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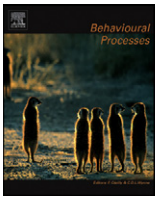

Ranging behaviour of little bustard males, *Tetrax tetrax*, in the lekking grounds

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ABSTRACT

We investigated the ranging behaviour during the breeding season of 18 radiotracked little bustard (*Tetrax tetrax*) males, a disperse-lekking species inhabiting the cereal pseudo-steppes. The average kernel 95% home range was 60 ± 50 ha and the average cluster 85% area was 17 ± 17 ha. Range structure was as relevant as home range size for explaining the variation in the ranging behaviour of males, which could be partially explained by age, habitat quality and site. Ranging behaviour varied from males defending small and concentrated home ranges with high habitat quality, to males holding larger home ranges composed by several arenas. Our results suggest that social dominance and resource availability may affect ranging behaviour of males during the breeding season. Also, mating systems constraints may play a role on the use of space of males within the lekking ground. The ranging behaviour of a given male may be determined by a tendency to reduce and concentrate the home range as age and social status increase, and several fine-tuning mechanisms adjusting the ranging behaviour to the prevailing environmental or social factors on a given site and year.

1. Introduction

The ranging pattern of particular individuals is the result of a complex process by means of which they try to fulfil all their needs, involving food, shelter, mates and the reduction of predation risk or competition. Extrinsic factors such as time of the year, habitat quality or population density, as well as intrinsic factors, such as age, gender, body condition or social status, may interact to finally shape the way in which a given individual ranges across space (Alonso and Alonso, 1992; Combreau et al., 2000; Garza et al., 2005; Novoa et al., 2006; Sardà-Palomera et al., 2011; Rhim, 2006). Although resource availability constraints are the factors most frequently identified as ultimately determining the home range shape and size in birds, in lekking species social interactions may also affect the ranging behaviour of males (Alonso and Alonso, 1992; Combreau et al., 2000; Jiguet et al., 2000; Wegge et al., 2003). In lek mating systems, males defend small, clustered courts visited by females to mate (Ligon, 1999). The social organisation of males within a lek is hierarchical, and only a few males contribute to the next generation (Ligon, 1999). The little bustard (*Tetrax tetrax*) is a near-threatened steppe-land bird (BirdLife, 2004) exhibiting a so-called exploded lek mating system (Jiguet, 2002; Morales et al., 2001). From their second year of life onwards, little bustard males exhibit breeding ornamental plumage and territorial behaviour and typically spend most of the breeding season displaying at the same place (called arena), preferably situated in fallow fields with low herbaceous vegetation (Martínez, 1994). In exploded leks, displaying males are considerably separated and aggregation is not detectable until they are mapped over a large area (Bradbury, 1981). It has been argued that this low aggregation potentially allows females to reduce male harassment. It may also allow males to hold larger territories, so they can include larger amounts of the female preferred habitat for foraging or nesting (Jiguet et al., 2000; Ligon, 1999), which differs from the males' preferred displaying habitat (Morales et al., 2008). In that situation, we would expect that higher ranking males would have larger and less concentrated ranges than lower ranking ones, and we would not be talking about a real lek mating system, but about a resource-based polygyny system (Jiguet et al., 2000). Alternatively, higher status males may simply try to occupy or defend optimal displaying places. In this case, higher status males will tend to have smaller home ranges in optimal displaying habitat. The aim of our research was (1) to analyse the variation in the ranging behaviour of little bustard males during the mating season; (2) to identify the main underlying factors causing ranging behaviour variation; (3) to discuss the implications of our findings in relation to the understanding of the mating system of the species.

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2. Material and methods

2.1. Study area

The Lleida Plains are situated on the northeastern edge of the Ebro Valley (Catalonia, Spain). The annual rainfall is low (between 300 and 450 mm) and the climate is continental (Bosch, 2004). The little bustard population in the area has been estimated at 700–1300 breeding males (Bota et al., 2004). We conducted our research in two pseudo-steppe Special Protection Area (SPA) sites: Bellmunt-Almenara (ES0000477) and Secans de Belianes-Preixana (ES0000479). The Bellmunt area (1769 ha) (41°47′ N, 0°57′E) was dominated by cereal crops (ca. 80%) with dispersed patches of scrub-steppe or fallow fields (ca. 12%). Female density in this area was estimated at 0.68 ± 0.80 female/100 ha and displaying male density at 2.9 ± 0.5 males/100 ha (unpublished results). The Belianes study site (2583 ha) (41°35′N, 0°59′E) was a farmland area dominated by cereal crops (ca. 83%) with a lower availability of scrub-steppe patches or fallow fields (ca. 3%). Female density in Belianes was estimated at 1.44 ± 0.82 female/100 ha and displaying male density at 3.2 ± 0.6 males/100 ha (unpublished results).

2.2. Home range descriptors

During the breeding season, we caught 18 males (8 in Bellmunt and 10 in Belianes) using snares (Ponjoan et al., 2010). We fitted all birds with TW-3 backpack transmitters with a 3-year lifespan battery (Biotrack, Dorset, UK) and 32 g of weight, which corresponded to 4.4% of the bodyweight of the smallest bird and 3.6% of the mean weight of captured birds. These percentages are below the 5% safety threshold indicated by Kenward (2001) for harness-mounted tags. We classified males as young (first spring), young adult (second spring), or adult (third spring or older). Young adults and adults males exhibit breeding ornamental plumage and territorial behaviour (Johnsgard, 1994), but they can be distinguished by means of plumage pattern (Otero, 1985). We determined the sex of first spring female-like males by genetic analyses of blood samples (0.1 ml collected by femoral vein puncture). Marked males were tracked once a day and five days per week from 1st April to 15th June over one to three mating seasons from 2002 to 2005. We monitored birds from ground vehicles using a handheld 3-element Yagi antenna and a portable scanning receiver (ATS R4000; Advanced Telemetry Systems Ltd.). The incremental analysis of the Ranges7 software (South et al., 2005) indicated that 14 locations were sufficient to obtain stable range estimates, similar to those used in previous bustard studies (Hingrat et al., 2004; Jiguet et al., 2000). The four locations recorded immediately after a bird was released were not taken into account, in order to avoid confusion resulting from possible alterations in the ranging behaviour associated with the capture (Kenward, 2001).

We described two characteristics of the ranges, their size and the distribution of fixes within them, using different estimators implemented in Ranges7 (South et al., 2005). As estimators of size (ha) we used the following parameters: (i) *MCP95*, the area of the Minimum Convex Polygon encompassing 95% of the bird locations (the 5% locations farthest away from the recalculated arithmetic mean centre were excluded); (ii) *Kernel95*, the area of the 95% core-weighted kernel density estimator, using the reference method to determine the smoothing parameter. This home range size estimator has been successfully used in other little bustard studies (Jiguet et al., 2000); (iii) *Cluster85*, the area resulting from a cluster analysis joining 85% of fixes in groups based on the nearest neighbour distance.

To describe the distribution of fixes within the ranges, we first estimated the following parameters: (i) *Units*, the number of independent clusters per range identified by the cluster 85% analysis; (ii) *Partial*, the proportion between the sum of the area of the separate clusters divided by the area of a single minimum convex polygon encompassing all of them. Then we conducted a Principal Component Analysis to summarise the information conveyed by *Units, Partial* and *Cluster85.* We used the resultant first component, called *Aggregation*, as an indicator of the level of aggregation of fixes within each range.

In ranges composed of several cluster units, these can be used simultaneously by moving constantly from one to the next, or sequentially by conducting very few movements between clusters. We calculated the proportion of movements within a single unit in relation to the total number of movements, as an index of sequential (high proportion) or simultaneous (low proportion) use of the cluster areas.

2.3. Habitat use

Each year, we mapped patches of scrub-steppe and fallow fields of the entire area used by each male. These land uses are considered the most suitable habitats for displaying, because the structure of the vegetation provides both conspicuousness and potential food resources (Martínez, 1994; Salamolard and Moreau, 1999). We used digital 1:5000 maps and Arcview 3.2 software (Environmental Systems Research Institute Inc., 1996) to estimate habitat use by calculating: (i) *Habitat C85*, the area (ha) of optimum display habitats within the clusters 85%; (ii) *%Habitat C85*, the proportion of area of optimum display habitats within the clusters.

2.4. Display rate

In 2003, we estimated the number of snort calls/min and the number of wing-flashes/min on 10 young adult or adult males (7 in Bellmunt and 3 in Belianes), in the peak of the mating season (from 5th until 23rd of May). We conducted 32 focal observation sessions (median: 3 sessions/individual) during the two hours after dawn or before sunset. During 20 min, we counted the number of snort calls (the basic display, consisting of a brief vocalisation uttered with a sharp toss of the head), and the number of wing-flashes (foot stamping, snort calling and finally a wing beating with the feet on the ground or jumping 20–100 cm) (Jiguet and Bretagnolle, 2001) performed by each male. Snort calls involve male–male interactions, while the wing-flash display is performed in the presence of females, supporting its inter-sexual function (Jiguet and Bretagnolle, 2001).

2.5. Statistical analyses

In order to avoid pseudoreplication caused by including individuals tracked during several years, we calculated the mean value for each home range descriptor and individual across years, and used every individual average as a sample unit (Hurlbert, 1984). We used the chi-square test to assess the assotiation between categorical variables. We checked for normality and homogeneity of analyzed variables by visual inspections of plots of residuals against fitted values. We used ANOVA for continuous variables showing a normal distribution, and Mann–Whitney *U* or Kruskall–Wallis tests for non-parametric variables. Individual differences on home range descriptors between consecutive seasons were analyzed by means of two-related sample *t*-test. To assess associations between display rates and home range descriptors we used two-tailed Spearman rank correlation coefficient. Statistical analyses were performed using SPSS v.12.0 (SPSS, 2001).

We used general linear mixed models (GLMM) with normal error and link identity function to assess which factors determined the size and *Aggregation* of home ranges. We checked for normality and homogeneity by visual inspections of plots of residuals against