Habitat selection by Little Bustard *Tetrax tetrax* in a cultivated area of France

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The Little Bustard *Tetrax tetrax* is one of the most endangered species in Europe. The French populations breeding in cultivated areas have suffered a drastic decline during the last 20 years and have disappeared from several locations. In a political context, where management agreements are developed under EU agri-environment regulations, it has become urgent to identify the ecological requirements of this species, to predict its response to environmental changes and to suggest management tools, such as promotion of beneficial farming practices. Despite the fact that many studies have described the habitat of the Little Bustard, quantitative data are lacking. We measured habitat use in relation to availability in a cultivated plain in western France in 1995. Habitat use by the Little Bustard differed significantly from habitat availability. Some crops, such as oilseed rape and cereals, were avoided. Sunflower crops were used by Little Bustard males, but were avoided by females. Females used set-aside to a greater extent than males. Habitat diversity was significantly greater around the centre of male activity than in randomly selected areas. These differences were found for areas within a radius of 100 and 200 m around centres of male activity but not for those with a 300 m radius. Vegetation height was one of the most important variables for calling males, as low vegetation is needed to detect and be detected by conspecifics. The most important variables for females are food resources and, to a lesser extent, predator avoidance. For these reasons, recent changes in land use on arable plains are likely to have different effects on males and females. Conservation measures should take into account these differences, the importance of the scale of measurement and should incorporate specific ecological requirements.

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The Little Bustard *Tetrax tetrax* has suffered a severe decline during this century in most areas of its range, and has disappeared from many European countries.1,2 It was classified as ‘Globally Threatened’3 and is currently considered as ‘Near Threatened’4 and ‘Vulnerable’ in Europe.5,6 Populations breeding in France show a very strongly negative trend. The French population was estimated at 7200 to 8500 calling males in 1978–79.7,8 The estimate fell to 1400 calling males in 1995 according to the national census co-ordinated by BirdLife-France (∼80% decline).9 Another national census made in 1996 confirmed a further decline of about 20% over one year.10 The main decline seems to be related to populations breeding in cultivated areas: the population breeding in the steppic area of the Crau, Southern France, seems to have been stable since 1972;10,11 in contrast, the remaining French population inhabiting cultivated plains declined dramatically from 7800 to 700 (90% decrease) in 18 years, and the breeding range has been similarly reduced.12

The main reasons suggested to explain Little Bustard decline and the fragmentation of its...
breeding range are loss or degradation of habitat through agricultural intensification, including increasing application of agro-chemicals.

For these reasons, a precise analysis of habitat use and selection on arable plains is necessary to identify the specific ecological requirements of the remaining Little Bustard populations breeding in such areas. This is becoming increasingly urgent given recent reforms of the Common Agricultural Policy (CAP) and management agreements developed under EU agri-environment regulations. The determination of the ecological requirements of the Little Bustard may enable us to predict its response to environmental changes and will help in the design of management measures such as beneficial farming practices.

Although most papers on the Little Bustard describe habitat use, few authors have assessed it quantitatively. The areas inhabited by the Little Bustard are known to vary in terms of the proportion of cultivated areas, types of crops and farming practices. Breeding habitats range from areas resembling the original steppe-like habitat, such as the extensive sheep and cattle pastures of Sardinia, Southern France, Iberian Peninsula and Central Europe, to cultivated areas in extensively farmed parts of Spain and more intensively cultivated plains in France.

Whereas male Little Bustards are relatively easy to observe, very few studies have considered habitat use by females. Moreover, due to their polygynous mating system, habitat choice by both sexes of Little Bustard is not necessarily similar. Males need good detectability in order to attract the highest number of females, whereas females have to find good protected areas to place their nests.

In this study, we analysed habitat use quantitatively in relation to availability by male and female Little Bustards on a cultivated plain in France, where the population is threatened. Territory selection by males was analysed in relation to habitat diversity at different spatial scales.

METHODS

Study area

The study was carried out on a cultivated plain in west central France, in the Poitou-Charentes region. This region holds the main remaining Little Bustard population breeding on the French arable plains (35–50% of the total French population), The study area, southern Deux-Sèvres (SDS) (46°10′N, 0°22′W), comprises 17 000 ha. Within this study area, a study site of 1700 ha, called ‘SB’ was monitored particularly intensively.

All observations of Little Bustard collected in SDS, where the density of Little Bustard ranged from 0.21 to 0.34 males/10 ha, were used for habitat selection analyses. All the other analyses pertain only to data collected in SB (density of 0.54 territorial males/10 ha). SDS is a gently undulating plain with calcareous soil and few remaining hedgerows. Except for small woods and villages all the land is farmed, more than 90% is used for cultivated crops and the remainder is covered by permanent pastures.

Reorganization of farmland during the last ten years has led to field enlargement, drastic reduction of hedgerows and the decline of grasslands in favour of cultivated fields. For example, changes in the land cover of SB between 1970 and 1988 (SCEES-INSEE), include a decline in the area used for grasslands or hay fields (from 49 to 20%) while cereal land cover remained relatively stable (from 46 to 44%). The area used for new crops (such as flax, peas, oilseed rape and sunflower), increased from 2% in 1979 to 35% of the land surface in 1988. The region of SDS has been identified as an Important Bird Area, holding significant numbers of breeding Montagu’s Harrier Circus pygargus, Stone Curlew Burhinus oedicnemus and Little Bustard.

Data collection

Habitat availability (percentage of surface area) was estimated by mapping the vegetation cover of SB in May–June 1995. Habitats were assigned to one of the following categories: pasture, clover and alfalfa, ryegrass, set-aside (1-year or long-term set-aside fields), cereals, peas, flax, maize, sunflower, oilseed rape, ploughed fields (sown with maize or sunflower from May), vineyard and others (woods or gardens).

The whole study area (SDS) was intensively surveyed from March to July 1995. Birds were
located from the tight network of tracks that criss-cross the study area. For each observation made throughout the study area, exact location, sex (according to plumage), male behaviour (displaying or not displaying) and crop type were recorded. Additionally, at SB, individual males were observed regularly (one or two times per week) throughout the main displaying period, i.e. 15 April to 15 June in both 1994 and 1995. The sum of locations for each male in 1995 was considered as its ‘territory’ (4–19 observations made for each male).

Invertebrate availability in each crop type was assessed in June by means of three pitfall traps set for six days in randomly chosen fields.

**Data analysis**

We first studied habitat selection by comparing the habitats used by three different classes of Little Bustards (female-like plumage, displaying males and males not displaying) with the habitat availability in the SB sample area. To avoid biases caused by differential observation times among males, we calculated the percentage of sightings in each habitat for each individual bird (assuming that observations in the same territory or site belonged to the same individual) and then averaged the results for all individuals monitored. For females, as they are more mobile and could not be identified individually, all observations were considered as independent observations.

Secondly, in SB, habitat composition of circles around the centre of activity of territorial males \((n = 9)\) was compared with the habitat composition of circles centred on randomly selected points \((n = 9)\). These circles were termed ‘territory units’ and ‘random units’. Comparisons were made at three different scales, with circles of 100 m (as in a recent study in Spain\(^\text{16}\)), 200 m and 300 m radius. In each unit, we recorded the number of crop types present in the different categories. We also counted the numbers of fields, and of crop units (where adjacent fields with the same crop type would be considered as the same unit). The Shannon–Wiener index of diversity \((H' = \sum_{i=1}^{k} p_i \log p_i)\) was calculated from the proportion of crop type units \((p_i)\). Finally, the fields used by the territorial males were measured and compared with the mean size of other fields of each crop type in the study site. Statistical analyses were performed using the Logitheq statistical package.

**RESULTS**

**Habitat selection**

Overall, the mean proportion of sightings of the three classes of Little Bustard (displaying males, males not displaying, females) in different habitats differed significantly from the proportion of habitats available in the study area \((\chi^2 = 1526, 1518, 1549, \text{respectively}; P < 0.001)\). Moreover, we calculated a Kendall rank order correlation coefficient \((T)\) to assess the degree of association between habitat rankings of bustard observations (in terms of percentage use) and those in the study area (in terms of percentage availability) for each of the three classes of bustards (Table 1). The correlations between habitat rankings were not significant for any of these classes (Table 1), which shows that the bustards’ use of habitat differs significantly from random. Whereas cereals represent 45% and rape 11% of habitat available, few or no Little Bustards were observed in these crops (Table 1). In contrast, alfalfa/clover and set-aside fields were used by the different classes of Little Bustard (from 16.4% to 42.9%) to a higher degree than their availability in the study area would indicate (Table 1).

We also calculated Kendall’s coefficient of concordance \((W)\) to evaluate the degree of agreement in habitat use among the three classes of bustards. There was a significant concordance between them \((W = 0.66, k = 3, n = 10, P < 0.05)\). However, the actual proportions of observations (rather than the rankings) differed among classes. Alfalfa/clover fields were similarly used by all classes of Little Bustard (Table 1). In contrast, the females used set-aside fields more than males (Table 1), whereas sunflower fields seemed to be preferred only by males (either displaying or not displaying), and females used this crop less frequently (Table 1).

**Male territory choice**

Fields of alfalfa, set-aside, flax and sunflower seemed to be more frequently represented in the territorial units of displaying males than in...
random units, whereas the opposite was found for cereals, maize and oilseed rape. The habitat rankings (in terms of percentage surface) differed significantly between territory and random units at all scales (radii 100, 200 and 300 m), as seen by the lack of concordance between them (Spearman test, \( r_s = 0.61, r_s = 0.71 \) and \( r_s = 0.69, P < 0.05; \) Kendall coefficient = 0.57, 0.62 and 0.59, respectively). The number of crop type units and the Shannon index of diversity were significantly higher in territory units than in random units for circles of 100 and 200 m radius, but territory and random units did not differ at a radius of 300 m (Table 2). The number of fields (and thus average field size) was significantly higher only in the circles of 100 m radius (Table 2). Whereas mean sizes of sunflower and flax fields were very similar in territory and random units, pasture fields tended to be larger in territory units than random units (Table 3).

By monitoring territorial males in two years, we found that the unmarked birds used areas that overlapped between years (Fig. 1).

Prey availability and crop type
Alfalfa, clover and oilseed rape fields harboured the highest number of invertebrates (also a high number of taxa). The highest diversity of invertebrates (in terms of size and number of taxa) was found in pastures, flax and set-aside fields (Table 4).

DISCUSSION
Male territory selection
The main considerations in territory selection are related to mate acquisition, displaying sites and defendability. For polygamous male

Table 1. Mean percentage of sightings of Little Bustard in each crop category, and overall habitat composition (percentage of surface) of study area SB, 1995. A total of 29 calling males was sighted in 93 observations, 45 males not displaying in 79 observations and 35 females in 35 observations.

<table>
<thead>
<tr>
<th>Crop type</th>
<th>Calling males (%)</th>
<th>Males not displaying (%)</th>
<th>Females (%)</th>
<th>Habitat (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pasture</td>
<td>2.61</td>
<td>2.22</td>
<td>2.86</td>
<td>4.64</td>
</tr>
<tr>
<td>Alfalfa and clover</td>
<td>26.80</td>
<td>17.19</td>
<td>25.71</td>
<td>2.03</td>
</tr>
<tr>
<td>Ryegrass</td>
<td>0.58</td>
<td>11.93</td>
<td>2.86</td>
<td>4.06</td>
</tr>
<tr>
<td>Set-aside</td>
<td>16.38</td>
<td>20.37</td>
<td>42.86</td>
<td>3.19</td>
</tr>
<tr>
<td>Cereal</td>
<td>0.00</td>
<td>2.22</td>
<td>5.71</td>
<td>45.22</td>
</tr>
<tr>
<td>Peas</td>
<td>0.69</td>
<td>8.89</td>
<td>5.71</td>
<td>2.61</td>
</tr>
<tr>
<td>Flax</td>
<td>2.65</td>
<td>0.44</td>
<td>8.57</td>
<td>4.06</td>
</tr>
<tr>
<td>Maize</td>
<td>13.49</td>
<td>3.32</td>
<td>0.00</td>
<td>7.25</td>
</tr>
<tr>
<td>Sunflower</td>
<td>36.82</td>
<td>33.41</td>
<td>5.71</td>
<td>15.65</td>
</tr>
<tr>
<td>Oilseed rape</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>11.31</td>
</tr>
</tbody>
</table>

Kendall coefficient (T) –0.227 –0.227 –0.477
Spearman coefficient –0.305 –0.317 –0.523

Table 2. Statistics of variables in territory units used by calling males of Little Bustard and in random units of the same surface. Each sample unit was a circle with a radius of 300, 200 or 100 m.

<table>
<thead>
<tr>
<th>Unit radius (m)</th>
<th>Variable</th>
<th>Territory units (N = 9)</th>
<th>Random units (N = 9)</th>
<th>Mann–Whitney U</th>
</tr>
</thead>
<tbody>
<tr>
<td>300</td>
<td>Number of fields</td>
<td>17.2 ± 4.3</td>
<td>16.0 ± 4.9</td>
<td>32, ns</td>
</tr>
<tr>
<td></td>
<td>Number of crop type units</td>
<td>10.0 ± 4.2</td>
<td>7.4 ± 3.1</td>
<td>23.5, ns</td>
</tr>
<tr>
<td></td>
<td>Index of diversity</td>
<td>2.2 ± 0.3</td>
<td>2.0 ± 0.3</td>
<td>36, ns</td>
</tr>
<tr>
<td>200</td>
<td>Number of fields</td>
<td>9.8 ± 2.6</td>
<td>10.0 ± 2.8</td>
<td>39.5, ns</td>
</tr>
<tr>
<td></td>
<td>Number of crop type units</td>
<td>7.3 ± 2.3</td>
<td>5.0 ± 2.1</td>
<td>18, P ≤ 0.05</td>
</tr>
<tr>
<td></td>
<td>Index of diversity</td>
<td>2.2 ± 0.1</td>
<td>1.7 ± 0.4</td>
<td>16, P ≤ 0.05</td>
</tr>
<tr>
<td>100</td>
<td>Number of fields</td>
<td>5.8 ± 1.4</td>
<td>4.5 ± 1.7</td>
<td>21, P ≤ 0.05</td>
</tr>
<tr>
<td></td>
<td>Number of crop type units</td>
<td>4.7 ± 1.2</td>
<td>3.0 ± 1.5</td>
<td>14, P ≤ 0.01</td>
</tr>
<tr>
<td></td>
<td>Index of diversity</td>
<td>1.8 ± 0.3</td>
<td>1.3 ± 0.4</td>
<td>18, P ≤ 0.05</td>
</tr>
</tbody>
</table>

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Habitat selection by Little Bustard

Little Bustards to attract many females, they must be easily detectable and make use of a variety of acoustic and visual signals. Thus, the criteria that define good displaying sites are good visibility, defendability and easy rapid detection of prelaying females.

The main cues which seem to operate in the selection of calling places are probably the physical features of the site, particularly the height of vegetation. Crop height is likely to be more important than crop type. In our study, calling males were more often observed in crops without vegetation, such as ploughed fields, or with very low and scattered vegetation, such as sunflowers in the early stages of growth, and in low vegetation, such as set-aside. Unusual locations with low

Table 3. Mean field sizes for the main crops used by the territorial males (n = 9) of Little Bustard and available in the study site SB, 1995.

<table>
<thead>
<tr>
<th>Crop type</th>
<th>Mean size of field used by territorial male</th>
<th>Size of fields not used by territorial males</th>
<th>Mann–Whitney U</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sunflower</td>
<td>3.4 ± 2.1 (19)</td>
<td>3.6 ± 2.8 (41)</td>
<td>375, ns</td>
</tr>
<tr>
<td>Flax</td>
<td>4.0 ± 2.5 (4)</td>
<td>4.8 ± 3.1 (10)</td>
<td>19, ns</td>
</tr>
<tr>
<td>Set-aside</td>
<td>5.5 ± 5.1 (4)</td>
<td>3.0 ± 3.1 (10)</td>
<td>15.5, ns</td>
</tr>
<tr>
<td>Alfalfa and clover</td>
<td>3.4 ± 2.4 (7)</td>
<td>2.8 ± 1.7 (16)</td>
<td>52.5, ns</td>
</tr>
<tr>
<td>Pastures</td>
<td>2.7 ± 1.3 (6)</td>
<td>1.7 ± 1.3 (30)</td>
<td>48, P ≤ 0.05</td>
</tr>
</tbody>
</table>

Results are mean ± se with n in brackets.

Figure 1. Locations of the territories of Little Bustard males in 1994 and 1995, in the study site SB. – – – –, Territories in 1994; ––––––, territories in 1995.

Table 4. Number of invertebrates caught per pitfall trap, Shannon index (invertebrate size class diversity) and number taxa (mean ± se).

<table>
<thead>
<tr>
<th>Crop type</th>
<th>Number of invertebrates</th>
<th>Shannon index</th>
<th>Number of taxa</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pasture</td>
<td>55.20 ± 27.95</td>
<td>0.83 ± 0.16</td>
<td>6.40 ± 1.14</td>
<td>5</td>
</tr>
<tr>
<td>Alfalfa and clover</td>
<td>88.00 ± 12.49</td>
<td>0.57 ± 0.10</td>
<td>5.67 ± 0.58</td>
<td>3</td>
</tr>
<tr>
<td>Ryegrass</td>
<td>69.14 ± 33.15</td>
<td>0.63 ± 0.15</td>
<td>5.00 ± 1.00</td>
<td>7</td>
</tr>
<tr>
<td>Set-aside</td>
<td>24.50 ± 12.02</td>
<td>0.68 ± 0.00</td>
<td>5.50 ± 0.71</td>
<td>2</td>
</tr>
<tr>
<td>Cereal</td>
<td>39.07 ± 32.35</td>
<td>0.62 ± 0.16</td>
<td>4.86 ± 1.17</td>
<td>14</td>
</tr>
<tr>
<td>Peas</td>
<td>60.50 ± 64.35</td>
<td>0.50 ± 0.02</td>
<td>4.50 ± 0.71</td>
<td>2</td>
</tr>
<tr>
<td>Flax</td>
<td>70.33 ± 53.41</td>
<td>0.69 ± 0.07</td>
<td>5.67 ± 0.58</td>
<td>3</td>
</tr>
<tr>
<td>Maize</td>
<td>24.67 ± 23.46</td>
<td>0.65 ± 0.19</td>
<td>4.67 ± 1.53</td>
<td>3</td>
</tr>
<tr>
<td>Sunflower</td>
<td>55.14 ± 30.73</td>
<td>0.66 ± 0.12</td>
<td>5.43 ± 0.94</td>
<td>14</td>
</tr>
<tr>
<td>Oilseed rape</td>
<td>159.08 ± 96.57</td>
<td>0.63 ± 0.16</td>
<td>5.69 ± 1.38</td>
<td>13</td>
</tr>
<tr>
<td>Ploughed fields</td>
<td>42.50 ± 12.02</td>
<td>0.57 ± 0.12</td>
<td>4.50 ± 0.71</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>72.81 ± 66.04</td>
<td>0.64 ± 0.15</td>
<td>5.32 ± 1.14</td>
<td>68</td>
</tr>
</tbody>
</table>

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vegetation, such as potato fields, have been cited. Many studies have recommended pasture as a favourable habitat because of its similarity to the original steppe-like habitat of this species, but these studies were conducted in extensive pasture land. In our study, this habitat was not selected by Little Bustards.

Soon after Little Bustards arrive at their breeding areas, the oilseed rape and maize get very high (80–100 cm); this is the most likely explanation for these crops being avoided. That sunflowers, only recently cultivated, were so highly preferred by males, also highlights the major role of vegetation height. Other studies conducted in the same area demonstrated that, while sunflowers are very often selected by calling males, this crop is not used when the vegetation exceeds 30–40 cm in height, when males switch to other crops.

A certain level of site fidelity was found among the males between the two years of the study, as reported in Portugal. This might be related to the polygamous mating system of the Little Bustard. In our study area, males have been observed displaying in the same locations, even though the land cover was greatly changed between the two years. For this reason, findings on habitat selection of Little Bustard males in highly cultivated landscapes, like ours, have to be considered with caution.

Effect of food and predation risk

Food could be an important constraint for some Little Bustards. Although alfalfa and one-year set-aside represent a very small proportion of the land cover, they are selected by all Little Bustard classes. The importance of alfalfa has been reported in other areas by empirical observation (for nesting sites, at certain seasons and in quantitative studies) as has been reported for the Great Bustard Otis tarda. Vegetable matter appears to make up most of the diet prior to the autumn migration in France. The preference for alfalfa could be explained by its high nutritive value and digestibility. Birds observed in alfalfa were mainly recently arrived groups, which may be restoring their body reserves after the spring migration. They included females, whose energy requirements are high during the prelaying period.

The preference for alfalfa by all classes of Little Bustard could also be linked with the invertebrate abundance in that habitat being higher than in other cultivated crops such as cereals, maize and sunflower. Invertebrates constitute a large part of the diet of Little Bustards in spring and the young are fed mainly upon insects, especially large species such as grasshoppers, in the first days after hatching. The selection of set-aside fields found in this study has been recorded by other authors. The diversity of invertebrates in this crop is also high, but a more important reason for this preference might be the higher floristic diversity of set-aside and fallow lands, providing a better supply of suitable plant food.

Except for pastures, the mean field size selected by calling males was not significantly larger than the other fields of the same crops in the study area. Boutin indicated that field sizes should be larger than 2 ha (as was the case in this study) because, as field area increases, distances between birds and field borders also increase, reducing the risk of mammalian predation and human disturbance. We could therefore expect calling males to prefer the largest fields. However, it has been suggested that predation would be a less important constraint on territory selection than mate acquisition and displaying sites. Further, as the spatial distribution of Little Bustard males in extensive farming areas in Spain shows no influence from sources of disturbance such as villages and roads, we believe it is unlikely that it plays a major role in territory selection.

Sex-related differences in ‘mobility’

Male Little Bustards need to stay in their calling place as long as possible, to increase the probability of attracting potential mates and to defend this area from other males. Consequently, their movements are reduced. Areas are selected where both displaying and feeding can be carried out, either in the same field or in fields which are close together. In
intensive farming areas, cultivated plants have a very high growth rate during spring. We noticed that males were located in areas of greater crop diversity than other, randomly chosen, units. These sites probably offered suitable habitats for the whole courtship period. The importance of diversity has been noted in other studies and selection for highly diverse areas has been demonstrated with the same methodology applied in Spain (radius 100 m). However, the importance of this variable could depend on the scale of measurements used. Crop unit diversity was relevant only in the vicinity of the calling places: at a radius of less than or equal to 200 m. A study in Spain, with unit areas enlarged to 75 ha, found a negative relationship between calling male density and the crop diversity.

In contrast, females are more mobile than males during the courtship period and are thus able to place their nests several kilometres outside the males’ territories. We could expect that females would be located in less disturbed foraging areas, and probably in the vicinity of the nest site. Moreover, nest sites should be located in areas with less risk of predation and as close as possible to the foraging areas for providing plentiful and easily handled food for the newly hatched nidifugous chicks. Set-aside fields provide high floristic and invertebrate diversity, and protection due to the vertical heterogeneity of the vegetation which aids in predator detection. These factors could explain the strong selection of set-aside fields by females. One recent study, in a nearby area, confirms the use of set-aside fields by females for nesting.

Conclusion

Changes in agricultural practices and land cover have probably had different effects on habitat selection for females and males. The transformation of permanent crops into new cultivated crops, such as sunflower, is not likely to affect the males’ choice of calling places unless this change reduces crop diversity.

Females, however, and to a lesser extent males engaged in activities other than displaying, are likely to be severely affected by the changes in land use, with reduction of permanent crops, especially alfalfa and set-aside, which could be essential as nesting places.

This study highlights the importance of the scale of measurements to detect biologically significant variables and is the first to show sex-related differences in habitat selection by the Little Bustard. We hope that these results will be useful for subsequent studies and plans for the conservation of this species in arable areas.

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