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# The benefits of extensive agriculture to birds: the case of the little bustard

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**Summary**

**1.** The little bustard *Tetrax tetrax* is among many birds thought to be declining be cause of agricultural intensification in western Europe. In contrast with the situation elsewhere, bustard numbers have greatly increased during the last 50 years in the Crau, southern France, as agriculture has been developing. We wished to ascertain which features of agricultural development might have supported this population increase.

**2.** Using data on habitat-specific densities obtained by surveys of the Crau in 1998 and 1999, we assessed how breeding male little bustards used habitats representing various levels of agricultural intensification. We also documented historical changes in bustard numbers and agricultural trends in the Crau, comparing them with present patterns of habitat use, to determine how changes in farmed landscapes may have driven population trends.

**3.** Male bustards used natural steppe and extensive agricultural habitats (fallow, grazed crops, legume crops), whereas more intensive agricultural habitats (hay-meadows, grain crops) were little used. Mean densities on extensive agricultural habitats were always high, but densities on steppe varied with landscape composition: densities were low where steppe was dominant in the landscape, but high where steppe and extensive agriculture were mixed.

**4.** Available literature showed that little bustards settled in the Crau around 1950, after 40% of the original steppe had been converted into arable land. We estimate a current population of 473-539 breeding males. Only 17% of the original steppe remains, but extensive agricultural habitats still represent 30% of arable land.

**5.** Both historical data and present habitat use suggest that little bustard population trends in the Crau are driven by the development of extensive agriculture. Extensive agricultural habitats may provide little bustards with resources unavailable or scarce in natural steppe. Severe declines in little bustard numbers observed elsewhere could be reversed within a few decades by restoring extensive agricultural habitats. The potential impact of current European agricultural policies is discussed, with special reference to agri-environmental measures and set-aside policy.

**6.** This work provides an example of an avian species that benefits from cultivated landscapes, providing that they are extensive rather than intensive. We propose a simple conceptual model to illustrate how little bustards, and possibly grassland birds in general, might respond where natural habitats are modified along orthogonal axes representing cultivation and agricultural intensification.

*Key-words:* farmed landscapes, grassland birds, habitat use, intensification, *Tetrax tetrax.*

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## Introduction

Although recent concerns about the erosion of biodiversity mainly focus on the clearing and transformation of natural habitats, many managed landscapes also hold declining species (Tucker 1997). Traditional agricultural landscapes, especially those Colonized early in human history, are typical of this situation. As natural habitats have been transformed into agricultural land during the last 10 000 years, many species have colonized these new habitats (O'Connor & Shrubb 1986; Bouma, Varralyay & Batjes 1998). Traditional farmed landscapes often consist of complex and extensive mosaics with high levels of biodiversity (Potter 1997; Walk & Warner 2000). Over recent decades, however, farmland in many industrialized countries has been profoundly altered, mainly through the intensification of farming techniques and related changes in land-use (Fuller *et al.* 1995; Chamberlain *et al.* 2000; Siriwardena *et al.* 2000). Farmland is altered at various scales, from single habitats, for example by mechanization, spraying, changes in vegetation phenology and composition, to the entire landscape, for example by changes in landscape composition and structure. The numbers and range of many farmland species have declined as a result of these changes (Tucker & Heath 1994; Green 1996; Pain & Dixon 1997; Blanco, Tella & Torre 1998; Bouma, Varralyay & Batjes 1998; Chamberlain *et al.* 2000; Ormerod & Watkinson 2000; Söderström & Part 2000; Donald, Green & Heath 2001). In western Europe, this phenomenon is so marked that farmland hosts the highest proportion of bird species with unfavourable conservation status (Tucker 1997). Similar declines have been noted in farmed landscapes in North America (Jobin, DesGranges & Boutin 1996; Herkert 1997).

The diversity of changes in farming practices often makes it difficult to identify the exact mechanisms through which wildlife populations are affected (Fuller *et al.* 1995; Signal & McCracken 1996; Chamberlain *et al.* 2000). Moreover, different species are likely to show contrasting responses to given modifications. The definition of sound conservation measures for species or habitats affected by changes in farming practices relies upon precise resolution of these apparently complex patterns, for example by understanding exactly how species use habitats.

The little bustard *Tetrax tetrax* L. is a medium-sized ground-nesting bird (weight 565-960 g; Cramp & Simmons 1980) that inhabits steppes and lowland farm-land of Europe, western Asia and north Africa. Until the early 1900s, the little bustard was common in open fields in many parts of Europe. Since then, the species has disappeared from a large part of its former range (Cramp & Simmons 1980; Schulz 1985), with remaining populations declining continuously, especially in France, Italy, Ukraine and parts of Spain (Goriup 1994; De Juana & Martínez 1996; Jolivet 1996, 1997). The species is listed as 'near-threatened' (Collar, Crosby & Stattersfield 1994), and the intensification of farming systems is thought to be the main cause of decline (De Juana *et al.* 1993; Goriup 1994). French populations, for instance, have declined during the last 20 years from 7200-8500 breeding males in 1978-79 (Métais 1985) to an estimated 1087-1256 in 1996(Jolivet 1997). However, the decline has not been homogeneous. Curiously, the only natural steppe of France, the Crau area (southern France), harboured no little bustards until the 1950s. Since then, the population in the Crau has reached several hundred males (Cheylan 1985) while the remaining French populations are in steep decline. Perhaps more surprisingly, this population increase has taken place while agriculture in the Crau has undergone profound changes by which arable land has been developed over the natural steppe. Little bustard population trends in the Crau thus contrast with the trend in the rest of Europe, suggesting that the relationship between agricultural development and decrease among little bustards may not be straightforward.

In this study, we analysed present and historical distribution patterns of the little bustard population of the Crau in an attempt to identify the links between farming changes and population trends. Surveys of little bustard breeding males, conducted in 1998 and 1999, were used to quantify how male densities varied among habitat types and landscapes. We documented historical trends in little bustard numbers and changes in landscape composition in the Crau in order to test the hypothesis that bustard numbers have increased as a result of landscape changes. We compared our results with patterns of little bustard population trends observed in farmed landscapes elsewhere in Europe, and used them to propose a guiding framework for studies relating changes in grassland birds to farmland.

## Methods

### STUDY AREA

The Crau is a 600-km$^2$ alluvial plain in Provence, south-eastern France, *c.* 50 km north-west of the city of Marseille. It is the ancient delta of the Durance river (Etienne, Aronson & Le Floc'h 1998), where the original habitat is a stony, semi-arid steppe dominated by the perennial grass *Brachypodium retusum* (Pers.) Beauv. (Molinier & Tallon 1949). This steppe has been grazed by sheep for at least 2000 years (Fabre 1998) and pastoralism has shaped vegetation composition and structure (Devaux *et al.* 1983). Irrigation schemes started in the 16th century eventually initiated the cultivation of the steppe, mainly as hay-meadows, which now cover 120 km$^2$. After World War II, highly intensive crops were developed, such as peach-tree orchards and green-house market gardening (Etienne, Aronson & Le Floc'h 1998). As a result of irrigation and urbanization, only one-sixth (about 100 km$^2$) of the original steppe remains.

Our study area covered 378 km$^2$. It included all the remaining steppe habitat and most of the little bustard's range in the Crau. To facilitate mapping and surveys, the study area was divided into nine sectors ranging from 29·3 to 49·4 $km^2$ (Fig. 1).

SURVEY OF BREEDING MALES

The little bustards' mating system involves 'exploded leks' (Schulz 1985; Jiguet, Arroyo & Bretagnolle 2000), in which males display in clustered territories that are visited by females for copulation only. Females subsequently nest and raise the young alone while males keep on displaying. Surveys of little bustard populations therefore usually entail recording males in the spring when they display, because females are inconspicuous at this time. Surveys took place between 1 May and 15 June 1998 and 1999. They encompassed all open habitats in 1998, whereas in 1999 sampling effort was mainly restricted to habitats known to be favoured by little bustards, and was less extensive than in the previous year. Following Schulz (1985) and De Juana & Martinez (1996), survey sessions of 2 h each were conducted daily at peak display periods, i.e. one starting 30 min before sunrise and the other ending 30 min after sunset. Surveys were not conducted in adverse weather, i.e. when rain or wind reduced display activity and/or detection range. During each session, predefined routes, including all possible roads or paths in a given area, were travelled by car. We stopped every 500 m for 5 min to count calling males located by ear or by scanning the surroundings with 10 x 50 binoculars. At each stop, the amount of area surveyed was recorded on a 1 : 25 000 map. When topographical features impaired vision, the radius of the area considered as surveyed was set at 250 m, which was the distance at which any calling male was sure to be heard in fair weather. When topography and vegetation height allowed long-distance visibility, males could be detected up to 1 km away. All males were positioned on maps and the habitat in which they displayed was recorded. Habitat categories included steppe, fallow, grazed crop, other pasture, legume crop, hay-meadow, grain crop and others. Routes were surveyed at random in order to avoid sampling bias.

LANDSCAPE COMPOSITION

Permanent habitats were mapped using 1 : 17 000 infra-red aerial photographs taken in July 1997. Annual crops were mapped in the field during the survey of breeding males in spring 1998, as well as any modification in permanent habitats that had taken place since the aerial photographs were taken. Maps were updated during the 1999 male survey. Land-use maps were redrawn on Geographic Information System (GIS) software MAPINFO Professional™ 5·0 (MapInfo Corporation 1992) to allow precise calculation of habitat areas. This information was used to group the nine sectors previously defined according to the pro-portion of steppe habitat retained, which provided an index of the structural change caused by agricultural development at a local scale.

STATISTICAL ANALYSIS OF MALE DISTRIBUTION

To estimate the density of breeding males by habitat type, survey maps were divided into square sampling units of 0·0625 $km^2$ (250 x 250 m). Squares were only considered for analysis when > 75% of their area had been surveyed. We recorded the number of males and the dominant habitat within each surveyed square, as well as the agricultural zone (see the Results) in which the square was located. The scale used was designed to keep sampling unit size relevant to the bird's ecology, with square size approximately equal to the median size of a male territory (0·067 $km^2$; Jiguet, Arroyo & Bretagnolle 2000).

We used GLIM 3·77 software (Payne 1985) to investigate whether male abundance differed among habitats and agricultural zones, by modelling the number of breeding males per sampling square against habitat type and agricultural zone. Model parameters were estimated by fitting a Poisson distribution to the data, using log-transformation as a link function (Crawley 1993), The fit of all possible models, including the complete model and all its subsets, was assessed using Akaike's information criterion (AIC; Lebreton *et al.* 1992; Burnham & Anderson 1998), with AIC = DEV + 2 np (where DEV = model deviance and np = number of estimated parameters). The model with the lowest AIC was selected as the most parsimonious model that fitted the data, i.e. the one that incorporated the most variation using the smallest number of estimated parameters. A total of 19 models was tested, considering that main effects were required to figure in any model in which their interaction term was specified.

Once the factors that appeared to influence male abundance significantly were identified by model selection, we examined in more detail how male abundance varied among habitats and agricultural zones by simplifying the most parsimonious model, a procedure equivalent to comparison of means in classical analysis of variance (Crawley 1993). Model simplification was performed by pooling factor levels together according to least differences. Factor levels were considered to differ significantly if pooling them caused an increase in model AIC, in which case they were specified separately in the next steps. They were considered not to differ if pooling them caused a decrease in model AIC, and were therefore considered jointly in further steps.

Parameter estimates resulting from model simplification were used to extrapolate the number of males in areas not surveyed. These estimates were then added to the number of males counted during the 1998 survey to obtain an estimate of total population size. Mean density estimates per unit square and associated 95% confidence interval limits were calculated using the outputs of model simplification (on a logarithmic scale) then exponential-transformed prior to extrapolation.


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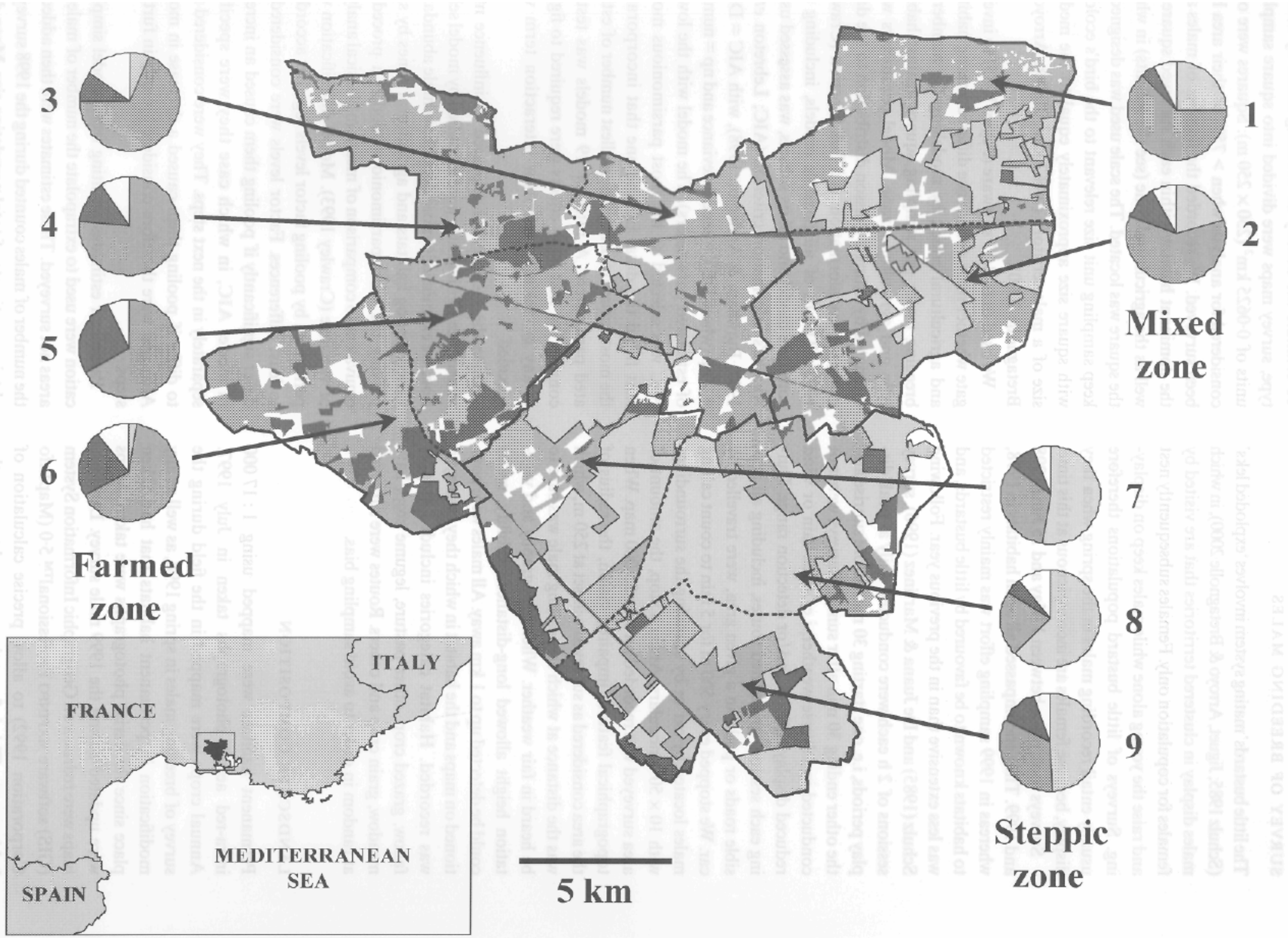


**Fig. 1.** Land-use in the study area during spring 1998. Light grey, natural steppe; medium grey, agriculture; dark grey, other land-uses; white, not recorded: dotted fines, sector limits; continuous lines, agricultural zone limits. Pie charts represent proportions of land-use types for each sector, numbered 1–9.

LANDSCAPE CHANGES AND HISTORICAL STATUS OF LITTLE BUSTARDS

Scientific and general literature were reviewed in search of data on landscape dynamics in the Crau and on the historical status of the little bustard population, particularly emphasizing the work of Cheylan (1985, 1998) which provided an extensive review of both bustard and landscape changes before the 1980s. Steppe area in 1983 was calculated by digitizing the map drawn by Devaux *et al.* (1983). These data were combined with our estimates of present population size and steppe area to plot the evolution of both variables in time.

## Results

LANDSCAPE COMPOSITION

Natural steppe habitat now covers only 102 km$^2$ in the study area (Table 1). Cultivated land covers about 52% (198·1 km$^2$), with permanent hay-meadows predominant (76·2 km$^2$). Fallow land, encompassing long-term fallow as well as rotational set-asides, also represents a significant proportion of the agricultural land (46·4 km$^2$, 12·3% of the study area). Most is grazed by sheep, but a small proportion of set-asides, under Common Agricultural Policy agreements, is not. On the whole, low-intensity land-uses linked to pastoralism (fallow, grazed crops, legumes and other pastures) represent nearly 30% of all the agricultural land. Steppe, fallow and grazed crops (winter-sown dry legume and/or cereal crops) are grazed by sheep from March to late June, although some fallow and steppe patches may also be grazed in autumn and winter. Stocking rates vary from about 2·4 sheep ha$^{-1}$ on fallow and steppe, to 20·25 sheep ha$^{-1}$ on grazed crops (Fabre 1998).

Recently planted orchards are the dominant intensive crop, covering 39·9 km$^2$ (10·5% of study area), while intensive grain crops (cereals + tilled + oilseeds + ploughed; Table 1) cover 15 km$^2$.

The nine sectors of the study area fell into three clusters on the basis of the proportion of steppe habitat they retained (Fig. 1): sectors 7, 8 and 9, located in the centre of the study area, were predominantly steppe (minimum 49·3%, sector 9; maximum 62·3%, sector 8; Table 1); sectors 1 and 2, in the north-east, were dominated by a mixture of extensive and intensive agriculture (62·9% sector 1, 60·5% sector 2; Table 1) but still retained from 20·4% (sector 1) to 24·8% (sector 2) of steppe habitat; sectors 3, 4, 5 and 6, located in the north-west of the study site, were also largely dominated by a mixture of extensive and intensive agriculture (minimum 64·4%, sector 6; maximum 76·3%, sector 4; Table 1) but had lost most, of their natural steppe habitat (minimum 0%, sectors 4 and 5; maximum 6·6%, sector 3). This zoning reflected similarities in land-use that followed from the distribution of irrigation facilities. This clustering of the sectors into steppic (sectors 7, 8 and 9), mixed (sectors 1 and 2) and farmed (sectors 3, 4, 5 and 6) zones was used to investigate differences in little bustard abundance with regard to landscape composition.

MALE LITTLE BUSTARD ABUNDANCE AND DISTRIBUTION

In 1998, 160·5 km$^2$ of open habitat was surveyed (42·5% of the study area; Fig. 2a), in which a total of 328 little bustard males (Fig. 2b) was counted (overall density 2·0 males km$^{-2}$). Breeding male abundance varied strongly among agricultural zones (Fig. 2b): males were most abundant in the mixed zone (51% of all males; 4·2 males km-2), while the

**Table 1.** Land-uses in the study area of the Crau during spring 1998 (area in km$^2$). 'Grazed crops' are dry winter-sown cereals and/or legumes grazed by sheep in the spring, and 'Other pastures' are permanent or semi-permanent sown pastures for horses or cattle. See Fig. 1 for zone limits

| | Steppic zone | Mixed zone | Farmed zone | Total |
|---|---|---|---|---|
| Steppe | 76·60 | 21·80 | 3·68 | 102·08 |
| Wetlands | 7·31 | 3·04 | 14·92 | 25·27 |
| Forests | 0·01 | 1·57 | 1·76 | 3·34 |
| **Total natural habitats** | **83·92** | **26·40** | **20·37** | **130·68** |
| Hay-meadows | 8·86 | 25·98 | 41·39 | 76·23 |
| Fallow | 13·25 | 12·05 | 21·12 | 46·41 |
| Fruit-tree orchards | 14·19 | 12·62 | 13·05 | 39·85 |
| Cereals | 1·09 | 1·81 | 8·42 | 11·31 |
| Greenhouse market gardening | 0·57 | 3·61 | 4·14 | 8·33 |
| Grazed crops | 0·82 | 2·35 | 2·92 | 6·09 |
| Legumes | 0·23 | 0·23 | 3·56 | 4·02 |
| Tilled crops + oilseeds | 0·26 | 0·42 | 1·71 | 2·40 |
| Other pastures | 0·89 | 0·16 | 1·12 | 2·17 |
| Ploughed fields | 0·35 | 0·01 | 0·94 | 1·30 |
| **Total agriculture** | **40·52** | **59·24** | **98·36** | **198·12** |
| Urban and industrial areas | 4·25 | 2·83 | 8·34 | 15·42 |
| Not recorded | 10·51 | 7·54 | 15·58 | 33·63 |
| **Total** | **139·20** | **96·01** | **142·64** | **377·85** |

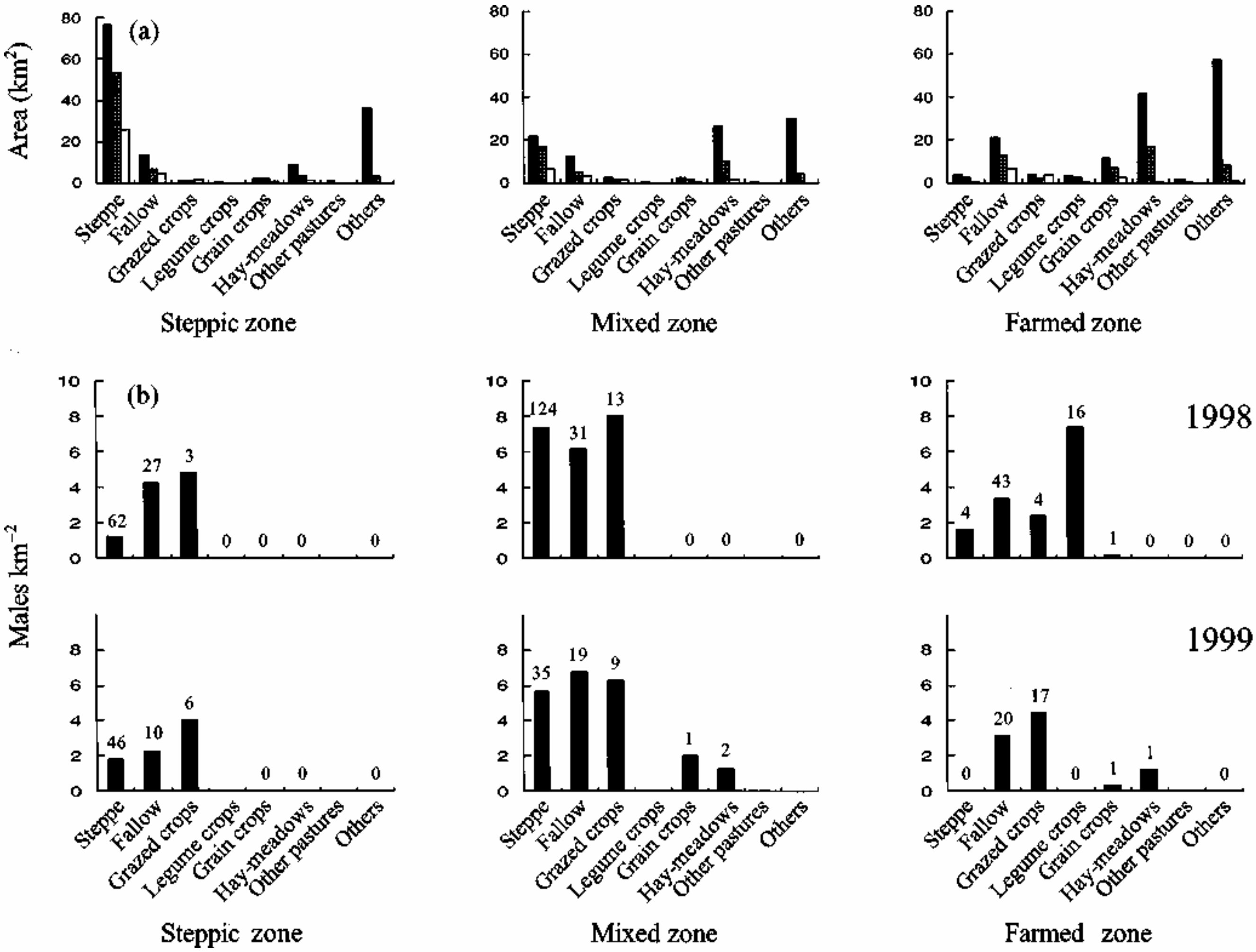


**Fig. 2.** (a) Mean area of open habitats ('Steppe' to 'Other pastures') and other or undetermined habitats ('Others') within each agricultural zone (black bars) and area surveyed during the 1998 (grey bars) and 1999 (white bars) seasons, (b) Little bustard male densities per habitat type in each agricultural zone in 1998 (top) and 1999 (bottom). Numbers represent the actual number of males recorded.

farmed and steppic zones held, respectively, 21% and 28% (1·3 males $km^{-2}$ in both zones). About 58% (2·6 males $km^{-2}$) of all males displayed on steppe habitat, of which most were found in the mixed zone (124 males). Fallow land also held a significant proportion of males (31%, 4·2 males $km^{-2}$). Overall densities were highest in grazed crops and legume crops (5·2 and 6·7 males $km^{-2}$, respectively), but these crops held only 36 males due to their restricted area (3·9 and 2·4 $km^2$ surveyed, respectively; Fig. 2a). Other open habitats were seldom used; only one male was observed in a cereal field and none in any of the remaining habitats (Fig. 2b).

In 1999, the survey of 60·8 $km^2$ (16·1% of the study area; Fig. 2a) yielded a count of 167 males (Fig. 2b), with patterns of distribution and habitat use similar to 1998: the highest densities were in the mixed zone, and the majority of males displayed on steppe habitat (48·5%, 2·5 males $km^{-2}$) and fallow land (29·3%, 3·6 males $km^{-2}$). Grazed crops again showed the highest densities (4·7 males $km^{-2}$) despite low area of cover, but no male was recorded on legume crops due to restricted survey of this habitat. Two males were recorded displaying on grain crops and three and three on hay-meadows, but overall densities in these habitats remained low.

Overall, only steppe, fallow land, grazed crops and legume crops were used regularly by displaying males in the Crau, of which only the two former were large enough to hold a significant proportion of recorded males (Fig. *2V),* totalling 88% in 1998 and 78% in 1999.

### VARIATIONS IN MALE LITTLE BUSTARD DENSITIES

For the statistical analysis of male abundance, we included only the most commonly used habitats, namely steppe, fallow land, grazed crops and legume crops; the latter were pooled into a single category because they only covered a reduced area and were similar structurally. Factors incorporated in the initial model were years (1998, 1999), zone (mixed, farmed and steppic) and habitat (steppe, fallow and grazed/legume).

The most parsimonious model (Table 2) showed no significant effect of year on breeding male density, but there were significant effects of agricultural zone, habitat type and their interaction (model 5). Further simplification of the most

**Table** 2. Model selection for number of male little bustards per sampling square. The most parsimonious model, i.e. with the lowest AIC, is highlighted. Out of 19 possible models, only models with AIC less than 10 units above the most parsimonious model (listed in decreasing number of estimated parameters) are shown. Model parameters: year (YEAR: 1998, 1999), agricultural zone (ZON: mixed, farmed and steppic) and habitat (HAB: steppe, fallow, grazed/legume crops). No., model number; np, number of estimated parameters; DEV, model deviance; AIC, Akaike's Information Criterion (AIC, DEV + 2 np)

| No. | Model parameters | np | DEV | AIC |
|---|---|---|---|---|
| 1 | YEAR x ZON x HAB (full model) | 18 | 1634·3 | 1670·3 |
| 2 | YEAR + ZON + HAB + ZON.HAB + YEAR.ZON + YEAR.HAB | 14 | 1640·9 | 1668·9 |
| 3·1 | YEAR + ZON + HAB + ZON.HAB + YEAR. ZON | 12 | 1640·9 | 1664·9 |
| 3·2 | YEAR + ZON + HAB + ZON.HAB + YEAR.HAB | 12 | 1643·9 | 1667·9 |
| 4 | YEAR + ZON + HAB + ZON.HAB | 10 | 1643·9 | 1663·9 |
| **5** | **ZON + HAB + ZON.HAB** | **9** | **1643·9** | **1661·9** |
| 6 | ZON + HAB | 5 | 1660·9 | 1670·9 |

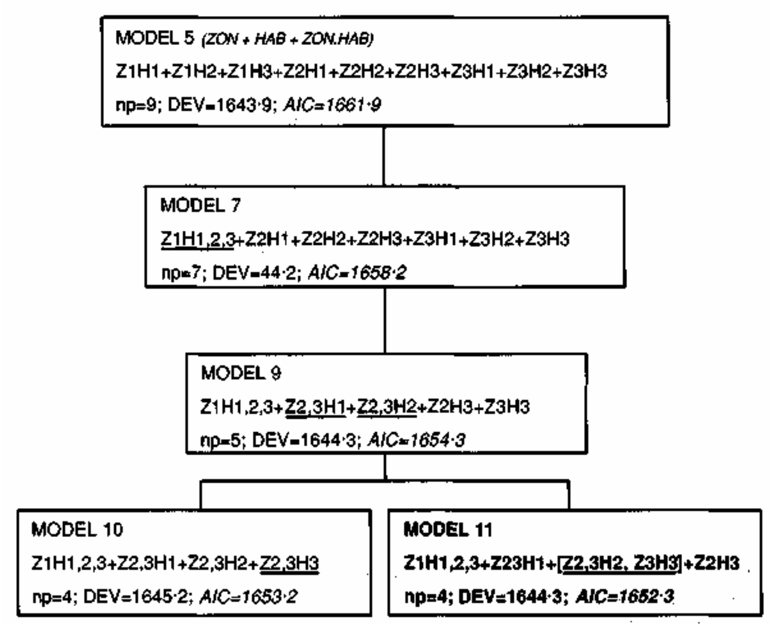


**Fig. 3.** Simplification of model 5, the most parsimonious model found by model selection (simplified diagram). At each step, parameter estimates that show the least differences (see Table 3) are pooled. Parameters pooled from the previous model are underlined. Model with lowest AIC is highlighted, np, number of estimated parameters; DEV, model deviance; AIC, Akaike's information criterion (AIC = DEV + 2 np). Factor modalities: zone, Z1, mixed zone; Z2, farmed zone; Z3, steppic zone; habitat, H1, steppe; H2, fallow; H3, grazed + legume crops.

parsimonious model by pooling parameters (model 11; Fig. 3 and Table 3) allowed us to clarify bustard response to agricultural zone and habitat type, and showed that: (i) steppe, fallow and grazed/legume crops all held particularly high densities in the mixed zone, averaging 6·7 males $km^{-2}$, with no significant differences among habitats; (ii) steppe habitat in the steppic and farmed zones held an average of only 1·4 males $km^{-2}$; (iii) other habitats in the steppic and farmed zones held intermediate densities, 4·4 males $km^{-2}$ for grazed/legume crops in the farmed zone and an average of 2·9 males $km^{-2}$ for fallow in the farmed zone and fallow and grazed/legume crops in the steppic zone.

Total population size (Table 3) was extrapolated by applying estimated densities per habitat type and agricultural zone, derived from model 11, to 55·4 $km^2$ (i.e. 14·7% of the total study area of 378 $km^2$) of suitable habitat not surveyed in 1998. To this end, areas not surveyed were calculated for each of the three types of habitats included in the model in each agricultural zone, using habitat area not covered by sampling squares in the land-use map of 1998. The estimated number of males in areas that were not surveyed was added to the actual number of males found during this season. This method led to an overall estimate of 503 breeding males in the study area (95% confidence interval 473 - 539).

## LANDSCAPE DYNAMICS AND LITTLE BUSTARD TRENDS IN THE CRAU

Natural steppe covered about 600 $km^2$ in the Crau before the first irrigation schemes were initiated in 1552 (Cheylan 1998); steppe habitat was lost slowly over several centuries, and 360 $km^2$ was left by the mid-1800s (Fig. 4). Steppe has since been converted into arable land at a mean rate of about 2 $km^2$ $year^{-1}$; (Cheylan 1998), falling to 260 $km^2$ in 1930. Digitizing the map

**Table 3.** Estimates of the density of breeding male little bustards and extrapolated population estimate. Parameter modalities: zone, Z1, mixed zone; Z2, farmed zone; Z3, steppic zone; habitat, H1, steppe; H2, fallow; H3, grazed + legume crops. Model 11 was the most parsimonious model resulting from step-down selection (see Fig. 3). Male densities (males $km^{-2}$) were calculated by exponential-transformation of model estimates. 95% C1 = 95% confidence interval limits of male densities, calculated using standard errors of estimates at the original log-scale prior to exponential transformation. Estimated densities from model 11 were used to estimate the number of males on areas not surveyed and associated 95% CI (1), which were added to actual counts from 1998 (2) to produce an estimate of total population
(1+2)

| | Step I: model selection and simplification | | | | Step II: extrapolation and population estimate | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Model 11 | | Not prospected (1) | | | | Total estimate (1 + 2) | |
| | Density | 95% CI | Density | 95% CI | Area ($km^2$) | Estimate | 95% CI | Counts (2) | Estimate | 95% CI |
| | 6·90 | (5·90-8·07) | | | 5·23 | 35 | (31-40) | 124 | 159 | (155-164) |
| | 6·48 | (4·92-8·52) | 6·74 | (5·92-7·67) | 6·98 | 47 | (41-54) | 31 | 78 | (72-85) |
| Z1H3 | 6·20 | (4·03-9·55) | | | 0·96 | 6 | (6-7) | 13 | 19 | (19-20) |
| Z2H3 | 4·44 | (3·19-6·19) | 4·44 | (3·19-6·19) | 2·61 | 12 | (8-17) | 20 | 32 | (28-37) |
| Z3H3 | 3·03 | (1·44-6·35) | | | 0·24 | 1 | (1-1) | 3 | 4 | (4-4) |
| Z3H2 | 2·89 | (2·09-3·99) | 2·88 | (2·24-3·68) | 4·75 | 14 | (11-18) | 27 | 41 | (38-45) |
| Z2H2 | 2·81 | (2·16-3·67) | | | 8·30 | 24 | (19-29) | 43 | 68 | (63-73) |
| Z3H1 | 1·41 | (1·17-1·70) | 1·40 | (1·17-1·69) | 25·16 | 35 | (28-44) | 62 | 97 | (90-106) |
| Z2H1 | 1·33 | (0·50-3·54) | | | 1·18 | 2 | (1-2) | 4 | 6 | (5-6) |
| Total | | | | | 55·41 | 176 | (146-212) | 327 | 503 | (473-539) |

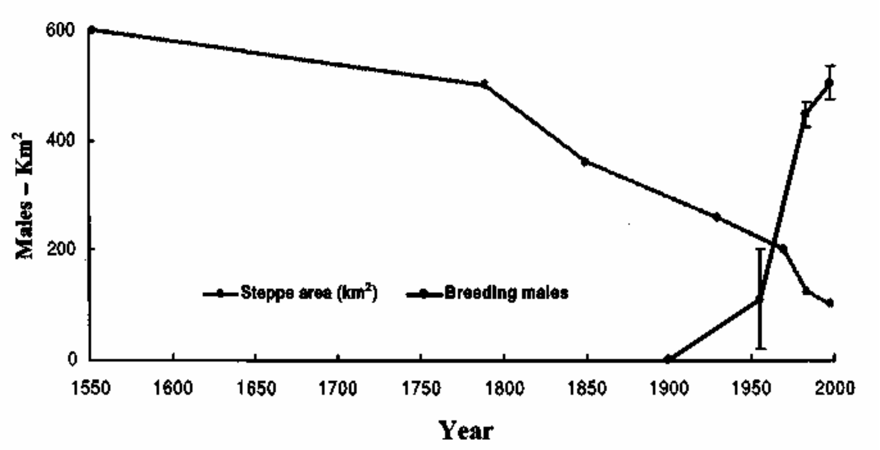


**Fig. 4.** Reduction of natural steppe area in the Crau between 1550 and 1998, and evolution of little bustard breeding male estimates. Data on steppe area from Devaux *et al.* (1983), Cheylan (1998) and present study. Data on male estimates from Cheylan (1985) and present study. Error bars indicate confidence interval of estimates; for 1955, the highly conservative range of 20-200 males stands for the 'few breeding couples' reported by Levêque & Ern (1960).

from Devaux *et al.* (1983) led to an estimate of 124 $km^2$ of steppe habitat remaining by 1980. The number of sheep grazing in the Crau dropped from about 200 000 heads (including the neighbouring Camargue area) at the beginning of the century to 140 000 in 1963 and around 100 000 in the 1980s (Fabre 1998). However, as the area of natural steppe was also cut by a half during the same period of time, overall grazing pressure on the steppe probably remained the same.

Little bustards were unknown in mediterranean France before the 20th century (Cheylan 1985); it was a rare wintering species in the Crau at the beginning of the century, and was not even mentioned in specialized hunting books (Samat 1906). The first documented record of breeding was in 1955 (Levêque & Ern 1960), when 'a few breeding pairs' were reported. Cheylan (1985) proposed an estimate of 425-470 breeding males (Fig. 4) from plot surveys performed between 1974 and 1983.

## Discussion

### DISTRIBUTION AND HABITAT USE OF BREEDING MALES IN THE CRAU

We observed little bustard breeding males mainly in steppe (58% and 48·5% of recorded males in 1998 and 1999, respectively) and extensive agricultural habitats (42% and 48·5%). Extensive agricultural habitats held high male densities, local averages ranging from 2·8 to 6·5 males $km^{-2}$. These habitats have often been reported as selected by bustards (Cheylan *et al.* 1983; Schulz 1985; Belik 1992; Martinez 1994, 1998; Salamolard, Bretagnolle & Boutin 1996; Salamolard & Moreau 1999). In contrast, more intensive agricultural habitats, such as grain crops and hay-meadows, were generally avoided, although they may be used transiently in the early stages of vegetation growth. Hay-meadows, usually considered to be extensive habitats, are managed rather intensively in the Crau: fields are flooded every 10 days in spring and summer, and hay is cut three times between May and August. After harvest, vegetation height reaches 70 cm within 1 month (A. Wolff, unpublished data), and hay-meadows rapidly become too high and dense for little bustards.

Although natural steppe held more than half the estimated breeding male population during our study (262 males; Table 3), densities in this habitat varied considerably. We suggest that this variation depended mainly on landscape composition: densities were low in the farmed zone where only a few, small (0·9-1·3 $km^2$) patches of steppe remain, and in the steppic zone where steppe is very abundant (1·3 males $km^{-2}$ in both zones). In contrast, bustard density was high (6·9 males $km^{-2}$) in the mixed zone where rather large (up to 6·5 $km^2$) steppe patches are interspersed with agricultural habitats. Although little bustards are commonly regarded as steppe birds (Cramp & Simmons 1980), vast areas of semi-arid steppe in the Crau were apparently not as suitable as extensive crops and fallow. In fact, arid or semi-arid steppes do not appear to be optimal for little bustards in western Europe: in Spain, the species is abundant in farmed pseudosteppes, where landscapes are dominated by dry cereals and medium-to long-term fallow grazed by sheep, but is absent or scarce in the most arid steppe areas (Pleguezuelos & Manrique 1987; De Juana *et al.* 1988; Suárez *et al.* 1992; Díaz, Asensio & Tellería 1996).

Habitat diversity in agricultural landscapes can benefit grassland birds that require several habitats for foraging and breeding (Söderström & Part 2000). The abundance of little bustard males in Spanish pseudosteppes is positively correlated with habitat diversity (Martínez 1994) and landscape fragmentation (Cam-pos & López 1996). In the Crau, higher male abundance on steppe in the mixed landscape suggests that breeding bustards may require a minimum degree of habitat diversity. This may reflect complementation or supplementation among habitats (Dunning, Danielson & Pulliam

1992), which may occur through various processes: (i) steppe may not provide males with sufficient resources during the breeding season (e.g. food may be obtained from adjacent agricultural habitats); (ii) steppe may be a poor nesting habitat for females, prompting males to display in the vicinity of better nesting habitats where they are likely to attract more females; (iii) cultivated land may be selected outside the breeding season (winter or post-breeding), so that constraints on breeding dispersal distances may result in higher densities near agricultural wintering or post-breeding grounds. Differential habitat use depending on landscape composition and on the spatial arrangement of patches influences the distribution of several birds (Whitcomb, Whitcomb & Bystrak 1977; Clark & Weatherhead 1987; Petit 1989) and other organisms (Law & Dickman 1998; Pope, Fahrig & Merriam 2000). Alternatively, direct edge effects between steppe and agricultural patches (modification of steppe vegetation structure, composition, and/or arthropod abundance) may also influence bustard distribution.

Extensive agricultural habitats could be more attractive to bustards than semi-arid steppe because they have higher plant productivity or higher insect biomass, although these hypotheses have not been tested. Similarly, extensive agricultural habitats are probably more attractive than intensive crops because (i) they hold higher plant diversity and arthropod biomass and diversity, providing adult and chick food (Donazar, Negro & Hiraldo 1993; Brickle *et al.* 2000; Henderson, Vickery & Fuller 2000); (ii) vegetation is lower, less uniform and/or less dense (Henderson *et al.* 2001), which might represent a better compromise between protection cover, long-distance vision and mobility.

### DYNAMICS OF FARMED LANDSCAPES AND LITTLE BUSTARDS

Our results show that 473-539 little bustard males were present on a 378-km$^2$ study area that encompassed most of the potential breeding habitats in the Crau. The Crau therefore holds the largest little bustard population in France, representing 38-49% of the most recent national estimates (Jolivet 1997). The contrasting trends between the little bustard populations of the Crau and other French regions may reflect different phases in the evolution of their farmed landscapes. In the Crau, pastoralism has remained the main vector of agricultural development, so that 30% of arable land in the study area is still devoted to extensive sheep-rearing. In most other cultivated lowlands in France, such mixed agriculture started to disappear after World War II, when increasing production demands led to a progressive abandonment of live-stocking in favour of intensively managed grain (Potter 1997). Little bustard male densities in the Département des Deux-Sèvres (western France) experienced a 90% decrease between the late 1970s (1000 males; Métais 1985) and 1999 (110 males; V. Bretagnolle & Groupe Ornithologique des Deux-Sèvres, unpublished data), during which time the area of permanent agricultural grasslands dropped from > 50% to less than 8% of the total area (Recensement Général Agricole & V. Bretagnolle, unpublished data). Even with varying accuracy of surveys, such changes in population estimates are large.

There are extensive agricultural landscapes similar to the Crau in several regions of Spain and Portugal where many lowland grassland birds with unfavourable conservation status are still abundant (De Juana & Martínez 1996; Delgado & Moreira 2000; Lane, Alonso & Martin 2001). However, irrigation schemes in these regions are currently reducing the availability of extensive agricultural habitats (Donazar, Negro & Hiraldo 1993; Bignal & McCracken 1996), affecting many grassland species (Suárez, Naveso & De Juana 1997; Lane, Alonso & Martin 2001) including little bustards (De Juana & Martínez 1996).

### IMPLICATIONS FOR LITTLE BUSTARD CONSERVATION

The current breeding distribution of little bustards in the Crau suggests that the availability of extensive agricultural habitats in the landscape is a key factor determining little bustard abundance. If effects were similar elsewhere, the general decline of little bustards in Europe may simply result from the reduction of extensive habitats linked to livestock rearing and cultural rotation, although additional effects of other processes linked to agricultural intensification cannot be ruled out (Chamberlain *et al.* 2000). Bustard population trends in the Crau suggest that restoring a significant proportion of extensively managed agricultural habitats in farmed landscapes might allow declining populations to recover within a few decades. Since 1992, the European Union Common Agricultural Policy (CAP) has led to an increase in the area of set-aside, which may benefit various grassland birds (Wilson *et al.* 1997; Chamberlain *et al.* 1999; Brickle *et al.* 2000; Henderson *et al.* 2000; Henderson, Vickery & Fuller 2000). However, several factors limit the effects of current set-aside regulations. First, compulsory mechanical destruction of the green cover on set-asides in May or June risks nest or brood destruction; secondly, 'industrial crops' (e.g. oilseed rape for biodiesel production) are grown on a significant portion of set-asides, especially in France (24% of French set-aside area in 1997-98; European Communities 1995-2000), with limited benefits to grassland birds; thirdly, set-aside policies are subject to changes according to economic pressures (Henderson *et al.* 2001). More reliable agri-environment schemes are therefore required to ensure the restoration of farming practices appropriate for wildlife. Agri-environment schemes developed in the Crau since 1991 have maintained extensive management practices over large areas of open habitat (Boutin 1998; Fabre 1998).

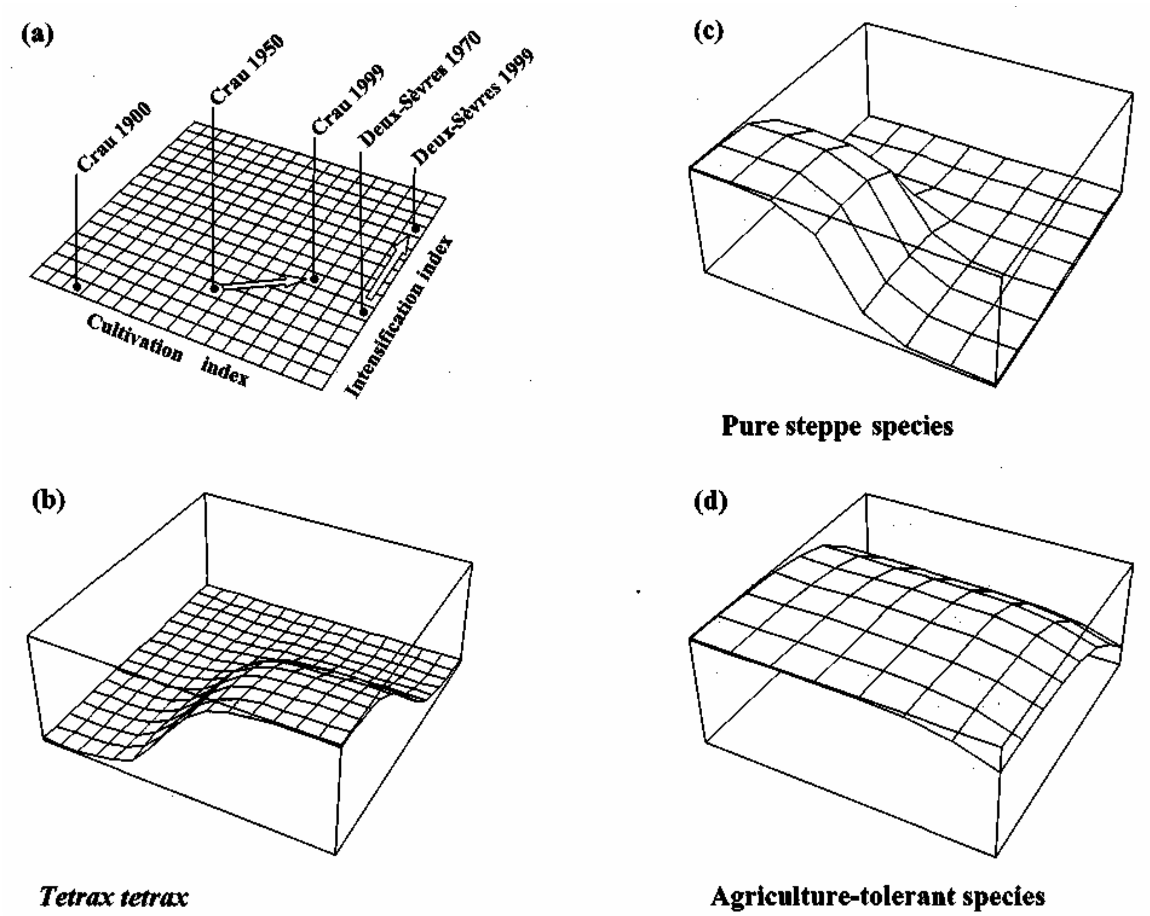


**Fig. 5.** Schematic representation of farmland changes and trends in grassland bird populations, (a) Classification of farmed landscapes according to the ratio of agricultural habitats to natural habitat, e.g. grassland or steppe (cultivation index), and the degree of intensification of farming practices (intensification index); (b) expected population levels (arbitrary scale) of *Tetrax tetrax* based on data from the Crau and the Département des Deux-Sèvres; expected trends for steppe birds either (c) restricted to extensively managed steppe habitat (e.g. pin-tailed sandgrouse *Pterocles alchata,* Duponts'lark *Chersophilus duponti)* or (d) tolerant to higher degrees of modification of their original habitat (e.g. stone curlew *Burhinus oedicnemus,* Montagu's harrier *Circuspygargus).*

## A FRAMEWORK FOR STUDYING BIRD/ LANDSCAPE RELATIONSHIPS IN FARMLAND

Based upon our results, we propose a guiding framework for studying changes in farmed landscapes and the population dynamics of grassland birds. We suggest that our understanding of bird/landscape relationships in farmland could be clarified by distinguishing two processes (Fig. 5a): (i) the replacement of natural habitats by agricultural habitats; (ii) the intensification of farming practices. The ratio of agricultural vs. natural habitats is easily measurable, although in some cases it may be difficult to distinguish between purely natural and anthropogenic grasslands. Intensification may be more difficult to quantify, due to the variety of changes it encompasses (Chamberlain *et al.* 2000; Donald, Green & Heath 2001). In the Crau, an intensification index for open habitats should for instance reflect both grazing pressure and crop management intensity (e.g. chemical and pesticide input, crop yield, labour intensity).

Landscapes at a local or regional scale may be classified according to these two variables. The two processes can act independently, as their chronological occurrence in European farmland suggests. In most of western Europe, natural habitats had disappeared long before farming intensification experienced the sharp increase observed during the 20th century (e.g. Deux-Sèvres 1970 vs. 1999; Fig. 5a). In contrast, farmed landscapes in southern Europe are often still characterized by a significant proportion of natural habitats, and their replacement by arable land is synchronous with the intensification of farming practices (e.g. Crau 1950 vs. 1999; Fig. 5a).

Bird species' responses to landscape changes (e.g. their abundance) can also be classified according to their reaction to cultivation and intensification. The recent dynamics of little bustard populations in various western European landscapes suggest that population levels may increase with the proportion of agricultural habitats in the landscape, and decrease with intensification (Fig. 5b). The abundance of bird species more typical of steppic habitats (e.g. sandgrouse *Pterocles* sp.) would be expected to decrease as both indices increase, although individual species may differ in their sensitivity to either process (Fig. 5c,d).

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