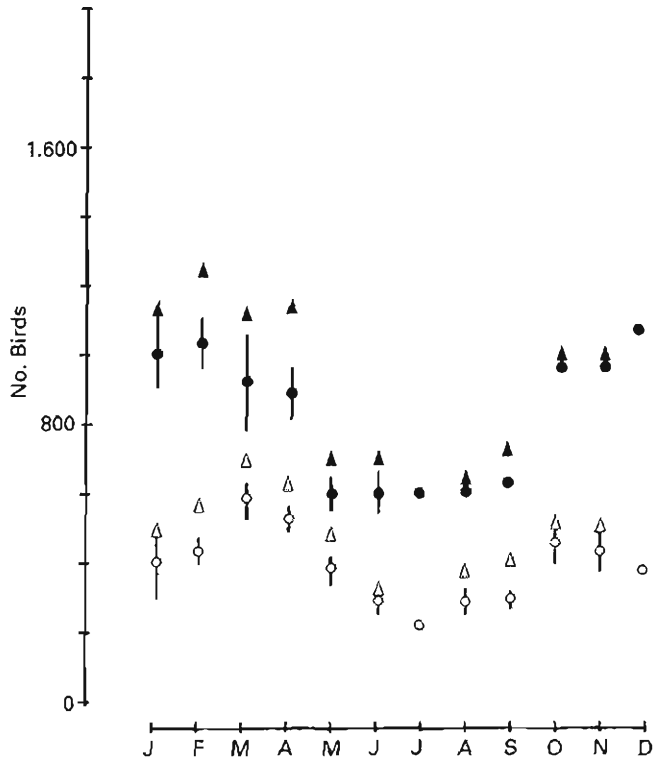

FIG. 2.—Monthly changes in mean numbers (dots) and maximum numbers (triangles) of great bustards older than 1 year censused in Villafáfila Reserve between January 1987 and December 1994. Males: open symbols; females: black symbols. Monthly samples were 2, 5, 3, 6, 4, 3, 1, 3, 8, 2, 3 and 1 censuses. Vertical bars represent ± 1 SE.

[Variación mensual de las cantidades medias (círculos) y máximas (triángulos) de avutardas de más de un año de edad censadas en la Reserva de Villafáfila entre enero de 1987 y diciembre de 1994. Machos: símbolos blancos; hembras: símbolos negros. Las cantidades de censos por mes fueron, respectivamente: 2, 5, 3, 6, 4, 3, 1, 3, 8, 2, 3 y 1. Los trazos verticales representan ± 1 error estándar.]

occasionally seen outside the Reserve (once in summer, and once in early winter), but close to its border (see Fig. 1).

With respect to those adult males marked with wing-tags as young birds, we have information from 38 individuals after their juvenile dispersal period (i.e. from their third year on). Two of these birds (a 5 %) probably lost their wing tags and could not be located since then. Both had lost one of the two wing-tags soon after marking, and later we sometimes sighted one male wearing just the rivets of the tags in the same areas. Twenty-one birds (a 55 %) dispersed definitively from the Reserve as juveniles. Another 7 birds (a 18 %) returned from their juvenile dispersal and established their home ranges in the Reserve, where they remain all the year round. Finally, 8 birds (a 21 %) are regularly seen at display sites in the Reserve only during late winter and spring, and later disappear and spend the rest of their annual cycle in some unknown place.

With regard to the seasonal movements of marked adult females, since all were marked as young in the Reserve, and females are strongly philopatric (Alonso & Alonso 1992 and pers. obs.), we still have no observations of individual birds confirming the inflow in October and outflow in May shown by the

census data (see Fig. 2). However, we have some preliminary data on seasonal movements of marked females that move between summer and winter sites within the Reserve, which will be analysed elsewhere.

Discussion

Our radio-tracking results show that all males and about 40 % of females hatching in the Reserve dispersed as juveniles to sites located at relatively far distances from their natal areas. Nine of the 22 males sighted outside the Reserve, or 21 of the 38 males known to have survived after their second year, never returned to the Reserve as adults. They settled as breeding adults on display sites at variable distances from it. These figures represent respectively a 41 % and a 55 % of all males born in the Reserve, which means that there is a very important flow of male genes from Villafáfila into the surrounding zones, and the area of influence of Villafáfila Reserve amounts approximately 2800 km^2, far more than the 327 km^2 occupied by the Reserve itself. In a previous paper (Alonso & Alonso, 1992) we showed that juvenile dispersal was male-biased in the Great Bustard and discussed that, as in many other species, long distance dispersal is probably a necessary mechanism to avoid inbreeding and/or reduce intraspecific competition for resources (see Dobson, 1982; Greenwood & Harvey, 1982; Greenwood, 1984; Shields, 1984; Dobson & Jones, 1985). However, in that study we only worked inside the Reserve and were unable to know the precise extent of juvenile dispersal distances, since birds were not radio-tagged and could not be followed along their dispersal outside the study area. Now we know that Great Bustard juveniles dispersing from Villafáfila can reach sites as far as 63 km from their natal sites. This has important consequences for the management and conservation of the species. For example, if the areas surrounding protected zones such as Villafáfila Reserve are not adequately managed, mainly conserving an appropriate habitat and avoiding disturbances, survival of long distance dispersing juveniles might be seriously endangered. Current conservation policy should change from the former system of protecting just a series of Reserves, to the more appropriate of trying to conserve the habitat unaltered in much wider areas, in order to assure maintenance of suitable feeding and nesting sites for the great bustards at a regional scale (see Sanz-Zuasti & Sierra, 1993). Our results showing how large the area used by the great bustards of Villafáfila is, provide basic information to support and encourage such large-scale conservation policy, which is in fact still to be adequately implemented. Most areas of the Tierra de Campos, the region represented in figure 1, are indeed still poorly managed in this sense, and disappearance of suitable habitat at these distant areas could seriously endanger local Great Bustard populations but also indirectly affect the population of Villafáfila. 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.

The great bustards from Villafáfila show a tendency to disperse to northeast. Only a few birds dispersed to south, and none to west. The extent of appropriate habitat to the west of the Reserve is in fact small, due to the proximity of the Esla valley, and westwards of it, the highlands preceding the mountains of La Culebra. To the south of Villafáfila the dispersal probabilities are possibly reduced by the presence of partly unsuitable habitat along the Duero river, where there are many irrigated fields. The next area with a relatively high density of great bustards southwards of Villafáfila lies at about 100 km from it, near Madrigal, in the province Avila (Martín & Martín, 1989). Our data suggest that there is little, if any, genetic exchange between this area and our study area. On the contrary, to the north and east of Villafáfila the region of Tierra de Campos continues uninterrupted until the area of La Nava, where our farthest dispersing juveniles were seen. In-between there are several areas of relatively high Great Bustard density in the provinces of León, Palencia and Valladolid (Otero, 1985; Lucio & Purroy, 1990; Sanz-Zuasti & Sierra, 1993). According to our data, most of these areas are temporally visited by juveniles dis-

persing from Villafáfila, and some of these birds eventually establish in these areas as breeding adults. A preliminary analysis of our data suggests that the geographical dispersal pattern is probably determined by the current distribution pattern of the species at a regional scale, and the latter could be limited by the availability of suitable habitat, with large areas of irrigation farmland constituting artificial barriers to the dispersal process. Large extents of unsuitable habitat could thus represent in the future a serious danger to the necessary genetic exchange between populations and ultimately determine the extinction of some isolated breeding groups.

With respect to the seasonal movements of the adult population at Villafáfila, the results of our censuses show that the numbers change seasonally between a maximum during winter or early spring and a minimum during summer. This seasonal movement pattern occurs every year in our study area and has also been observed at other Great Bustard sites (e.g. Lukschanderl, 1971; Hutterer & Lütkens, 1974; Sterbetz, 1981; Carranza *et al.*, 1989; Martín & Martín, 1989; Alonso *et al.*, 1990a;b; Lucio & Purroy, 1990; Trucios & Carranza, 1990; Hellmich, 1990; 1991). However, incomplete series of censuses at given areas and lack of individually marked birds had traditionally prevented field biologists from knowing to what extent these seasonal changes in numbers were a consequence of a lower detectability of the birds due to the higher herbaceous vegetation in summer. Our results show that a 20-30 % of the males displaying in spring in the Reserve spend the rest of the year outside it, at close to moderate distances. Altogether, about a half of the males displaying in spring in the Reserve abandoned not only the display sites but also the Reserve soon after the peak copulation period in March-April, remaining far from it at least until the next autumn and, in a number of cases, until the next spring. These seasonal movements clearly reflect the lekking reproductive behaviour of the species, with adult males clustering at traditional arenas where they display to attract females. We still do not know if there is any relationship between remaining or leaving the Reserve and breeding success in males. With respect to the adult females, around 40 % of those wintering in the Reserve leave it to nest, after the copulation period. This is probably a density-dependent dispersal, determined by the need to have enough resources to rear young, because unsuccessful females, but also a number of females with their young (pers. obs.), return again to the Reserve more or less suddenly in October, coinciding with a marked increase in their gregariousness. At that time families join in progressively larger flocks with unsuccessful females at favourable feeding sites, remaining there throughout the winter. Although the described patterns are probably present in most Great Bustard areas, further individual marking is necessary in order to confirm them, as well as to find out other important behavioural trends.

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The Junta de Castilla y León gave us the permits to capture and mark Great Bustards, but during the last two years the directors of the Reserve, M. Rodríguez and J. Palacios, made it extremely hard to carry out research by inventing many objections. Their narrow-mindedness and lack of interest in research and knowledge of the species, and the inability of their superiors in the Dirección General del Medio Natural of the regional government to place science and conservation in front of political interests, are seriously damaging the progress of knowledge. Scientific marking was finally prohibited in 1994, against the recommendations from the Consejo Superior de Investigaciones Científicas and the Universidad Complutense, and ignoring the wish of local people to continue research.

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