

Sex-dependent habitat selection in a high-density Little Bustard *Tetrax tetrax* population in southern France, and the implications for conservation

PIERRICK DEVOUCOUX,^{1,2*}  AURÉLIEN BESNARD² & VINCENT BRETAGNOLLE¹

¹Centre d'Études Biologiques de Chizé, UMR 7372, CNRS & Université de La Rochelle, 79360 Villiers-en-Bois, France

²PSL Research University, CEFE, UMR 5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, 1919 route de Mende, 34293 Montpellier, France

Conservation measures often rely on habitat management, so knowledge about a species' habitat use is a prerequisite for effective conservation planning. The Little Bustard *Tetrax tetrax*, a medium-sized bird native to the Palaearctic steppes and today found in extensively farmed habitats, is a threatened species. Its population experienced a 94% decline in farmland habitats in France between 1982 and 1996, and populations all over Europe have suffered equally sharp declines. Due to this steep negative trend, this species has been the subject of a number of habitat selection studies in order to develop relevant conservation measures based on its habitat requirements. In this study, we investigated the habitat selection of a range of habitat types by both sexes and at two nested spatial scales: plot scale and landscape scale. In addition, we analysed intra-specific social interactions by incorporating conspecific density in the statistical models of habitat use. The study was conducted on a very high-density population, perhaps the highest ever recorded for this species at around 50 Bustards per 100 ha of suitable habitat. Our methodology combined two field approaches (point counts and quadrat counts). The findings showed rather limited sexual dimorphism in terms of habitat selection at a local scale, with only vegetation height differing between sexes at a micro-habitat scale, no selection at landscape scale, and a prevailing role of social factors at both scales. The implications for future conservation strategies in relation to population density and landscape composition are discussed.

Keywords: buffer effect, habitat use, landscape, social factors, spatial scale.

Although conservation usually targets species, conservation measures actually often depend on habitat management (Sutherland & Hill 1995, Ausden 2007). Thus the habitat use of species of conservation concern is the cornerstone of most species-orientated conservation strategies (Simberloff 1998). A thorough understanding of a species' habitat selection is thus essential for planning sound habitat-management initiatives (Morris 2003, Ruckstuhl & Neuhaus 2005, Morrison *et al.* 2006). Theoretical considerations suggest that the spatial distribution of individuals is driven not only

by the distribution of resources (mainly food, shelter and nesting sites) (Fretwell & Lucas 1969) but, given that individuals are usually unequal competitors (Sutherland 1996), also by individual interactions such as competition (Svårdson 1949, Martin 1993, Petit & Petit 1996), intra-specific attraction (Danchin *et al.* 1998, Forsman *et al.* 1998) and interactions resulting from resource depletion (Martin 1993, McCollin 1998).

Habitat use is defined as the way individuals use habitats to meet their biological needs (Block & Brennan 1993). Individual characteristics such as sex, age, experience and physical condition, all of which underlie different needs or competitive ability, influence behaviour and therefore habitat

*Corresponding author.

Email: pierrick.devoucoux@gmail.com

selection. Sex in particular often plays a crucial role, as sexual dimorphism results in different resource use or sex-dependent behaviour (e.g. Evans & Gates 1997, Trebatická *et al.* 2008). Habitat selection is a hierarchical process that takes place across spatial and temporal scales (Jones 2001). In particular, when species require more than one resource to complete their life cycle, their abundance is predicted to be higher when both (or more) resources are present (Dunning *et al.* 1992), the so-called landscape complementation effect (Ens *et al.* 1992, Barbaro *et al.* 2008). As habitat selection is a scale-dependent process and studies of this process are based on comparing 'used' and either 'unused' or 'available' habitats (Jones 2001), the scale on which an analysis is carried out may affect 'used' vs. 'available' habitats. An unused habitat at micro-scale may become a used habitat at macro-scale simply because habitats may be mixed on a large scale and are thus more likely to include favourable habitats, particularly in patchy mosaic habitats such as farmland. In the latter habitats, human land use has dramatically modified both landscape structure and habitat quality (Wiens 1986, 1989, Newton 1998). In these contexts, the distribution of individuals may depend not only on the quality of each habitat patch but also on the spatial configuration of the patches (Pope *et al.* 2000, Soderstrom & Part 2000). Habitat selection is therefore influenced by a number of variables: landscape structure and heterogeneity, resource distribution and abundance, and also social behaviour and sex (Jones 2001, Tarjuelo *et al.* 2013). Little evidence has been obtained on how these various factors interact in the habitat selection process (although see Oehlers *et al.* 2011, Roever *et al.* 2014).

The Little Bustard *Tetrax tetrax* is a medium-sized bird native to the Palearctic steppes that is now found in extensively managed agricultural habitats (Wolff *et al.* 2002, García la Morena *et al.* 2006). Since 1970, this species has disappeared from at least 10 European countries; its population experienced a 94% decline in Western and Northern France between 1982 and 1996 (Suárez *et al.* 1996, Jolivet & Bretagnolle 2002, Inchausti & Bretagnolle 2005), a situation that contrasts with the increasing population in Southern France. The decline of the Little Bustard results from a combination of factors: direct causes include a marked decrease in invertebrate food resources (in part due to the use of agricultural chemicals) as well as

nest destruction during harvesting (which can destroy eggs, clutches, and kill broods or even females; Inchausti & Bretagnolle 2005). These direct effects are amplified by habitat simplification, loss of grasslands and the mechanization of agriculture (De Juana *et al.* 1993, Bretagnolle *et al.* 2011). Due to this species' precipitous decline and unfavourable conservation status, the habitat use of the Little Bustard has been the focus of many recent studies (see Table 1 for a review).

The Little Bustard uses an 'exploded lek' mating system (Jiguet *et al.* 2000, Jiguet & Bretagnolle 2014): displaying males defend small territories visited by females for mating purposes only, and females incubate and raise chicks alone nearby, often close to breeding males (Jiguet *et al.* 2002, Morales *et al.* 2013, Silva *et al.* 2014). Habitat selection is therefore expected to be strongly sex-dependent (Morales *et al.* 2008). As males display in open habitats in order to be visually (and acoustically) detected by females, most studies on this species' habitat selection have been conducted on males. However, conservation measures actually target breeding females (Bretagnolle *et al.* 2011). Thus an understanding of whether (and how) habitat selection patterns are sex-dependent in this species is of critical interest for conservation purposes. In the few studies available to date on both sexes, strong sexual dimorphism has been detected in both macro- and micro-habitat selection (Morales *et al.* 2008, Faria *et al.* 2012a, Table 1). Other studies have additionally detected landscape effects on habitat selection in Little Bustards (Wolff *et al.* 2001, Santangeli & Dolman 2011, Table 1), but it is not clear which landscape features, and at what scale, affect which sex. Lastly, only one study has investigated the role of conspecific attraction between sexes in the habitat selection of the Little Bustard (Tarjuelo *et al.* 2013), despite its acknowledged role in the closely related Great Bustard *Otis tarda* (Alonso *et al.* 2004, Osborne *et al.* 2007).

Our aim in this study was to address these gaps by simultaneously investigating the habitat use of both sexes at two spatial scales: the micro-habitat scale (1 ha) and the macro-habitat scale (approximately 20 ha). Additionally, in the statistical models of habitat use, we further incorporated conspecific density as a proxy of social interaction, as well as its interaction with habitat use. Another unique feature of our study is that it was conducted on a population in which individual density

Table 1. Synthesis of habitat selection studies.

	Males		Females	
	Selected for	Selected against	Selected for	Selected against
Landscape heterogeneity/diversity	Campos and López (1996), Martínez (1994), Morales <i>et al.</i> (2005, 2006, 2014), Salamolard and Moreau (1999), Santangeli and Dolman (2011), Wolff <i>et al.</i> (2001, 2002)	McMahon <i>et al.</i> (2010), Moreira <i>et al.</i> (2012)		
Landscape composition				
% of grassland, pastures, fallows, alfalfa and legumes	Jiguet <i>et al.</i> (2002), Morales <i>et al.</i> (2005), Moreira <i>et al.</i> (2012), Santangeli and Dolman (2011), Wolff <i>et al.</i> (2001, 2002)	Morales <i>et al.</i> (2014) Moreira <i>et al.</i> (2012)	Jiguet <i>et al.</i> (2002), Wolff <i>et al.</i> (2002)	
% of ploughed soil				
% of irrigated crops				
Field land use				
Cereals	Delgado and Moreira (2000)	Delgado <i>et al.</i> (2010), Martínez (1994), Salamolard and Moreau (1999)		Morales <i>et al.</i> (2013), Salamolard and Moreau (1999)
Grassland, pastures, fallows, alfalfa and legumes, set-asides	Delgado and Moreira (2000), Faria <i>et al.</i> (2012b), Martínez (1994), McMahon <i>et al.</i> (2010), Morales <i>et al.</i> (2006), Salamolard and Moreau (1999), Santangeli and Dolman (2011), Silva <i>et al.</i> (2010), Wolff <i>et al.</i> (2001)		Faria <i>et al.</i> (2012b), Jiguet <i>et al.</i> (2002), Morales <i>et al.</i> (2013), Salamolard and Moreau (1999), Tarjuelo <i>et al.</i> (2013)	
Ploughed soil		Delgado <i>et al.</i> (2010), Martínez (1994) Silva <i>et al.</i> (2010)		Morales <i>et al.</i> (2013), Tarjuelo <i>et al.</i> (2013) Morales <i>et al.</i> (2013)
Ligneous Field size	Faria <i>et al.</i> (2012b), McMahon <i>et al.</i> (2010), Salamolard and Moreau (1999), Silva <i>et al.</i> (2010) Moreira (1999)		Silva <i>et al.</i> (2014)	
Vegetation height		Campos and López (1996), Martínez (1994), Morales <i>et al.</i> (2008), Salamolard and Moreau (1999), Santangeli and Dolman (2011), Silva <i>et al.</i> (2010)	Faria <i>et al.</i> (2012b), Morales <i>et al.</i> (2008), Salamolard and Moreau (1999)	Silva <i>et al.</i> (2014)
Vegetation height heterogeneity	Silva <i>et al.</i> (2010), Morales <i>et al.</i> (2008)			Silva <i>et al.</i> (2014), Morales <i>et al.</i> (2008)
Vegetation cover	McMahon <i>et al.</i> (2010), Santangeli and Dolman (2011)			Morales <i>et al.</i> (2008), Moreira (1999)

(Continued)

Table 1. (Continued)

	Males		Females	
	Selected for	Selected against	Selected for	Selected against
Floristic richness	Faria <i>et al.</i> (2012a), Salamolard and Moreau (1999)		Faria <i>et al.</i> (2012a), Salamolard and Moreau (1999)	
Arthropod availability	Faria <i>et al.</i> (2012a), Salamolard and Moreau (1999), Traba <i>et al.</i> (2008)		Faria <i>et al.</i> (2012a), Jiguet <i>et al.</i> (2002), Salamolard and Moreau (1999) Wolff <i>et al.</i> (2002)	
Surrounding male density	Morales <i>et al.</i> (2014)		Faria <i>et al.</i> (2012b), Jiguet <i>et al.</i> (2002), Morales <i>et al.</i> (2013), Silva <i>et al.</i> (2014), Tarjuelo <i>et al.</i> (2013)	
Presence of opposite sex	Morales <i>et al.</i> (2014)			

may be the highest ever recorded (approximately 50 Bustards per 100 ha) – a factor that is likely to increase social interactions and therefore enhance the detection of their effect. In light of our results, we discussed the impact of density on habitat selection in this species (Delgado *et al.* 2010, Morales *et al.* 2014) and its consequences on conservation strategies for the Little Bustard, and possibly other species with similar habitat preferences.

MATERIALS AND METHODS

Study area

Our study area was located within the Costière Nimoise, a stony, sandy plateau 40 km long located near the city of Nîmes in the Mediterranean region of southern France (Fig. 1a). The area is used for agriculture and is dominated by open landscape and vineyards, with a mosaic of mixed crops, fallow land and unfarmed land (Table S1). The median field size is 1.16 ha (range = 0.01–36.32 ha, mean = 1.77, $n = 8021$). Since 2006, 13 377 ha of the plateau has been designated as a Special Protection Area (SPA) (Natura 2000 site FR9112015), consisting of seven unconnected subareas of agricultural land between villages and roads (Fig. 1a,b,e). It was designated as a protected area mainly because of the presence of the population of Little Bustards.

Little Bustard surveys: transects and quadrats

Given that male Little Bustards are very easy to detect, whereas females are notoriously more difficult to spot and do not call as males do (Morales *et al.* 2008, Tarjuelo *et al.* 2013), we used two types of surveys: one designed to investigate simultaneously male and female densities at a local scale, and the other designed to investigate only males at a landscape scale (the SPA).

In the local-scale survey, we used a ‘flush count’ protocol, which is the only method that allows an accurate count of Little Bustard females (Wolff *et al.* 2002). We randomly chose 582 quadrats (Fig. 1b) in habitat categories that may be used by females (excluding only buildings, roads, forest, water and bare-ground vineyards; Table S1). Using the randomness function in GIS software (ESRI® ARCMAP™ 10.3; Environmental Systems Research Institute, Redlands, CA, USA), an initial sampling

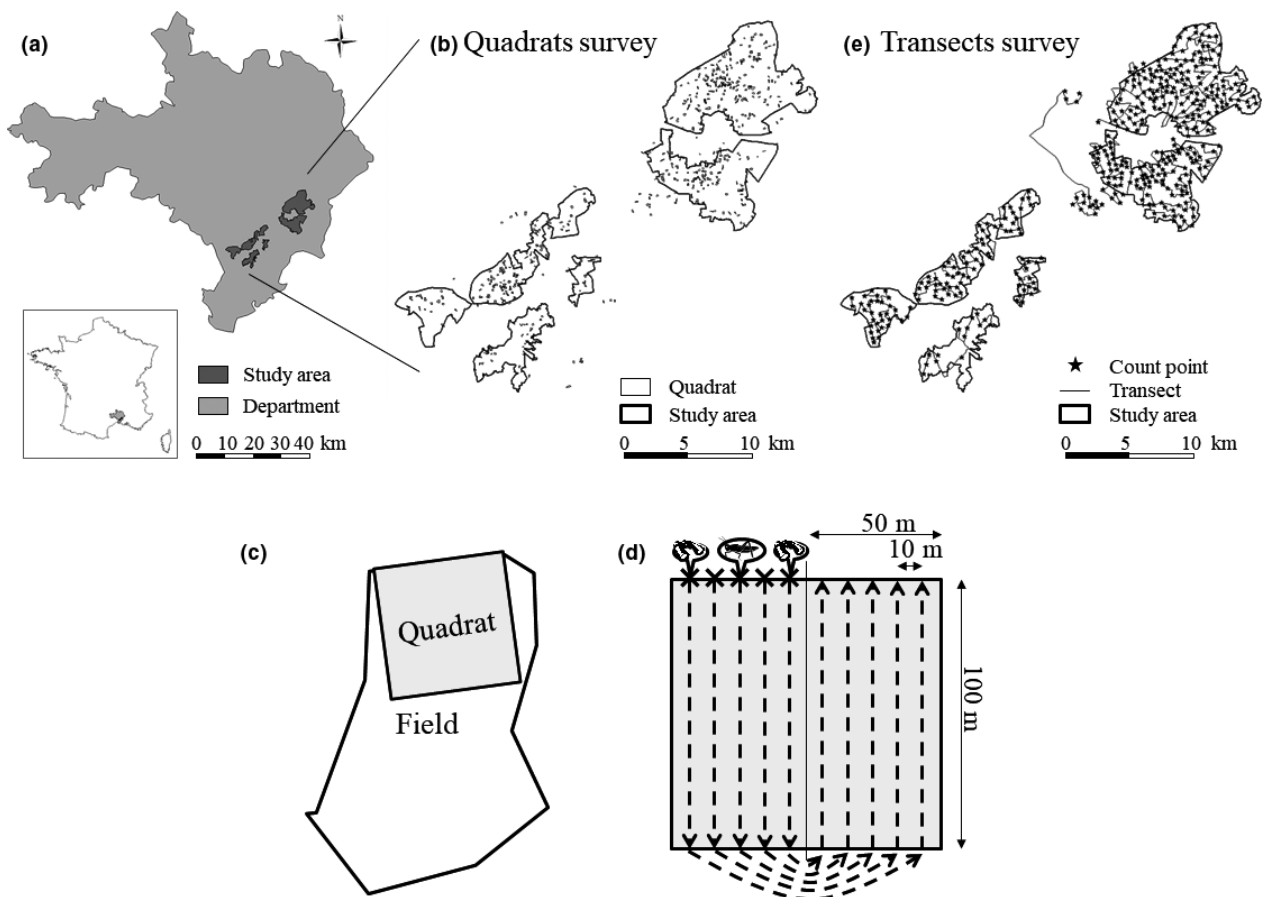


Figure 1. (a) Location of the study area in southern France and the study area within the Gard department. (b) Complete map of all quadrats prospected in 2011 and 2012. (c) Example of a quadrat (in grey) within a field. (d) How quadrats were prospected (transects along dotted lines) by observers (each cross represents an observer; binoculars represent ornithologist observers; a grasshopper represents an observer counting orthopterans). (e) Complete map of transect surveys with count points.

of at least 30 quadrats per habitat type were selected whatever the total surface area of the habitat category in the studied area (see below for habitat description). However, due to logistical constraints, in some cases fewer than 30 quadrats were available (Table S1). Each quadrat was located in a different field (no quadrat overlapped two different fields, see Fig. 1c). In some cases (12% of the quadrats, $n = 65$), we had to shift a quadrat to its closest neighbouring field because the selected quadrat was not accessible (e.g. restricted access or the presence of aggressive cattle, modification of land use (cutting, ploughing) or access denied by landowner (especially cereal fields where walking would have had an impact)). At the landscape scale, we evaluated the proportions of different habitat types in a 250-m buffer zone around the quadrat centroid. As land use had

only been recorded within the SPA, the buffer zones for quadrats near the edge of the SPA resulted in large areas of unknown land use. Quadrats for which $< 75\%$ of the land use was known were thus excluded, leading to an analysis of 488 quadrats. The mean size of a sampled field was 3.21 ha (range = 0.28–36.32 ha). The planned standardized quadrat area was around 1 ha, consisting of a 100×100 m square. Because of readjustments due to actual field shape on the ground, the effective mean quadrat area was 0.84 ha. A small quadrat size was deliberately chosen, both to be representative of field size in the area (median = 1.17 ha) and to avoid double counts (flushed birds may land nearby and be flushed out again). A complementary telemetry study in the area showed that males preferentially use a single field (mean = 1.88, median = 1, range = 1–5

fields) to display during the breeding season (study based on $n = 27$ individuals in 2012, P. Devoucoux unpubl. data). The total prospected area including all quadrats was 409.51 ha, i.e. 3.06% of the SPA.

Each quadrat was searched by five people walking side by side at the same speed, at a distance of 10 m from each other. The observers searched two consecutive transects 50 m in width (i.e. a 100-m transect if the quadrat was 1 ha: see Fig. 1d). The walking speed was high in order to reduce disturbance as much as possible. When a Bustard was flushed out, its precise location was recorded by GPS, and its age and sex were determined by one of two experienced observers with 10 \times binoculars who stood at either end of each walking line. As 1-year-old males can be difficult to distinguish from females (see Jiguet & Wolff 2000 for criteria), in case of doubt, female-like birds were discarded from the analysis (four individuals). To avoid double counts, flying birds were monitored until they were considered out of the surveyed quadrat. The sampling of the quadrats was performed from 07:00 to 12:00 h and from 15:00 to 20:00 h, avoiding high temperatures and harsh weather, which can be detrimental to unprotected eggs and chicks. In 2011, 292 quadrats were sampled, and in 2012, 290 were sampled. A quadrat was sampled in 1 year only (i.e. no quadrat was monitored over 2 years). The fieldwork was carried out twice a week during the female nesting period: either from 12 May to 21 June 2011 or from 23 May to 22 June 2012.

For the landscape-scale survey, we used a large-scale census of displaying males using transect counts (see Wolff 2001 for a general description of this method for this species). These censuses took place once per breeding season, from 2 to 11 May 2011 and from 3 to 12 May 2012, when displaying males are very demonstrative and easy to count. They were conducted in optimal weather conditions (without rain or wind). All useable roads or paths were predefined so that a transect of about 16 counting points occurring on average every 500 m could be easily covered in 3 h (Fig. 1e). Calling males were located by ear or visually detected with binoculars during 5-min point counts and were recorded on a map for each point. Transect counts were performed during the hours of maximum male activity (i.e. 3 h after sunrise or before sunset) to ensure maximum detection (Jiguet & Bretagnolle 2001).

Habitat covariates: land use and resource availability

The sampled surface area (c. 1 ha) was far smaller than the home-range of an individual of this species. To study covariates at home-range scale for both sexes simultaneously, we tested the impact of some covariates on species presence at the quadrat scale, and others at the landscape scale in the modelling procedure (Table 2). Landscape scale was chosen to fit home-range size. The home-range for displaying males has been estimated at 27–83 ha (Schulz 1985), 17 ha (Ponjoan *et al.* 2012) and 19 ha (Jiguet *et al.* 2000). For nesting females, home-ranges have been found to vary from 3.1 ha ($n = 1$, Schulz 1985) to 17–25 ha ($n = 2$, Lett *et al.* 2000) in natural and semi-natural areas, or from 10 to 430 ha ($n = 8$, Lapiedra *et al.* 2011). In our study area, we radiotracked three females fitted with UHF radio-transmitters during 2012 and found their home-ranges were 1.2, 4.9 and 5.5 ha (P. Devoucoux unpubl. data). Therefore, for the landscape scale, we used a buffer zone with a 250-m radius around the quadrat centroid, representing a total surface area of 19.63 ha, which fits reasonably well with known estimates of home-ranges in this species.

At the quadrat scale (micro-habitat), we identified the vegetation height using five height classes: 0–10, 10–30, 30–50, 50–70 and > 70 cm. Height was estimated by visual observation. The percentage of vegetation cover was recorded with 10% precision. For each quadrat, two measurements (by two different observers) were made, and these were then averaged for each height class. A principal component analysis (PCA) was performed on the five values per quadrat (see Table S2): the first component (PC1) described vegetation height (explaining 41.2% of the variance) and PC2 described vegetation height heterogeneity (28.6%) and contrasted quadrats that contained both high and low vegetation heights to quadrats with homogeneous vegetation height. Tables of eigenvalues, the contribution percentage and correlation by factors for the two main components are detailed in Table S2. At the quadrat scale, we also determined an index of food availability by measuring grasshopper abundance. For females, the breeding period can be divided into three consecutive stages: lek-visiting, nesting and then brood-rearing (Silva *et al.* 2014). Although coleopterans are a

Table 2. Definition of the covariates analysed at each scale to investigate habitat selection by the Little Bustard in the Costière Nimoise.

Covariate	Scale	Definition
Vegetation height	Quadrat	Mean of visual estimates by two observers of the percentage of cover of five vegetation height classes
PC1	Quadrat	First PCA axis values calculated on vegetation height classes, correlated to vegetation height
PC2	Quadrat	Second PCA axis values calculated on vegetation height classes, correlated to vegetation height heterogeneity
Land use	Quadrat	Land use of the quadrat, based on three categories (see Table S1)
Orthopteran density	Quadrat	Count of jumping grasshoppers within a 1-m-wide transect along the central line
Plot size	Quadrat	Area of the whole plot within the quadrat
Area	Quadrat	Area prospected in the quadrat (used as an offset in the abundance model)
Opposite sex abundance	Quadrat	Number of individuals of the other sex from one of three categories (0, 1 or > 1)
Surrounding landscape composition	Landscape	Ratio of land use in a 250-m buffer zone around the quadrat centroid, based on four categories (see Table S1)
Surrounding landscape diversity	Landscape	Shannon index of land-use categories calculated in a 250-m buffer zone around the quadrat centroid
Surrounding landscape fragmentation	Landscape	Number of plots within a 250-m buffer zone around the quadrat centroid
Surrounding male density	Landscape	Density of displaying males counted within a 250-m buffer zone around the quadrat centroid

main food source for Bustards during the breeding season (Jiguet *et al.* 2002), grasshoppers are preferred during the nesting period, especially during the chick-rearing period (Bretagnolle *et al.* 2011). Quadrats were surveyed during both the nesting and the chick-rearing period, so grasshopper abundance should be a good proxy of food availability at this time. For each quadrat, the observer who walked the central line counted all the jumping grasshoppers within an imaginary transect 1 m in width (50 cm on each side, for a length of 100 m), which was converted into orthopteran density per m² for each quadrat (Fig. 1d).

Land use within the entire area of the SPA was recorded for both years and stored on GIS software (MAPINFO PROFESSIONAL 8.0; Pitney Bowes Software, Troy, NY, USA). Land use was divided into 19 categories, 10 of which we sampled (excluding all habitats that are totally unsuitable for this species, as mentioned above). In the SPA, land use remained relatively constant between 2011 and 2012 (paired *t*-test, $t = 0.69$, $df = 11$, $P = 0.50$). To limit the number of land use categories in the models, all sampled quadrats were identified as one of three types of habitat categories (Table S1): perennial herbaceous crops ('grasslands', 21.69% of the SPA surface area) (including herbaceous and fallow land with medium-

height vegetation, alfalfa and pastures, $n = 352$); annual crops ('crops', 12.20% of the SPA surface area) (including cereals and artificial prairies, $n = 44$) and woody crops ('ligneous', 26.90% of the SPA surface area) (fruit orchards, arboreal fallow land, fallow vineyards and grass-covered vineyards, $n = 92$). These habitat categories represented approximately 8075 ha (61%) of the total area of the SPA. The size of the field was also recorded for each quadrat. Finally, as we were interested in testing hypotheses regarding social factors and interactions between sexes, we also used as a covariate the number of individuals of the other sex counted in the quadrat. This covariate was used in the model as a factor with three levels (0/1/> 1 individual).

In the model, we finally incorporated the macro-habitat scale by including the surface area of habitat types in the 250-m buffer zone centred on each quadrat centroid. In these buffer zones, we calculated the proportions of land use pooled into three habitat categories similar to those used at the quadrat scale ('crops', 'grasslands' and 'ligneous'), plus an 'unsuitable' category (Table S1). We calculated the percentage of each land-use category, the Shannon–Wiener index of land use, and an index of landscape configuration based on the total number of fields within the buffer zone. To

test the importance of social factors in the habitat selection process, we also calculated the number of males recorded during the transect counts in a buffer zone carried out in the macro-scale survey.

Data analysis

We modelled habitat selection separately for males and females. We used generalized linear models (GLMs) and a multimodel inference approach to determine which models best fit the counts based on a set of candidate covariates. All quantitative continuous variables were standardized prior to analysis to allow direct comparison of their slope estimates. Given the highly skewed response variable distribution (i.e. strongly zero-inflated), we separately modelled the presence/absence of Little Bustards with a binomial distribution and a logit link function, and the abundance (given presence) with a zero-truncated Poisson distribution using the 'countreg' R package (Zeileis *et al.* 2008) and a log-link function. In all models, the area of the quadrat was used as an offset (log-transformed) and vegetation height was tested with simple and quadratic terms.

As the number of candidate covariates was high, we fitted all combinations of the covariates in addition (using the 'dredge' function of the MUMIN package; Barton 2015). We then kept all the best models (delta Akaike's information criterion (AIC) < 4 compared with the best model) and obtained the estimates through a model-averaging procedure following Burnham and Anderson (2002) (using the 'model.avg' function of the AICCMODAVG package; Mazerolle 2015). Only significant covariates ($P < 0.05$) from this model-averaging procedure were considered. Spatial correlation of residuals of the null model was visually explored using plot. We also visually inspected variograms plotted using the 'GSTAT' package (Pebesma 2004, Gräler *et al.* 2016). No spatial structure was detected (Fig. S1). All statistical analyses were performed using R 3.4.1 (R Core Team 2017).

RESULTS

In 114 of the 488 quadrats, at least one Little Bustard was flushed out and detected (67 quadrats for females and 67 quadrats for males), for a total of 198 individuals (102 females and 96 males) (Table S5). At this local scale, the highest male density

was 4.92/ha (five males on one quadrat), and the highest female density was 5.15/ha (five females on one quadrat). By totalling up the birds counted over the entire prospected area (409.51 ha), the mean male density per 100 ha was 23.44 and the mean female density 24.91, for an average total density of about 50 individuals per 100 ha.

Model selection identified only vegetation height and social factors as significant drivers of habitat selection for both males and females, at least in terms of presence (Table 3). Field land-use category only affected female presence (Table 3). None of the other tested covariates, field size, vegetation height heterogeneity, macro-scale characteristics (e.g. land-use category, Shannon index, number of fields in the 250-m buffer zone) or insect abundance, had any statistical effect (coefficient table in Table 3, model selection tables in Table S3). Female presence probability was only affected by micro-scale parameters: field land-use category, vegetation height and male abundance (Fig. 2). Male presence probability was affected by vegetation height, female presence at plot scale (Fig. 2) and a single macro-scale factor: male presence was positively correlated to male density in the 250-m radius (Fig. 3). In both sexes, a significant negative correlation between vegetation height (PC1) and presence probability was detected (Fig. 2). However, the effect of vegetation height differed between sexes: whereas females showed a quadratic response to vegetation with an optimal height (estimated at around 30 cm, converting from PC1 units: Table S2), males showed a strict decrease in presence probability with vegetation height (Fig. 2).

In both sexes, local habitat selection was strongly and positively correlated to the abundance of the other sex: the more individuals of the opposite sex, the higher the presence probability (Fig. 2). The role of the opposite sex presence was significant for male abundance. Indeed, the abundance of males was positively correlated with the presence of females. None of the other tested covariates was significant after the model-averaging procedure regarding the abundance (given presence) modelling (coefficient table in Table S4, model selection tables in Table S3).

DISCUSSION

At a micro-scale (i.e. vegetation structure), previous studies have found that male Little Bustards prefer vegetation of low height (Campos & López

Table 3. Model-averaged coefficient tables with estimates and *P*-value for models with $\Delta\text{AIC} < 4$. *P*-values: '***' = 0.001, '**' = 0.01, '*' = 0.05, '.' = 0.1, '' = 1.

(a) Presence of males						
Males (presence/absence)	Estimate	se	Adjusted se	Z value	Pr(> z)	Significance
(Intercept)	-2.95	0.22	0.22	13.70	< 2e-16	***
Female presence = 1	0.69	0.42	0.42	1.64	0.10	
Female presence > 1	1.35	0.51	0.51	2.65	0.01	**
Vegetation height proxy (PC1)	-0.65	0.26	0.26	2.48	0.01	*
Quadratic vegetation height proxy (PC1 ²)	-0.15	0.63	0.64	0.23	0.82	
Vegetation height heterogeneity proxy (PC2)	0.01	0.16	0.16	0.09	0.93	
Field size (log)	0.45	0.30	0.30	1.53	0.13	
Orthopteran density (by linear metre)	0.20	0.27	0.27	0.75	0.45	
Field land-use category: Ligneous	-0.37	0.52	0.53	0.71	0.48	
Field land-use category: Crops	-0.39	0.54	0.54	0.73	0.47	
Surrounding male density (250-m buffer)	0.48	0.14	0.14	3.51	< 0.01	***
Land-use categories Shannon index (250-m buffer)	-0.28	0.18	0.18	1.59	0.11	
Number of fields (250-m buffer)	0.27	0.20	0.20	1.34	0.18	
Unsuitable habitat ratio (250-m buffer)	0.48	0.39	0.39	1.22	0.22	
Low height habitat ratio (250-m buffer)	1.33	0.93	0.93	1.43	0.15	
High height habitat ratio (250-m buffer)	1.36	0.93	0.93	1.45	0.15	

(b) Presence of females						
Females (presence/absence)	Estimate	se	Adjusted se	Z value	Pr(> z)	Significance
(Intercept)	-2.46	0.20	0.20	12.45	< 2e-16	***
Male presence = 1	0.67	0.40	0.40	1.67	0.10	.
Male presence > 1	1.35	0.56	0.56	2.42	0.02	*
Vegetation height proxy (PC1)	1.46	0.76	0.76	1.92	0.06	.
Quadratic vegetation height proxy (PC1 ²)	-1.54	0.69	0.70	2.21	0.03	*
Vegetation height heterogeneity proxy (PC2)	-0.27	0.18	0.18	1.54	0.12	
Field size (log)	0.46	0.30	0.31	1.50	0.13	
Orthopteran density (by linear metre)	0.29	0.28	0.28	1.04	0.30	
Field land-use category: Ligneous	-1.21	0.57	0.57	2.12	0.03	*
Field land-use category: Crops	-0.96	0.65	0.65	1.48	0.14	
Surrounding male density (250-m buffer)	0.06	0.14	0.14	0.43	0.67	
Land-use categories Shannon index (250-m buffer)	-0.24	0.15	0.16	1.57	0.12	
Number of fields (250-m buffer)	-0.23	0.18	0.18	1.28	0.20	
Unsuitable habitat ratio (250-m buffer)	0.34	0.32	0.32	1.05	0.29	
Low height habitat ratio (250-m buffer)	0.89	0.73	0.73	1.22	0.22	
High height habitat ratio (250-m buffer)	0.88	0.74	0.74	1.18	0.24	

1996, Moreira 1999, Silva *et al.* 2010), i.e. around 20–30 cm in height (Martinez 1994, Morales *et al.* 2008). At a macro-scale (i.e. land-use composition and configuration), they have been found to select natural pastures, fallow land or annual spring-sown crops (Delgado *et al.* 2010, Santangeli & Dolman 2011). Females have been shown to differ from males in this respect rather strongly, seeking habitats with more and higher vegetation to remain hidden from predators during laying and incubation (Morales *et al.* 2008, 2013, Silva *et al.* 2014). Females also positively select for sites with more legume crops (Salamolard & Moreau 1999, Jiguet

et al. 2002, Faria *et al.* 2012a). Most previous studies have shown some selectivity for crop types, in males (Martinez 1994), females (Morales *et al.* 2013) or both (Salamolard & Moreau 1999, Morales *et al.* 2008, see Table 1 for a compilation). At a larger spatial scale, males have been found to select for heterogeneous landscapes with high crop diversity (Campos & López 1996, Wolff *et al.* 2001, 2002, Suárez-Seoane *et al.* 2008). However, we found little selection based on crop types or land use, no significant effect of landscape structure, very little sexual dimorphism in macro-habitat selection, and no selection or effect of food

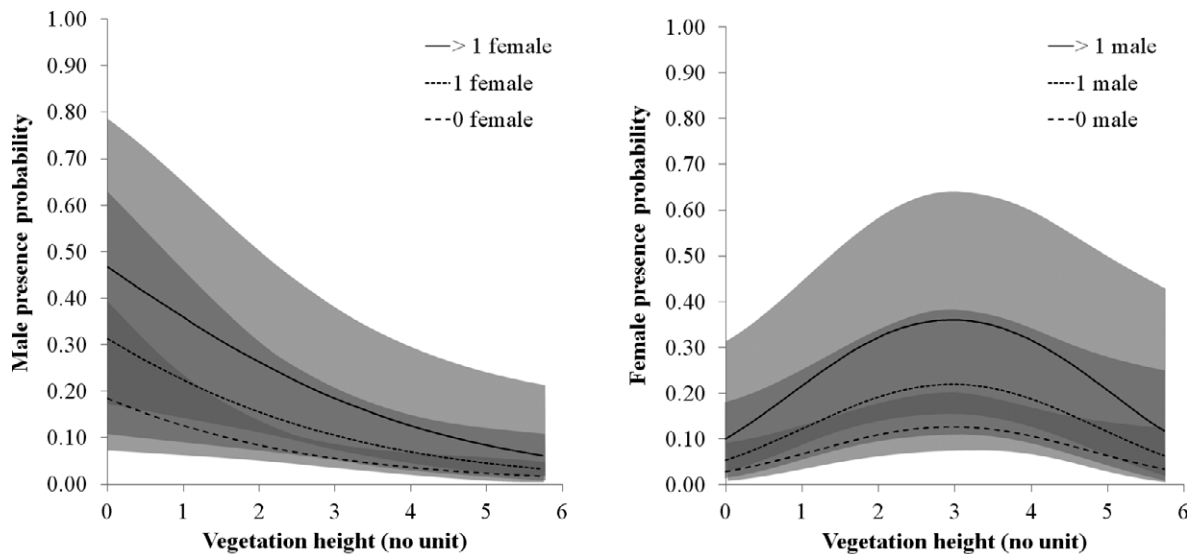


Figure 2. Presence probability of male and female Little Bustards in the grasslands of the Costière Nimoise in 2011/12 (males on the left, females on the right) according to vegetation height and the number of individuals of the opposite sex.

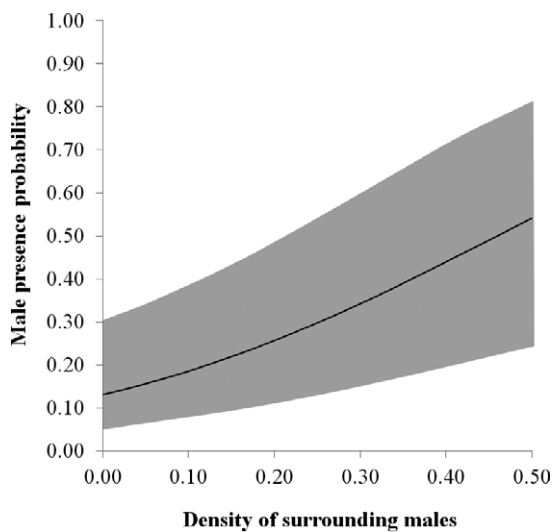


Figure 3. Presence probability of male Little Bustards in the grasslands of the Costière Nimoise in 2011/12 according to the density of surrounding males in a 250-m buffer zone with more than one female.

availability. Yet there was a strong sex-dependent micro-habitat selection for vegetation height.

Micro- and macro-scale habitat selection patterns in relation to sex

First, as in almost every related study to date (Table 1), we found a significant avoidance of high

vegetation in both sexes. Both males and females were negatively influenced by vegetation height. However, males and females differed quite strongly in their preference patterns with regard to vegetation height, with females preferring relatively higher vegetation. PCA results indicated that females' preferred vegetation height class was 30–50 cm, which is consistent with the results of other studies (> 30 cm in Morales *et al.* 2008, and < 42 cm in Silva *et al.* 2014). Vegetation cover and structure were not investigated in this study, except the PC2 axis of the PCA, which was interpreted as a proxy of vegetation height heterogeneity within a field (see Morales *et al.* 2008).

In contrast, we failed to detect sex-dependent habitat selection at the macro-scale. In our study area, females did not significantly favour any kind of crop type, even herbaceous fallow land, as has been found in most other studies (Morales *et al.* 2008, 2013, Silva *et al.* 2014), or alfalfa fields (Salamolard & Moreau 1999). Nor did males show any significant crop-type preference, whereas other studies have indicated that males strongly select for alfalfa fields, fallow land or set-aside land in extensive farmland habitats (Moreira 1999, Delgado & Moreira 2000, Suárez-Seoane *et al.* 2002, Wolff *et al.* 2002, McMahon *et al.* 2010) or spring-sown crops or alfalfa in intensive farmland habitats (Jiguet *et al.* 2002). There was significant avoidance of ligneous fallow land and fruit-tree

orchards (Tarjuelo *et al.* 2013), but only for females, whereas we found some males displaying in olive groves, at least when grass vegetation was present. Vegetation of ligneous habitat was too high for nesting females. Females seem therefore to be more selective than males according to field land-use.

Similarly, despite a significant habitat effect on presence probability (mainly vegetation height), we failed to detect any habitat effect on abundance either in quadrats or at the larger landscape scale. This unusual pattern was demonstrably due to the fact that males and females were found in most suitable habitat types (Table S4), possibly suggesting that the overall habitat was favourable and/or saturated in our study population. The landscape characteristics of this SPA may partly account for these unique results: alfalfa availability is limited in the SPA (around 2% of the surface area) and spring-sown crops barely exist, which may explain this lack in crop-type selection. Moreover, while many previous studies on this species have detected a positive effect of landscape heterogeneity (Wolff *et al.* 2001, 2002, Morales *et al.* 2005, 2006), we did not find such an effect on the presence probability of either sex. Therefore, landscape complementation did not seem to be involved in the habitat selection of either sex. Field size has also been shown to affect Little Bustard distribution (Silva *et al.* 2010) but this was not detected in our study either. This discrepancy between our results and those in the literature might be explained by the relatively highly fragmented landscape mosaic in our study area (plot size ranged from 0.01 to 36.32 ha; the number of fields in a 250-m radius ranged from 1 to 43, with a median of 20). This level of heterogeneity may be the highest at landscape scale yet observed; previous studies have been conducted in steppe plains in La Crau (France) and Spain. These factors reinforce the hypothesis that the habitat structure in our study area may be globally highly favourable to the species, which may explain the lack of strong habitat selection signals.

The importance of social factors on Little Bustard habitat selection

The local density (50 birds/100 ha) found in this study is far above previously published densities for this species. In females, previously reported density ranged from 0.54 to 1.4 individuals per

100 ha (Morales *et al.* 2008). In males, values have ranged from 6 to 7.3 up to 16 individuals per 100 ha (Wolff *et al.* 2002, Silva *et al.* 2014), 6.05 per 100 ha (Silva *et al.* 2010), and 10 per 100 ha (Delgado & Moreira 2000). Values similar to our findings have only been found by Moreira and Leitão (1996) (47 males per 100 ha, but no indication of the number of fields encompassing this high density) and Silva *et al.* (2014) (40 males and 16 females per 100 ha, but based only on 10 males and four females found in a single field). The Costière Nîmoise area thus appears to be highly favourable for the species in terms of habitat quality, explaining the density of Little Bustards in our study area. Such high density may also result in a buffer effect (Brown 1969, Block & Brennan 1993, Gill *et al.* 2001, Jackson *et al.* 2004, Gunnarsson *et al.* 2005), leading some individuals to select suboptimal habitats, which may further partially mask the expected pattern of habitat selection that has been observed in other studies.

High density may exacerbate the pre-eminence of social factors driving habitat selection. This has so far been little studied in this species, although Tarjuelo *et al.* (2013) and Morales *et al.* (2013) have shown that male distribution depends on female presence, and Morales *et al.* (2014) have put forward the thesis that the presence of females drives male territorial behaviour. Despite a lack of data on social behaviour *per se* in our study (i.e. we did not collect data on social interactions such as behavioural information on social contact between male and female individuals), we did investigate the coexistence of sexes in a specific quadrat and the statistical interactions between the sexes and, hence indirectly, social interaction. We found strong statistical evidence that social factors such as conspecific density and the presence of the other sex significantly impacted habitat selection patterns. We found a positive relation between the local presence probability of males and surrounding male density, which would be expected in a lekking species (Höglund & Alatalo 1995, Widemo & Owens 1995, Danchin & Wagner 1997, Morales *et al.* 2001) and has indeed been observed in the Great Bustard, which is also a lekking species (Lane *et al.* 2001, Alonso *et al.* 2004, Osborne *et al.* 2007). In addition, given that female Little Bustards are known to be harassed by males (Jiguet & Bretagnolle 2006, Morales *et al.* 2014) and tend to nest close to but not necessarily within

fields occupied by displaying males (Jiguet *et al.* 2002), habitat selection by females is particularly strongly impacted by male presence. It could be that female presence in quadrats occupied by males was the result of high overall density, which might constrain females to use suboptimal habitats (e.g. close to males), resulting in a relatively high overlap in habitat selected by both sexes. In low-density populations of Little Bustards, such as those studied in intensively farmed habitats (Jiguet *et al.* 2000, Morales *et al.* 2005), these social factors may have remained undetected. When density increases (such as in extensively farmed habitats: Wolff *et al.* 2001, Morales *et al.* 2006), the Little Bustard may show little sexual dimorphism in habitat selection, as the sexes cannot be spatially segregated even should they prefer to be.

Consequences for conservation

The Little Bustard is a species of high conservation concern in Europe. The Costière Nîmoise provides a case study that this species is able to respond rapidly to a sudden improvement in habitat quality. The Little Bustard population in this area has steadily increased from only 123 males in 1998 to 683 in 2012, a spectacular population growth related to habitat change. Currently, the landscape is characterized by small patches (approximately 1 ha in size) of heterogeneous land use, with a high percentage of fallow land, with the result that it consists of a mosaic of vegetation of various heights and high food availability. In recent years, the habitat has largely improved for Little Bustards, as the proportion of fallow land has increased due to land abandonment caused by the decreased financial viability of vineyards and fruit orchards over the last 15 years, and has accelerated since 2005 due to the planned construction of a high-speed railway (construction started in 2014). It is likely that the overall favourability of the study area for this species resulted in our failure to find the strong habitat selection covariates that are usually used to help define habitat-management conservation measures. Nevertheless, this finding in itself allows us to postulate that the mosaic landscape composition of the SPA as it is now is critical to conserve; the target should be the maintenance of this habitat composition and structure not only for this site but for other similar sites where the species is currently in decline and/or at low density.

In a broader context, for heterogeneous landscapes, we encourage multi-scale habitat selection analyses such as the one carried out in this study, incorporating social relationships either directly or indirectly, and using dedicated statistical methods. Many habitat selection studies consider only one scale for analysis (in bird studies, typically the scale of individual territories) and considering at least two scales, although arbitrarily chosen, often improves model accuracy. However, the scale at which the studied species actually selects its habitat is usually unknown (Johnson 1980) and may be context-dependent (e.g. the size of a territory may change over space and time). In addition, farmland landscapes are very heterogeneous as a consequence of the spatial arrangement of fields. Hence, using an arbitrary scale of analysis may lead to erroneous conclusions if the chosen scale is not relevant. Investigating habitat selection across a continuum of scales from an individual's territory to landscape is now possible, and there are several studies on farmland birds that have shown that selection changes with scale (e.g. the Skylark *Alauda arvensis*: Miguet *et al.* 2013). Interactions between habitat and social factors have also been found statistically, in farmland bird specialists such as Montagu's Harrier *Circus pygargus* and the Little Owl *Athene noctua* (Cornulier & Bretagnolle 2006). Both these species, which have contrasting spatial distribution (aggregated in the harrier, and overdispersed in the owl), showed contrasting selection patterns when taking into account the interaction between habitat and social factors. Such analyses are not difficult to implement, but using the results for conservation action is more complicated, as only the habitat can be manipulated (in a way that minimizes or maximizes social interactions of the target species, depending on the overall goal). Despite this limitation, we argue that identifying the social factors that interact with habitat selection patterns and running the analyses at preferably two (or even more) scales, i.e. a local (micro-habitat) and macro (land-use) scale, should be a prerequisite in conservation studies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Plot of null model residuals geographical distribution and variograms for male abundance, female abundance, male presence and female presence. Negative residuals are shown as red dots and positive as blue dots.

Table S1. Details of the categories of land-use types, their definition, their percentage of the SPA surface area, the number of quadrats used for analyses, and the habitat category according to fine- or large-scale analyses.

Table S2. (a) Correlation circles from the PCA on vegetation height classes (H0 = 0–10 cm; H10 = 10–30 cm; H30 = 30–50 cm; H50 = 50–70 cm; H70 = 70 cm and over). Left panel: correlation circle with the quadrats; right panel: correlation circle with the variables. (b) Table of eigenvalues and percentage of variance explained by the first four components. (c) Table of percentage of variance explained by each factor for the first two components used in the analyses. (d) Table of correlations by each factor for the first two components used in the analyses.

Table S3. Model selection tables after dredging for models with $\Delta AIC < 4$, for male presence (a) and female presence (b), and male abundance (c) and female abundance (d)

Table S4. Model-averaged coefficient tables with estimates and *P*-value for models with $\Delta AIC < 4$.

Table S5. Table of female and male occurrence between quadrats and habitat categories.