

Landscape context and little bustard abundance in a fragmented steppe: implications for reserve management in mosaic landscapes

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Abstract

In mosaic landscapes, patch use by animals may depend on features associated with neighbouring patches, e.g. resources or predators. This is of concern for species living in fragmented remnants of natural habitats surrounded by man-modified habitats. We studied how landscape context influenced habitat use by a lekking grassland bird, the little bustard, in a landscape where protected patches of natural steppe were interspersed with improved pastures suitable to bustards, and other unsuitable habitats. At a scale equivalent to a lekking site (30–70 ha), the abundance of displaying males and nesting females on steppe plots increased with increasing availability of improved pastures within 1 km of plots. This concentration of breeding bustards on steppe habitat around modified pastures may partly result from the species' lekking system. We emphasize that increasing the suitability of managed habitats around protected natural areas may help in maintaining viable populations of native species by providing additional resources or breeding sites. © 2002 Published by Elsevier Science Ltd.

Keywords: Landscape context; Reserve management; Fragmentation; *Tetrax tetrax*; Leks

1. Introduction

The fast increase in human population has triggered massive changes in land-uses at a global scale (Houghton, 1994). As a result of these changes, large tracts of natural habitats have been transformed into reduced patches, surrounded by a matrix of habitats more or less modified by agriculture, forestry or urban development. Aboriginal species living in these modified landscapes face a vast array of constraints resulting from the reduction and fragmentation of their native habitats (Harrison and Bruna, 1999), but also from the development of new habitats around them (Janzen, 1986; Saunders et al., 1991). There is increasing concern about the fact that management of native habitat remnants for species conservation cannot ignore factors linked to surrounding modified habitats (Brussard et al., 1992; Hansson, 1992; Wiens, 1994; Law and Dickman, 1998; McIntyre and Hobbs, 1999; Baillie et al., 2000).

Indeed, the distribution of wildlife in mosaic landscapes does not uniquely depend on the intrinsic quality of each habitat, but may be influenced by factors linked to the spatial configuration and arrangement of patches (Pope et al., 2000; Söderström and Pärt, 2000). For instance, the use of a patch for breeding may be limited by predators or competitors from surrounding habitats (Janzen, 1986). In contrast, a species may perform better in its breeding patch by gaining access to complementary or supplementary resources (Tilman, 1982; Dunning et al., 1992) in neighbouring habitats (Kozakiewicz, 1995; Mahan and Yahner, 1998; Aebischer et al., 2000; Franklin et al., 2000; Sorensen and Fedigan, 2000). Understanding how surrounding modified habitats may positively or negatively influence the performance of species in native habitat patches is therefore a crucial prerequisite to the implementation of sound conservation strategies.

Social interactions may enhance the importance of landscape-level features of habitat selection in mosaics, because decisions at the individual level are constrained by the distribution of conspecifics. Gregarism or colonialism may for instance favour the use of larger rather

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than smaller patches (Rolstad and Wegge, 1987). Differences in habitat preferences between individuals may also favour the use of areas where the whole range of preferred habitats occurs in close proximity (Höglund, 1996). Species exhibiting complex mating systems such as leks possess several properties that make them interesting models for studying the influence of intraspecific interactions on habitat selection in mosaic landscapes: (1) breeding habitat requirements of males (display) and females (nesting) usually differ; (2) males need to aggregate for display; (3) the number of females that visit a lek for fertilization may be influenced by lek size and location with respect to female feeding or nesting habitats.

In this paper, we study how the breeding abundance of a threatened lekking grassland bird, the little bustard *Tetrax tetrax* L., is influenced by the availability and distribution of patches of natural steppe and modified habitats in a mosaic landscape of southern France, the Crau area. A recent study (Wolff et al., 2001) showed that in the Crau, overall little bustard abundance was higher on improved pastures (fallow and dry cereal and/or legume crops) than on natural steppe. Moreover, abundance on steppe habitat was much lower in a zone largely dominated by steppe than in a zone where steppe patches occur within a mosaic of improved pastures and other agricultural habitats. These results suggest that higher male abundance in the mosaic zone may occur because bustard abundance on steppe increases when the local landscape includes a larger proportion of improved pastures. Here, we specifically test this latter hypothesis, investigating whether breeding densities of male and female bustards, recorded on 30–70 ha plots of steppe and improved pastures during spring 2000, increase with the abundance of improved pastures around plots. We also investigate whether landscape context effects on bustard distribution may result from the species' mating system. In particular, we assess whether distribution patterns may result from differences in habitat preferences between sexes: in the little bustard, displaying males usually favour very low cover to maximize the efficacy of displays (Salamolard et al., 1996), whereas females tend to establish their nests in somewhat taller vegetation for better concealment (Salamolard and Moreau, 1999). The conservation implications of our results are discussed, with special reference to wildlife management in fragmented protected areas.

2. Methods

2.1. Study species

The little bustard *T. tetrax* is a medium-sized ground-nesting bird (weight 565–960 g, Cramp and Simmons, 1980) that inhabits pseudo-steppes and lowland farmlands of Europe, western Asia and north Africa. The

species, listed as “near-threatened” (Collar et al., 1994), has disappeared from several European countries (Tucker and Heath, 1994), and the intensification of farming systems is thought to be the main cause of decline (De Juana et al., 1993; Goriup, 1994). In north and west France, populations have experienced a 90% decline during the past 20 years (Jolivet, 1997). This however contrasts with southern France populations, which have remained relatively stable during that time, with a recent estimate of 473–539 breeding males for the single population of the Crau (c. 40% of the French population, Wolff et al., 2001).

The little bustards' mating system is classified under “exploded leks” (Schulz, 1985; Jiguet et al., 2000), in which males display in clustered and small (< 10 ha) territories that are visited by females for copulation only. Females subsequently nest and raise the young alone while males keep on displaying.

2.2. Study area

The Crau is a 600-km² alluvial plain in Provence, south-eastern France, c. 50 km north-west of the city of Marseille. The original habitat is a stony, semi-arid steppe, whose vegetation structure and composition have been shaped by twenty centuries of extensive pastoralism (Devaux et al., 1983). Steppe habitat has been reduced to 17% (102 km²) of its original size following the development of irrigation facilities (Wolff et al., 2001). Remaining steppe patches have been designed as Special Protection Area (SPA) under the European Union Directive on the Conservation of Wild Birds (79/409/EEC), 65% of which have recently been designated as Natural Reserve. The matrix surrounding the protected steppe is mainly covered by arable lands. Haymeadows, fallows and peach orchards are the dominant land-uses, whereas grain crops, grazed dry crops, greenhouses, wetlands and forests cover smaller areas within the matrix (Wolff et al., 2001). Steppe, fallows and grazed crops (winter-sown dry legume and/or cereal crops) are grazed by sheep from March to late June, although some fallows and steppe patches may also be grazed in autumn and winter. Stocking rates vary from about 2 to 4 sheep ha⁻¹ on fallows and steppe, to 20–25 sheep ha⁻¹ on grazed crops (Fabre, 1998). In the Crau, displaying little bustard males use natural steppe, but also grazed fallows and grazed dry crops. In the present study, fallows and grazed dry crops are grouped under the term “improved” pastures, in contrast to the “natural” steppe.

For this study, data were obtained on a 236-km² area where natural steppe and improved pastures cover 98 and 30 km², respectively. We distinguished two geographical zones according to the distribution of natural and modified habitats in the study area (Wolff et al., 2001): the “south” zone covers 140 km² and is largely

dominated by natural steppe (54% of zone area, Fig. 1); the “north-east” zone, covering 96 km², is a mosaic of steppe patches (23% of zone area) and various agricultural habitats including improved pastures (Fig. 1). Improved pastures cover 15.5 km² in the south zone and 14 km² in the north-east zone (Fig. 1), thus representing 17 and 39% of total potential breeding bustard habitat (improved pastures + steppe), respectively.

2.3. Male, female and nest abundance on plots

Surveys of little bustards were conducted on 30–70 ha plots from early May to late July 2000. Plots were covered either by steppe ($n=15$), by improved pastures ($n=11$, sometimes with various proportions of hay-meadows or irrigated crops), or were a mixture of steppe and improved pastures ($n=5$). For the latter category, the steppe and improved pasture portions of plots were treated as independent samples in statistical analyses, so that a single habitat type could be attributed to each plot. Sample size for analyses was therefore 20 steppe plots and 16 improved pasture plots. Plot location and size were constrained by two main factors: (1) access, which was subject to permission by land owners; (2) presence of visual boundaries such as field

margins or paths, which allowed observers to determine whether detected birds were located inside or outside plot limits. Nearest-neighbour distance between plot centres averaged 1.5 km (min. 0.85 km; max. 3.83 km).

To survey breeding bustards, two observers walked across plots in straight lines, respecting a 100 m spacing between lines, and regularly searching the area with binoculars. Each plot was surveyed every 8–10 days. Surveys were performed from 6:00 to 12:00 h (GMT + 1:00) in the morning, and from 15:00 to 22:00 h in the evening. Birds that were flushed or spotted (visually or by ear) were mapped. Nests were searched by visually scanning the ground while walking, or by searching the area (about 200-m radius) from which females suspected to be nesting were flushed; when neither nests or young were found, the area was searched again within the next 2 days during warmer day hours (to increase the chances of flushing the female close to its nest). Chicks were usually localized by the soft whistling call they produce when left alone.

Because we specifically wanted to contrast habitat preferences and distribution of males when displaying and females when nesting, we distinguished a pre-nesting period (5 May–26 May), when females visit displaying males on lekking sites for copulation, and a

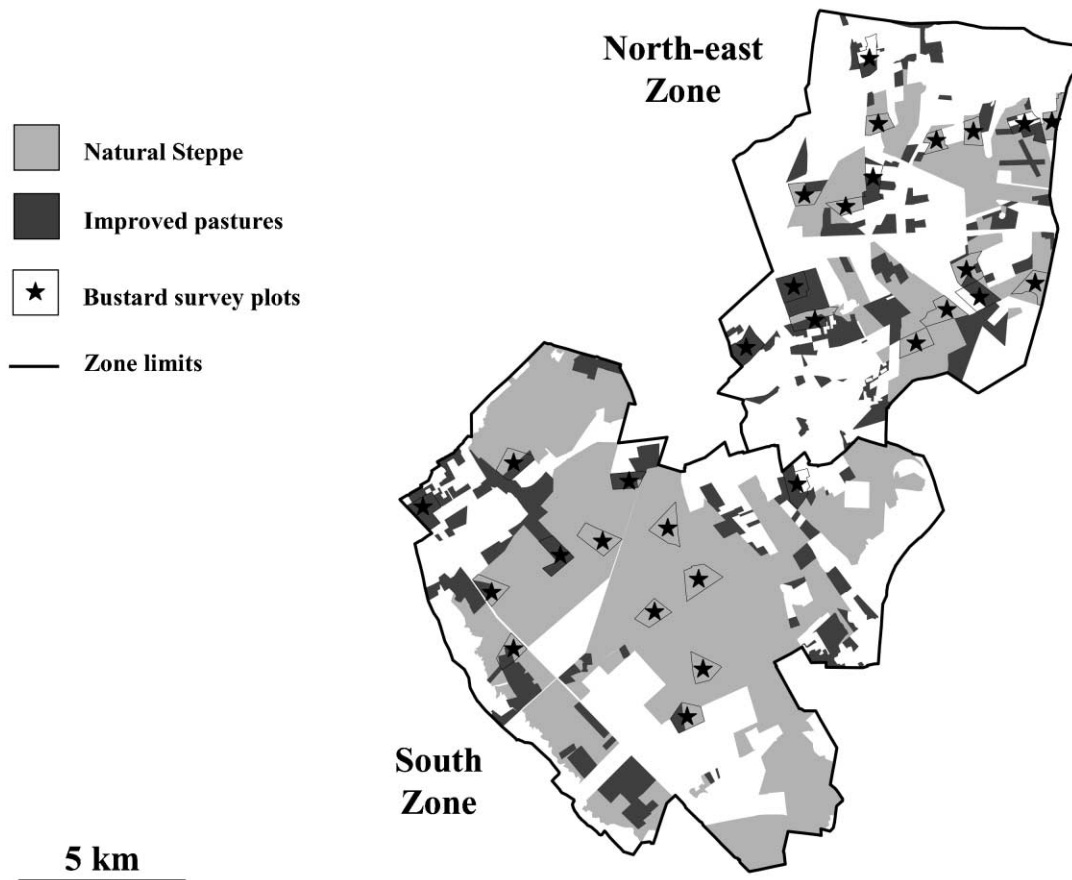


Fig. 1. Distribution map of natural steppe and improved pastures in the study area, and location of survey plots.

main nesting period (27 May–23 June) when most females can be considered to be either incubating or with young chicks (26 May was the median laying date in 1999–2000; $n=42$ nests, T. Dieuleveut & A. Wolff, unpublished data). Three visits were conducted during each period. We calculated male and female densities for 50 ha (the mean area of plots), averaging bird counts over the three visits of each period. Land-uses remain unchanged throughout the breeding season.

Little bustard nests are well camouflaged (Cramp and Simmons, 1980) and are notoriously difficult to find. However, the number of nests discovered on plots was correlated to the mean number of females observed at each visit during the nesting period ($r^2=0.51$, $P<0.001$, $n=36$; nest = $0.18 + 0.54$ female). The density of females during the nesting period was therefore used as an index of nest abundance on plots. Densities of displaying males were calculated during the pre-nesting period.

2.4. Statistical analyses

To investigate whether availability of improved pastures in the surrounding landscape influenced bustard abundance, we used GIS software MAPINFO Professional™ 5.0 (MapInfo Corporation, 1992) to calculate the proportion of improved pastures (extracted from a digitised land-use map of the study area, see Wolff et al., 2001) within a 1-km-wide buffer around each plot. This radius was chosen so that buffer area was about 1 order of magnitude larger than plot area (means 5.63 and 0.51 km², respectively). For plots located near the limits of the study area, the proportion of improved pastures in the surroundings was estimated using the area of 1-km buffer located inside the study area as ratio denominator (instead of total buffer area), since land uses had not been recorded outside the study area. For each plot type (steppe or improved pasture), densities of males before the nesting period and densities of females during the main nesting period were regressed against the proportion of improved pastures within 1 km of plots, using GLM procedure on SAS software (SAS Institute, 1994). Log (1 + bird density)

was used as the response variable to meet normality and homoscedasticity assumptions.

3. Results

3.1. Influence of surrounding improved pastures on bustard abundance

On steppe plots, male density significantly increased with increasing proportion of improved pasture within 1 km of plots (Table 1). Although male densities on steppe plots in the south zone were on average 35–51% lower than in the north-east zone (for plots with similar landscape contexts, i.e. 4.3–20.2% of surrounding improved pastures; Fig. 2a), male densities did not significantly differ between zones (Table 1). The density of females on steppe plots during the nesting period did not significantly differ between zones (Table 1), and the effect of surrounding improved pastures fell short of significance ($F_{1,16}=2.8$, $P=0.11$). When we excluded a single steppe plot that held an exceptionally high density of females (3.0 females/50 ha, vs. a maximum of 1.2 females/50 ha for other steppe plots, see Fig. 2a), the effect of surrounding improved pasture on female density became significant ($F_{1,15}=5.8$, $P=0.03$) while the effect of zone remained non-significant ($F_{1,15}=0.3$, $P=0.58$). When data from both zones were pooled, the effect of surrounding improved pastures on bustard densities on steppe plots was significant for both males and females (Fig. 2a). Model fit was again improved for females when removing the outlier plot referred to above ($r^2=0.33$; $F_{1,18}=8.5$; $P=0.01$).

On improved pasture plots, neither the proportion of surrounding improved pasture nor zone significantly affected male or nesting female abundance (Table 1; Fig. 2b). This indicates that, above a minimum patch size of 30–70 ha (our plot area), increasing patch size does not increase the attractivity of improved pastures for breeding bustards. Regressions remained not significant for males and females on improved pasture plots when data from both zones were pooled (Fig. 2b).

Table 1
GLM analyses of male and female densities on steppe and improved pasture plots^a

Dependent variable (sex and period)		Steppe plots ($n=20$)			Improved pasture plots ($n=16$)		
		Type III SS	F value	Pr. > $F_{1,16}$	Type III SS	F value	Pr. > $F_{1,12}$
Males pre-nesting	Surr. mod. past.	1.118	11.48	0.004	0.229	0.51	0.49
	Zone	0.275	2.83	0.11	0.038	0.08	0.78
	Zone × surr. mod. past.	1×10^{-4}	≈0	0.98	0.020	0.04	0.84
Females nesting	Surr. mod. past.	0.386	2.82	0.11	0.012	0.06	0.81
	Zone	2×10^{-4}	≈0	0.97	0.022	0.10	0.75
	Zone × surr. mod. past.	0.003	0.02	0.89	0.403	1.89	0.19

^a Analyses were performed on log (1 + birds/50 ha). Surr. mod. past., % of surrounding improved pastures within 1 km of plots; n = number of plots.

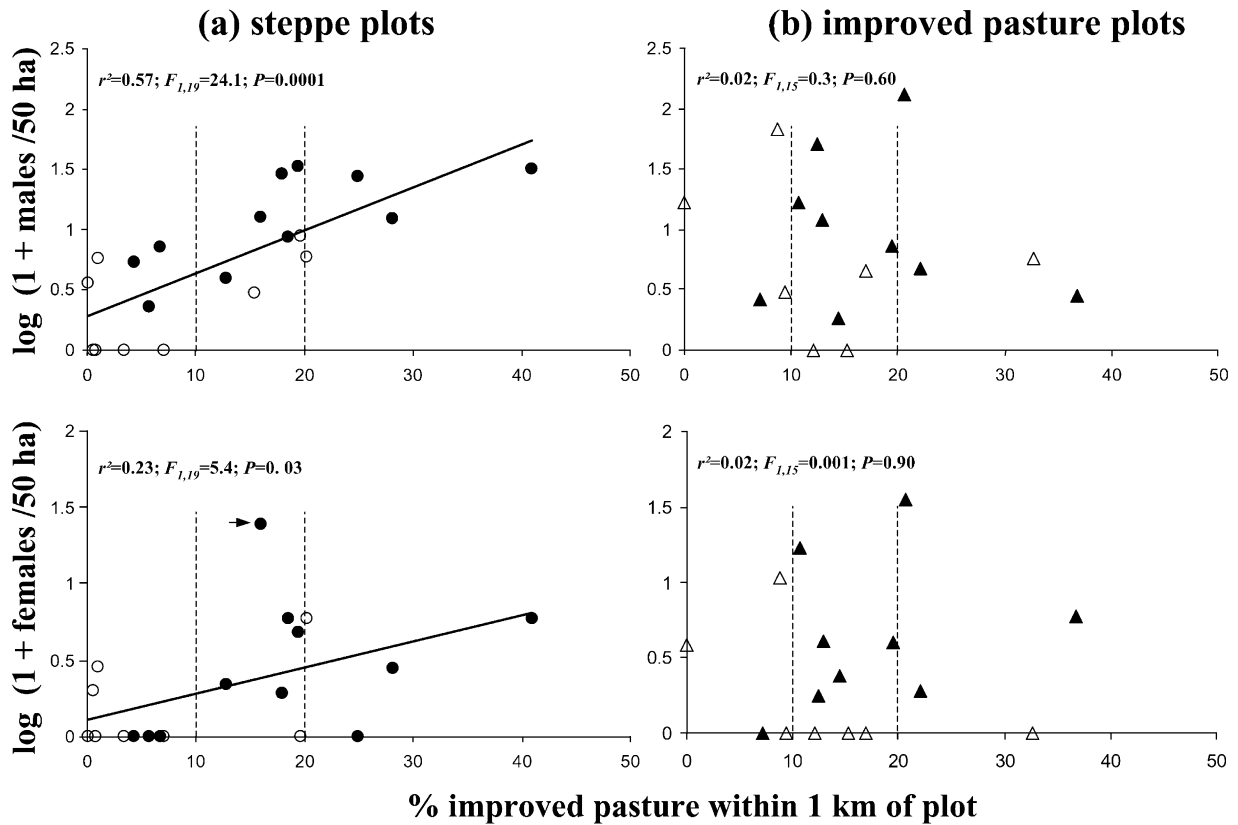


Fig. 2. Male and female densities as a function of proportion of improved pasture within 1 km of plots. Mean density of males (pre-nesting period, upper) and females during nesting (lower) on steppe plots (a, circles) and improved pasture plots (b, triangles) are plotted. Open symbols, south zone; black symbols, north-east zone. The steppe plot with exceptional female density (outlier, see text), shown by an arrow, is included in the regression analysis. F values from GLM analyses with data pooled across zones (see text). Only regression lines with probabilities <0.05 are plotted. Vertical dotted lines represent class limits used for comparisons of steppe and improved pasture plots in similar landscape context (see text).

To test specifically whether the differences in breeding bustard densities between habitat types increased with increasing area of improved pasture in the surrounding landscape, we compared bustard densities between steppe and improved pasture plots grouped into three categories of landscape contexts: <10 , 10 – 20 and $>20\%$ of improved pastures within 1 km of plots. Class limits were chosen to keep sample sizes of classes as equilibrated as possible (see Fig. 2). Data were pooled across zones for this analysis. No difference in either male or nesting female densities was detected between steppe and improved pastures for plots surrounded by 10 – 20% or $>20\%$ of improved pasture. However, male densities were significantly lower on steppe than on improved pasture ($P < 0.05$) for plots surrounded by $<10\%$ of improved pasture. Mean nesting female densities were more than five-fold lower on steppe than on improved pastures for plots surrounded by $<10\%$ improved pasture, but the difference failed to be significant ($P = 0.10$).

3.2. Relative locations of displaying and nesting sites

During the pre-nesting period, the density of females on plots was correlated with the density of displaying

males (linear regression: $r^2 = 0.24$, $P = 0.002$, $n = 36$; Fig. 3), suggesting that prospecting females preferentially attended sites with higher densities of displaying males. Similarly, the density of females during the nesting period was correlated with the density of males before the nesting period ($r^2 = 0.36$, $P = 0.0001$, $n = 36$; Fig. 3). In both cases, no significant difference in regression slopes between steppe plots and improved pasture plots was detected ($P = 0.98$ and $P = 0.29$ for females before and during the nesting period, respectively). The number of nests on plots was also correlated to the density of males during the pre-nesting period (Poisson regression: $\chi^2 = 6.33$, $P = 0.01$, $n = 36$).

4. Discussion

4.1. Effects of landscape context on bustard abundance

Our results show that the abundance of displaying male bustards on natural semiarid steppe increased in the vicinity of improved pastures. At a scale equivalent to a lekking site (30 – 70 ha plots), male density on steppe increased with increasing proportion of improved

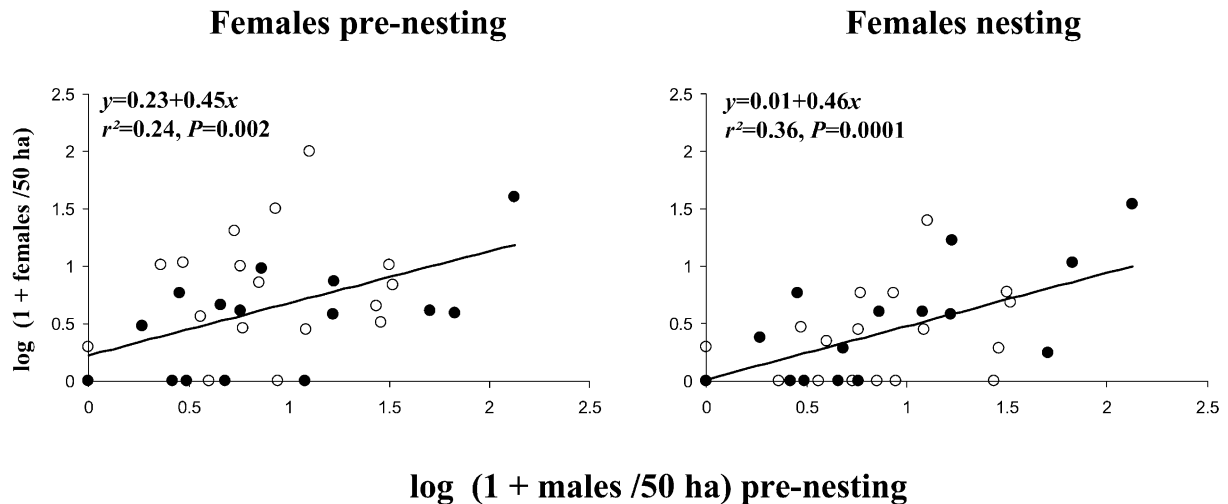


Fig. 3. Density of females during the pre-nesting period (left) and females during the nesting period (right) on plots, as a function of male density during the pre-nesting period. Open circles: steppe plots; closed circles: improved pasture plots. Plotted regression lines consider steppe and improved pasture plots jointly.

pasture within 1 km of plots. The availability of improved pasture around plots explained a large part of the variation in male abundance on steppe, especially within the north-east zone. The abundance of nesting females on steppe also increased with increasing proportion of improved pasture around plots. Although the trend was not as clear as with males, the lack of fit appeared to be caused mainly by a single atypical plot. Furthermore, the estimation of female densities on plots was more subject to sampling variations because of poor female detectability, as female abundance on plots during the nesting period was always very low (72% of all visits with no female, rarely more than two females detected per visit on the richest plots). The hypothesis that improved pastures locally increase bustard abundance on adjoining steppe patches is reinforced by the fact that bustard densities on improved pastures, although highly variable, were not influenced by local abundance of improved pastures (Fig. 3b), and were higher than densities on steppe only where improved pastures were scarce in the local landscape (<10%).

In this study, our working hypothesis was that differences in bustard abundance between the south zone (largely dominated by steppe) and the north-east zone (mosaic of steppe, improved pastures and more intensive agricultural lands) were explained by differences in landscape features which acted at smaller scales. Percent cover of improved pastures around plots explained most of the variation in male and female densities on steppe (Table 1; Fig. 2a), although our inability to detect differences between zones may partly result from small sample sizes, especially in the south. Some of the unexplained variation between zones may stem from differences in habitat characteristics (e.g. north–south aridity gradient, Devaux et al., 1983), or by differences in landscape composition or physiognomy

not accounted for in our analysis. With respect to the latter, it may be argued that patches formed by improved pastures and adjoining steppe habitat in the north–east form a more continuous network of areas of high bustard abundance than in the south: in the south zone, about 60% of steppe area lies within 1 km of improved pastures, whereas in the north–east 99% of steppe area lie within 1 km of improved pastures (Fig. 4). These aggregated bustard nuclei in the north–east may further attract more individuals than the more loosely connected nuclei in the south.

4.2. Possible causes of landscape context effects

Higher bustard abundance on and around improved pastures, i.e. fallow lands and dry legume/cereal crops, suggests that this habitat type holds resources more abundant or of higher quality than the semiarid steppe (e.g. food or cover, see Martínez, 1994). The fact that the attractivity of improved pasture patches extends beyond field limits suggests that birds establishing in nearby steppe habitat may benefit from the resource available in improved pastures. The mating system of little bustards (exploded leks) may also participate in the extent of landscape context effects in several ways. First, if males increase their expected reproductive success by aggregating, as admitted in most lek formation models (Höglund and Alatalo, 1995; Höglund, 1996), they may benefit from settling at the periphery of leks established on improved pastures even if their access to resources were limited. Second, leks may form where female encounter is maximized (“hotspot model”, Bradbury and Gibson, 1983), so that males may aggregate around improved pastures not because of the resources they hold, but because females preferentially settle in this habitat. In this respect, it was expected that

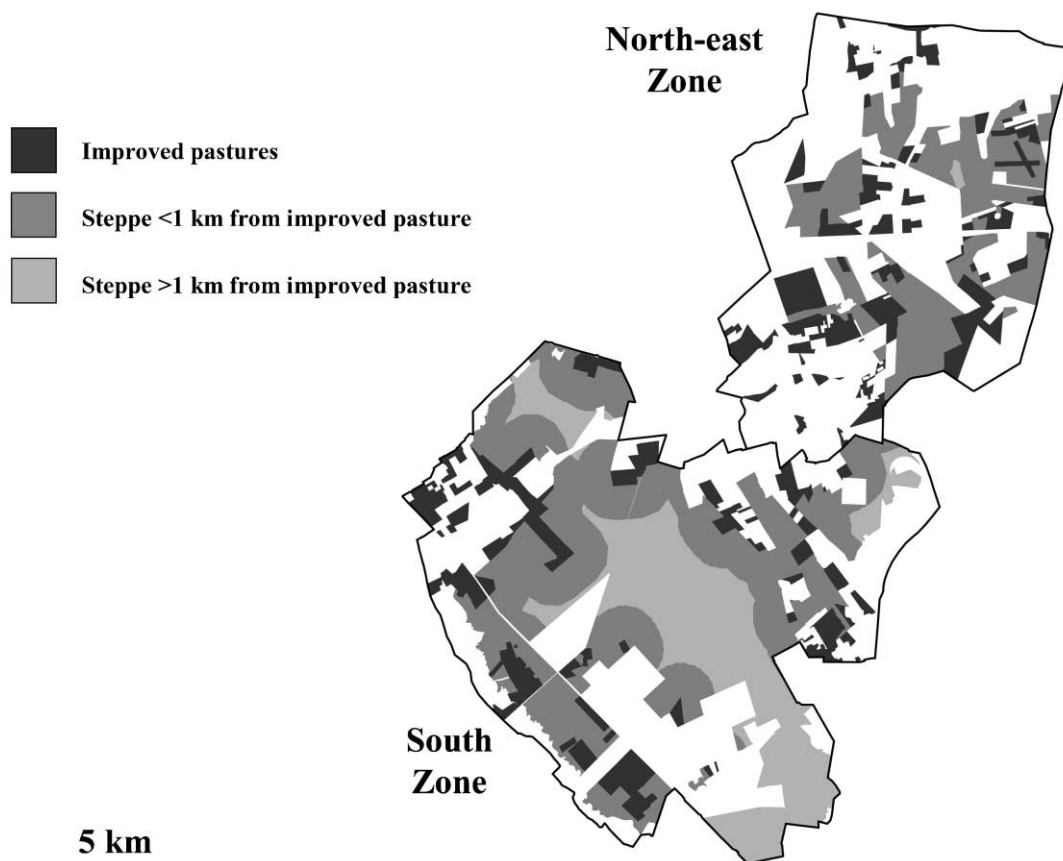


Fig. 4. Schematic map of the study area representing, in each zone, the area of steppe lying within or further than 1 km from patches of improved pastures.

the selection of vegetation types or patches would somehow differ between displaying males and nesting females, as reported in other studies (Salamolard and Moreau, 1999), because, at a finer scale, microhabitat selection in breeding little bustards is considered to differ between sexes. However, we found that: (1) nesting females did not appear to select improved pastures more strongly than males; (2) both males and females tended to be more abundant on steppe in the vicinity of improved pastures; (3) more generally, the number of nests and the density of females during the nesting period on plots were highly correlated with the density of males before the nesting period. This unexpected convergence in the selection of habitat types and patches for displaying and nesting may be explained by the spatial heterogeneity of vegetation structure in the types of extensive pastures used by bustards in the Crau (A. Wolff, unpublished results), which may allow microhabitat selection of displaying and nesting sites to operate at a smaller scale within the plots we surveyed. Moreover, on dry crops, where grazing pressure and plant growth are higher than on steppe and fallows, temporal variation in vegetation structure according to grazing and vegetation re-growth may result in males and females using the same field at different times.

Although the spatial correlation between male and female densities are consistent with the “hotspot” model, there was no evidence that male aggregation around improved pastures was specifically a consequence of female habitat selection, and further studies at a smaller scale are needed to clarify the relationships between bustard distribution patterns and resource selection.

4.3. Suitability of matrix habitats and reserve management

In the Crau, the abundance of little bustard males during the breeding season had previously been shown to be as high, and in some areas higher, in unprotected improved pastures than in the protected natural steppe, whereas more intensive open habitats of the matrix were little used (Wolff et al., 2001). The present study confirms this pattern of habitat use for males, and suggest that unprotected extensive improved pastures are a nesting habitat of equivalent or higher attractivity than the protected steppe.

Problems of matrix quality are of increasing concern for the management of protected areas (see e.g. Janzen, 1986; Andrán, 1994; Mesquita et al., 1999; Norton et

al., 2000; Söderström and Pärt, 2000). The nature and quality of habitats in the matrix have been shown to influence the population dynamics of target species in several ways, with an emphasis on negative consequences. For instance, the impact of border effects, e.g. nest predation by generalist predators, may depend on the nature of the adjoining habitat (Wiens, 1994; Andrén, 1995; but see Lahti, 2001). Lack of permeability of the matrix to dispersal increases the probability of local patch extinction, while decreasing recolonization probability and gene flow between protected patches (Laurance, 1991; Stouffer and Bierregaard, 1995; Gascon et al., 1999; Fahrig, 2001). In this study, we emphasize the potential for positive effects of suitable elements of the matrix on species subsisting in remnants of native habitats. First, improved (but extensively managed) pastures in the matrix provide bustards with additional area of suitable breeding habitat outside the protected area. The result is a net increase of the total carrying capacity at the scale of the whole landscape, which allows to sustain higher population levels than would be achieved by the protected habitat alone: in the Crau, 48% of breeding males occur in suitable matrix habitat around the protected steppe (Wolff et al., 2001). This in turn may reduce the risks of population extinction associated with demographic and genetic stochasticity. Second, suitable matrix habitats influence the abundance and distribution of bustards within the protected area, since breeding bustards on steppe concentrate near adjoining improved pastures. In many types of fragmented native habitats, the persistence of highly mobile organisms is likely to be improved by access to supplementary or complementary resources in nearby matrix habitats (Aebischer et al., 2000; Fisher and Merriam, 2000; Söderström and Pärt, 2000; Sorensen and Fedigan, 2000). Suitable matrix habitats surrounding fragments of native habitat also increase the area of effectively usable habitat, which benefits species whose distribution is constrained by large territorial requirement (Wilcove et al., 1986; Andrén, 1994; Maehr and Cox, 1995; Franklin et al., 2000) or by complex social systems (Höglund, 1996; Aebischer et al., 2000).

5. Conclusion

The example provided in this study stresses the need to conjugate conservation efforts within protected areas and in the “wider environment” (Saunders et al., 1991; Wiens, 1994; Kelson, 1998; Putz and Romero, 2001). Although the protection of steppes remain a priority because of the characteristic species they hold, we argue that the management of surrounding habitats may further improve population sustainability for many species living in fragmented steppe areas. Additional studies

conducted in the Crau indeed suggest that other birds such as stone curlews *Burhinus oedicnemus* use managed lands around steppe patches extensively (A. Wolff, M. Lepley and E. Hervet, unpublished results). Even species whose populations have declined as a result of steppe reduction, such as pintail sandgrouse *Pterocles alchata*, also use improved pastures to some extent (Cheylan et al., 1983). Little bustards are unlikely to persist in the protected steppe of the Crau if extensively managed matrix habitats are replaced by more intensive crops. Specific agri-environmental measures (under EU Regulation 2078/92) for bustard conservation are being developed in the Crau area, to promote and develop the extensive management of improved pastures around the protected steppe; economic incentives are also proposed to farmers willing to convert intensive crops into extensive pastures, with a special emphasis on large fields adjoining protected steppe patches. We believe that, when possible, wildlife biologists and managers of protected areas should be encouraged to develop and propose targeted management strategies for surrounding matrix habitats, with the aim of increasing the probability of persistence of animal species for which the protected areas were designed.

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