

MATING SYSTEM IN THE GREAT BUSTARD: A REVIEW OF PUBLISHED WORK IN LIGHT OF RECENT RADIOTRACKING RESULTS

EL SISTEMA DE APAREAMIENTO DE LA AVUTARDA (OTIS TARDA): REVISIÓN DE LOS ESTUDIOS PUBLICADOS, A LA LUZ DE NUEVOS RESULTADOS OBTENIDOS MEDIANTE RADIOSEGUIMIENTO

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Female and resource defense polygyny, as well as promiscuous mating in communal display areas (leks) are the mating strategies usually cited for the Great Bustard (*Otis tarda*) in most compilation works (Gewalt, 1959; Glutz *et al.*, 1973; Cramp & Simmons, 1980; Johnsgard, 1994). However, some of the published papers on the Great Bustard emphasize its highly variable mating system (Sterbetz, 1981; Carranza *et al.*, 1989; Hidalgo & Carranza, 1990). For example, Sterbetz (1981) lists several reproductive strategies for nine different populations in southeastern Hungary, ranging from monogamy to female defense based harems, including promiscuity, in which certain "unpaired" males display communally, limiting their relationship to females to the act of copulation. Carranza *et al.* (1989) state that mating system variability in the great bustard results from different ecological conditions such as degree of male and female dispersal, climate, food resource distribution, habitat stability or hunting pressure. Such flexibility would exist not only between populations but also between different years in the same population, ranging from resource and/or female defense based harems to several lek-like mating systems, such as exploded leks, thus allowing Great Bustards to maximize their reproductive success by adopting the mating strategy that optimizes their costs to benefits ratio after the prevailing set of environmental conditions. As pointed out by Hidalgo and Carranza

(1990), monogamy seems to be an unlikely strategy for a species as markedly dimorphic as the Great Bustard, for which no reliable evidence of male parental investment has so far been given. However, this possibility has been regarded in some compilation works (see, for example, Johnsgard, 1994). Hellmich (1991) rejects the existence of harems in Sierra de Fuentes, Cáceres province, emphasizing the high mobility of males, as well as the high frequency of male-male interactions during male daily movements, what suggests that the mating system of Great Bustards is basically the same in all healthy populations, rather than varying from a given strategy to a conceptually different one that works optimally in the new conditions. However, this conclusion is based on mere populational observations, lacking support from a study on individually marked birds that regarded the different factors affecting individual variance, such as age and social rank.

Here we review the work so far published, in the light of recent radiotracking results obtained by the authors, during 1994-96 at the Reserve of Villafáfila, NW Spain. Our discussion is based on tracking data from 17 adult males during the whole annual cycle and particularly during the breeding season, which are briefly set out below.

Seasonal movements

Male and female Great Bustard seasonal

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movements have already been discussed in a previous paper (Alonso *et al.*, 1995). About 40% of females wintering in the Reserve abandon it to nest and rear their young during spring and summer, most of them returning in October. A 20-30% of the males present at the display arenas in early spring only enter the Reserve during the exhibition and copulatory period. About half the males present at that time leave the Reserve once the peak copulation period is over, remaining at as far as 20 km from the exhibition areas. These results are supported by contacts with radiotagged males that spend the winter at distant areas and are later located at display sites in the Reserve. Marked adult females, on the other hand, were sighted in the same arenas year after year. In early April, the number of individuals in the Reserve decreases again, as shown by both censuses (Alonso *et al.*, 1997) and movements of marked birds (Alonso *et al.*, 1995), to reach its minimum during the summer.

Male gregariousness

Male gregariousness varies with time, so that some males segregate in early stages of the breeding season and display solitarily, while others do so in the later stages, even when some of the former are already back in the flocks. As a general rule, it seems that the younger an individual, the longer it remains in a flock. However, most marked birds eventually segregated from their flock and displayed solitarily at variable distances from other individuals, although their behaviour sometimes differed considerably between individuals. An idea of the great individual variance found in the marked sample is given by the behaviour of two males of the same known age, 4 years (they were marked when young in the same year). One of them remained in a flock during the whole breeding season, taking part in numerous fights, while the other segregated from the same flock and displayed solitarily during the later phases of the season.

Daily movements

Daily range of movements also varied between different marked individuals. Radio-tracking showed that some birds stayed in the

same parcel for a whole day, while others traveled long distances displaying at quite distant points at dawn and dusk, and taking the mid-day rest in some half-way suitable place. In no case whatsoever males seemed to defend a definite territory, displaying in apparently any point of their range and allowing other males to feed and display at practically the same sites used by themselves. Most radiotagged males seemed to have a movement and activity routine, although it cannot be stated that a given male's movement range represents a real territory, since there is a high level of overlap between ranges of several males. Moreover, a given male can be seen both alone and as a member of a flock at different moments of the same day's routine. Finally, one male displayed at various sites separated by more than 10 km and regularly repeated this pattern every year.

Display rates

Daily display rate was higher in solitary males. Therefore, some males that had remained gregarious, and whose daily display rate was low during the first stages of the breeding season, began to intensively strut when they became solitary late in the season, while some of the initially solitary males were already beginning to return to their flocks, thus lowering their display rate.

Main copulation period

The main mating period was obtained from the direct observation of copulations or from the number and intensity of struts seen in the display areas. It coincided in time with the beginning of a decrease in the number of females censused in the whole of the Reserve and some more intensively surveyed areas. In the years this study was carried out, such period occurred in the first half of April. The steepest fall in the number of females detected takes place between April and May and reflects how they successively begin incubation.

Discussion

Although the above mentioned results are

still preliminary, it is possible to discuss some aspects of the functioning and dynamics of the Great Bustard mating system that have been considered settled in previous works.

Monogamy should be considered a very rare possibility, found only in, if any, extremely fragmented populations. With regard to the seasonal defense of a group of females by a male, radio-tracking does not appear to support its existence in the Great Bustard. On the contrary, the high daily mobility of many males, the high variability of females detected in the proximity of marked males during whole periods of observation and the long distances traveled to nest by some marked ones, seen near displaying males, point against that possibility. In relation to female mobility, it is interesting the fact that certain areas of the Reserve hold no males during the breeding season or even all year round, but are important nesting and young rearing areas in which several marked females were hatched and

return to as breeding adults.

The defense of a resource rich territory might be a strategy undertaken by non mobile solitary males, though it might also be regarded as a special case of promiscuity rather than real harem polygyny (Davies, 1991). Male fights might be a consequence of disputes over those resource rich territories, although they have also been observed to occur between wandering males that meet in some point of their daily ranges.

Communal display in aggregations of different degree of tightness that fit what has been referred to as leks (Bradbury, 1981; Oring, 1982) is the only alternative strategy to that considered above. However, the classical, highly aggregated, lek model, proposed in the first papers on this type of mating system, does not properly suit Great Bustards. The few copulations by marked birds recorded (such small sample does not allow to draw any conclusion about individual bias in

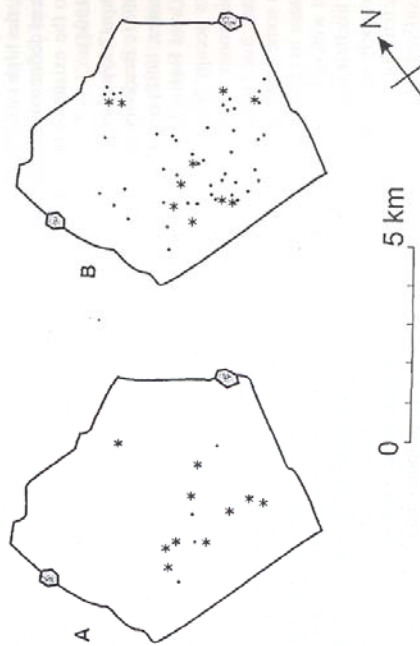


Fig. 1.- Temporal change of male flock size and distribution at the Corecinos valley during a given breeding season (1994). A: By late March, when the main copulation period has not yet begun, males are still aggregated in large flocks (asterisks). B: By late April, when copulation frequency is already in decrease, most males are displaying solitarily (dots) and there only are some small groups (asterisks, integrated mainly by immatures).

[Evolución temporal del tamaño de bando de machos de avutarda a lo largo de una estación reproductora (1994) en el valle de Corecinos. A: finales de marzo, antes del periodo principal de cópulas, los machos permanecen agregados en grandes bandos (asteriscos). B: finales de abril, pasado el pico de la frecuencia de cópulas, la gran mayoría de los machos se exhiben en solitario (puntos), quedando sólo pequeños bandos, fundamentalmente de inmaduros (asteriscos).]

mating distribution and its relationship to male physical condition, which is of great importance for some lek models) involved solitary individuals or members of loose aggregations. The main copulation period occurs when male gregariousness is lowest and the few remaining flocks are formed by immature individuals (birds younger than 3 years). Moreover, as solitary males return to flocks, female detectability markedly decreases, what suggests that most of them are incubating and the main copulation period is over.

The exploded lek hypothesis (Emlen & Oring, 1977) is much likelier than the classical one, since it does not require tight aggregations of displaying males, but rather that they be dispersed over a large, geographically limited area where levels of reproductive activity are high. Such is the situation found in some areas of the Reserve of Villafáfila like Cercinos and Tapioles (see figure 1) which hold the highest densities of males in the Reserve during the breeding season. Furthermore, the high mobility of males suggests the lack of definite displaying territories, and points to the existence of mobile arenas (Johnsgard, 1994).

The "hotspot" hypothesis of lek evolution (Bradbury, 1981; Bradbury & Gibson, 1983; Beehler & Foster, 1988) could gain some support in the Great Bustard from the fact that female flocks occupy from the beginning of the fall certain zones offering favourable feeding conditions. Such female distribution pattern could to some extent determine male distribution pattern in spring, although this is to be confirmed with more data.

The two likeliest mating strategies discussed above, namely exploded leks in mobile arenas and defense of a resource rich territory, are both considered here special cases of promiscuity since they do not imply any male-female relationship after copulation. From this point of view, those two strategies are not nearly differentiated, but form part of a gradient in aggregation level, which depends on multiple ecological factors such as population density, resource distribution and defendability and local physiography. The so far proposed alternative, based on the harem / lek duality does not seem to be supported by individual radiotracking.

Temporal variations in displaying male dispersion have also been described in other lekking species, such as the Buff-breasted Sandpiper (*Pyrangites subgriffollis*, see Pruett-Jones, 1988), what points it as a common pattern in promiscuous mating strategies.

More research effort is needed on this fundamental aspect of Great Bustard biology, not only because of its great theoretical interest, but also because of its usefulness in the species' management. A policy that does not regard the mating system of Great Bustards is in risk of falling in erroneous views of populations and the role individuals play in them, as it has occurred to the management of some hunting species. The final analysis of the preliminary results referred in this paper will help to settle some of the still unsolved questions on this topic.

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RESUMEN. - Se revisan los estudios publicados hasta la fecha sobre el sistema de apareamiento de la Avutarda (*Otis tarda*), a la luz de recientes resultados obtenidos mediante radioseguimiento de machos de avutarda durante los años 1994-1996 en la Reserva de Villafáfila. Estos resultados son aún preliminares, pero proporcionan nueva información sobre los movimientos estacionales de los machos, su grado de gregarismo, rango de movimientos y tasas de exhibición durante el celo, así como el período principal de cópulas y las áreas de nidificación de las hembras. Tal información apunta a un sistema de apareamiento básicamente promiscuo. Esta conclusión es todavía preliminar y ha de ser confirmada tras un análisis más detallado de los resultados presentados.

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