

Fate of unproductive and unattractive habitats: recent changes in Iberian steppes and their effects on endangered avifauna

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SUMMARY

Steppe ecosystems worldwide are affected by agricultural development and generally unprotected. Spanish shrub-steppes contain endangered avifauna, and this paper analyses their state of habitat conservation, the changes that have occurred in the last decade, primary productivity and its relationship with land exploitation and the richness of threatened birds, and avifauna responses to habitat loss. Fifty steppe remnants distributed throughout Spain and inhabited by Dupont's lark *Chersophilus duponti*, an endangered passerine representative of shrub steppe-like habitat, were studied. The study fragments were generally affected by agriculture exploitation, and steppe cover had significantly decreased in several isolated patches during the period 1991–1999. Steppe habitat recovered slightly in areas with low plant productivity indices, and decreased in extent in the most productive areas, in line with EU (European Union) agricultural policy recommendations to abandon marginal land of low productivity. The low overall primary productivity of Iberian steppes opened the way to industrial activities (mining, waste collection and wind-farming), which in the study areas occurred more frequently in steppe than in other habitat types that are more attractive to the public (woodland) or more productive (farmland). The emerging wind industry little affected the study plots, but the presence of anemometers suggests that the impact is likely to increase in the near future, especially in the largest steppelands. Dupont's lark was sensitive to the fragmentation of its habitat; crowding occurred in isolated and small fragments, possibly as a consequence of habitat constraints and species dispersal dynamics. Fragments inhabited by Dupont's lark also hosted other steppe birds with a high conservation value; the community of endangered birds, mostly adapted to arid conditions, was richest in the less productive sites. Only four shrub-steppe fragments are given some kind of protection throughout Spain, testifying to the limited public awareness about the value of this habitat. Urgent action is required to restore this habitat through abandonment of less productive farmland,

and to create a network of protected and connected steppelands, in order to assure the long-term viability of steppe specialists and the preservation of a habitat that is unique in Western Europe. This should be coupled to an effort to increase social consciousness of the ecological value of steppes and arid landscapes in general.

Keywords: agriculture intensification, birds, Dupont's lark, habitat loss, industrial development, steppe, wind farms

INTRODUCTION

Steppe ecosystems throughout the world have extensively collapsed through agricultural development, principally by conversion to arable lands and overgrazing of livestock (Fleischner 1994; Leimgruber *et al.* 2001; Sanchez-Zapata *et al.* 2003). Although many species of plants and animals are rare and threatened because of land transformations, steppe landscapes are generally under-protected (Barnard *et al.* 1998; Cofré & Marquet 1999; Hemstrom *et al.* 2002; Tella *et al.* 2004).

Steppes are included in Annex I of the EU (European Union) Habitat Directive (92/43/EEC) within the NATURA 2000 Network. Among European habitats, steppes comprise the greatest proportion of priority habitat types; 100% of steppe types are given priority for conservation. Eighty-three per cent of steppe avifauna show an unfavourable conservation status, a greater proportion than in any other habitat type (Tucker 1997), suggesting that steppe species represent the most threatened group of birds in Europe and could face serious risk of extinction in the near future (Tucker & Heath 2004).

In Europe, the best steppe landscapes are located in the Iberian peninsula. Despite including large areas of natural vegetation, these steppelands have been modelled by husbandry and traditional farming since the Neolithic (Alados *et al.* 2004). Like many other semi-agricultural landscapes, Spanish steppelands were subjected to rapid anthropogenic changes starting in the middle of the 20th century, which involved severe habitat loss and land transformation for intensive agricultural purposes (Suárez *et al.* 1997a; Brotons *et al.* 2004, 2005). The intensification of agricultural practices in Iberian pseudo-steppes (i.e. traditional dry-cereal cultivation) and its effects on the avifauna have received attention (Suarez *et al.* 1997b; Alonso *et al.* 2004; Moreira

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et al. 2004; Morales *et al.* 2005; Ursua *et al.* 2005), but less known is the state of steppe habitat where natural shrub vegetation is predominant (secondary steppes). This habitat hosts specialized birds, their basic requirements and responses to habitat loss being largely unknown; this lack of information could eventually weaken any attempt at conservation and management (Serrano & Astrain 2005).

We analysed the current state of the Iberian shrub-steppes, focusing on the remnants inhabited by one of the most representative birds of steppe-like habitat, Dupont's lark (*Chersophilus duponti*). Among European passerines, this lark is one of the most threatened; the species underwent substantial decline in Europe in 1970–1990, and its populations are now reduced to 1300–1900 territorial males in Spain (Garza *et al.* 2003a; BirdLife International 2004; Tella *et al.* 2005). It has been recently classified as Endangered in the Spanish Red List (Garza *et al.* 2003b) and as Nearly Threatened in the IUCN Red List (BirdLife International 2005). This ground-nesting and elusive lark is extremely habitat selective and sensitive, only inhabiting the flat patches of natural shrub-steppe (Cramp 1988; Garza *et al.* 2005; Seoane *et al.* 2006).

We first analyse land-use cover around 50 steppe fragments inhabited by Dupont's lark, addressing changes that occurred from 1991 to 1999, updating this information with further agro-forestry development in the period 2004–2005. We also test whether land-use changes were related to local productivity (primary productivity). Second, we examine impacts of industrial activities (mining, waste collection and wind-farming), the contributions of which to habitat loss are often neglected in conservation studies. Third, we analyse whether Dupont's lark was sensitive to the fragmentation of its habitat, relating male local densities to habitat availability, patch isolation and other eco-geographical predictors.

By focusing on a wide range of elements differently linked to agriculture, industry or public perception, we tried to better understand the present threats and the future ecological impacts that human activities can have on steppelands, in order to better guide future actions for habitat conservation and maintenance.

METHODS

Study areas and bird surveys

In spring 2004 and 2005, we visited 50 steppe fragments (plots) within Dupont's lark's distribution in Spain. The study sites were characterized by prevailing natural vegetation, which includes tall grass steppe (genera *Lygeum* and *Stipa*) and arid bushes (mainly *Genista*, *Rosmarinus*, *Cistus*, *Timus*, *Helianthemum* and *Artemisia*). The sampled plots were located in five broad geographic areas (Iberian Mountains, Ebro Valley, Southern Plateau, Northern Plateau and Southern Spain; Fig. 1), which differ in topography, degree of steppe fragmentation and amount of habitat suitable to Dupont's lark. The Iberian mountains include the greatest proportion of species suitable habitat, followed by the Ebro



Figure 1 Locations of the study fragments (squares), their grouping into broad geographic areas (ellipses), and known distribution of Dupont's Lark in Spain (grey shaded areas; modified from Garza *et al.* 2003b).

Valley, the two Plateau areas and Southern Spain (Laiolo & Tella 2006).

In each study plot, locations of Dupont's lark territorial males were established by surveys starting 1–0.5 hr before dawn (when vocal activity peaks) and ending at 9–10 am; we used a global positioning system (Garmin eTrex[®] Navigator) to mark territories. During survey, we also recorded bird vocalizations with a digital tape recorder. Spectrogram inspections allowed individual recognition, thus achieving a more precise estimate of bird abundance (P. Laiolo, M. Vögeli, D. Serrano & J.L. Tella, unpublished data, 2005). Territorial locations were then spatially referenced by means of a geographic information system (ArcView, version 3.1, ESRI, Redlands, CA, USA). The number of males divided by the area delimited by external territories was used to calculate male densities. We estimated densities only when more than three territories were recorded in a plot.

In order to verify whether Dupont's lark can be considered a convenient indicator of natural steppe-like habitat, we also recorded the occurrence of other typical steppe birds, all of which have Endangered, Vulnerable, Rare or Declining status in Europe (Tucker & Heath 2004). This avifauna includes eight species (Table 1), which are associated with, or more abundant in, areas with natural shrub-steppe vegetation.

Recent changes in steppe cover and the impact of agriculture and industry

In order to quantify land-use cover and its temporal variation, we used CORINE land-use/land-cover digital maps derived from orthodigital aerial photographs of the Iberian Peninsula

Table 1 Breeding birds of Spanish shrub-steppes (% frequency of occurrence in study fragments) which have Endangered, Vulnerable, Rare, Declining or Localized status in Europe (Tucker & Heath 2004). SPEC 3: species with an unfavourable conservation status, which are not exclusively concentrated in Europe (Tucker & Heath 2004). When considering overwintering birds, the percentage of fragments with skylark increases to 100% in the Ebro Valley.

Common name	Scientific name	Conservation status	Southern Plateau	Northern Plateau	Ebro Valley	Iberian Mountains	Southern Spain
Eurasian thick-knee	<i>Burhinus oedicnemus</i>	SPEC3	25.0	100.0	100.0	84.0	75.0
Black-bellied sandgrouse	<i>Pterocles orientalis</i>	SPEC3	16.7	40.0	100.0	69.2	50.0
Pin-tailed sandgrouse	<i>Pterocles alchata</i>	SPEC3	–	–	83.3	–	–
Calandra lark	<i>Melanocorypha calandra</i>	SPEC3	66.7	80.0	100.0	84.6	50.0
Lesser short-toed lark	<i>Calandrella rufescens</i>	SPEC3	16.7	–	94.4	–	50.0
Short-toed lark	<i>Calandrella brachydactyla</i>	SPEC3	100.0	100.0	100.0	100.0	75.0
Thekla lark	<i>Galerida theklae</i>	SPEC3	100.0	100.0	100.0	100.0	100.0
Skylark	<i>Alauda arvensis</i>	SPEC3	100.0	100.0	20.0	100.0	–

from 1991 and 1999 (Commission of European Community (CEC)-CORINE 1991, 1999; map resolution = 100 m). By means of ArcView (ESRI, Redlands, CA, USA), we built a buffer ring of 2500 m radius around the centroids of Dupont's lark territories in each plot: these buffers were then clipped with a land-cover digital map. In order to calculate the amount of suitable shrub-steppe habitat, we pooled the categories that proved to be selected by Dupont's lark in the five areas, namely natural grassland, sclerophyllous vegetation and sparsely vegetated areas (in keeping with Laiolo & Tella 2006). The resulting values of suitable habitat cover correspond to the land areas occupied by natural steppe vegetation in each region.

Recent fine-scale fragmentation was recorded during field work; the practices include agro-forestry (young conifer plantations and steppes ploughing in the last 5 years), wind farm development, refuse disposal (from small domestic to large rubbish dumps) and quarrying. We also recorded the presence of anemometers, which denote areas where the establishment of wind turbines is being assessed. To be considered as included in a site, the elements of fragmentation had to be placed in or near (distance < 2.5 km) the same steppe fragment or group of patches inhabited by Dupont's lark. These activities provided evidence of land uses that came after digital map production or were too fine-scale to be included. We also carried out a 230-km long transect crossing part of the Dupont's lark range in the Iberian Mountains and Ebro Valley (route Madrid–Zaragoza), recording where industrial land modifications (dumps, wind farms, anemometers and quarries) were located within the steppe habitat.

Changes in steppe cover were related to local primary productivity, which was expressed as a plant productivity index (PPI), namely the growth potential of vegetation under local rainfall and temperature conditions. The PPI was derived from satellite imagery (NOAA-AVHRR [National Oceanic and Atmospheric Administration – Advanced Very High Resolution Radiometer]), by calculating the monthly maximum value from NDVI (normalized difference vegetation index) images from the period 1984–2000. Vegetation variables from 166 satellite images were summed

up by principal component analysis in one component only (the PPI) (Diaz-Delgado & Pons 2001; Seoane *et al.* 2003). The resolution of the primary productivity map was 1 km.

Effects of habitat loss on Dupont's lark density

We used a generalized linear model (GLM) to investigate the relationships between Dupont's lark male density and habitat availability, geographical location and area productivity. Six predictors were considered. (1) Percentage of steppe habitat available in each site. (2) Straight line distance from the nearest patch occupied by the species. (3) Isolation from the nearest patch occupied by the species, expressed as the route between the Dupont's lark nearest patches that maximized the use of suitable habitat corridors. These 'least-cost paths' were calculated using habitat suitability models developed by Laiolo and Tella (2006). We expressed the probability of occurrence of Dupont's lark in 2 × 2 km squares of the species range, and calculated 'friction maps' representing the cost of movements through the landscape. The cost was expressed as a function of the probability of occurrence in each 2 × 2 km square, where $COST = (1 - \text{probability of occurrence}) \times 100$, so that the lower the probability of occurrence in a square, the higher the cost of crossing it (Laiolo & Tella 2006). Least-cost paths were extracted from friction maps using the extension PATHMATRIX for ArcView (Ray 2005) (Fig. 2). (4) Mean plant productivity index. (5) Latitude. (6) Longitude. The GLM was performed on log-transformed data, using a normal distribution and an identity link function.

RESULTS

Recent changes in Iberian steppe

The habitat matrix in the study plots was heterogeneous, with farmland covering on average half of the 2.5-km radius plots. Mean cover of steppe habitat was 33–79% in 1991 and 27–58% in 1999 (Fig. 3). Two-way ANOVAs using area and year as fixed factors showed that the five areas differed significantly in the proportion of steppeland cover, with Southern Spain

Figure 2 Examples of straight line distance (dotted line) and least-cost path (continuous line) measures of isolation, the latter calculated from the friction map expressing the cost of movements through the landscape.

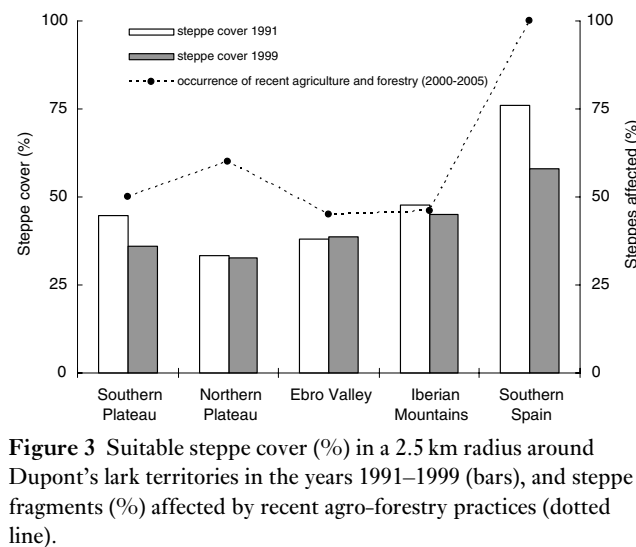
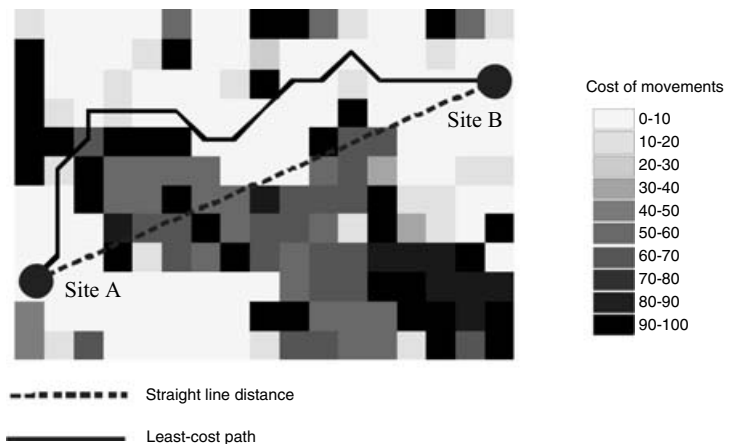


Figure 3 Suitable steppe cover (%) in a 2.5 km radius around Dupont's lark territories in the years 1991–1999 (bars), and steppe fragments (%) affected by recent agro-forestry practices (dotted line).

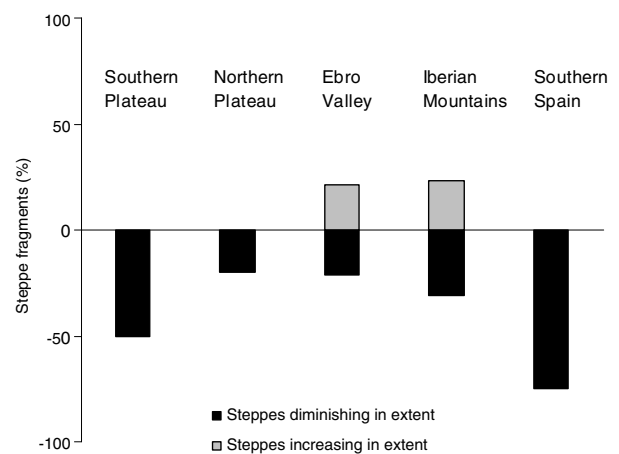


Figure 4 Steppe fragments (%) where a significant reduction (black bars) or increase (grey bars) of suitable steppe vegetation was ascertained in the years 1991–1999.

showing the greatest areas of steppeland and the two Plateaus the smallest ($F_{4,82} = 4.0, p < 0.01$). Significant differences were also found in the relative cover of farmland ($F_{4,82} = 7.3, p < 0.001$), urban-industrial areas ($F_{4,82} = 3.4, p < 0.05$) and woodland ($F_{4,82} = 2.7, p < 0.05$). The overall proportion of steppe, farmland and urban-industrial cover per plot did not change significantly in the eight-year period (all $F_{1,82} < 1.1$, and $p > 0.29$), whereas woodland cover slightly increased from 1991 to 1999 ($F_{1,82} = 4.3, p = 0.041$). When restricting the analysis at the plot level, the relative proportions of suitable steppe habitat decreased significantly in a large number of sites. In Southern Spain, steppe vegetation decreased significantly in three out of the four study fragments ($19 < \chi^2 < 176, p < 0.001$), in the Southern Plateau it diminished significantly in half of the plots ($70 < \chi^2 < 271, p < 0.001$), and it decreased in 20% of the Northern Plateau plots ($\chi^2 = 15, p < 0.001$), 31% of the Iberian Mountains plots ($5 < \chi^2 < 600, 0.05 < p < 0.001$) and 21% of the Ebro Valley plots ($5 < \chi^2 < 126, 0.05 < p < 0.001$). Overall, 35% of the Spanish steppe fragments diminished in extent, whereas

only 12% increased; the Ebro Valley and Iberian Mountains encompassed the few plots where steppe cover increased (Fig. 4).

Field work indicated that agro-forestry developed in the last five years (2000–2005) affected 52% of the steppe fragments considered; 42% of the fragments included recently ploughed fields and 32% young conifer plantations. All Southern Spain fragments were affected by recent agro-forestry, whereas in the other areas agro-forestry was involved in 45–60% of the fragments; differences among the five areas were significant ($\chi^2 = 12.8, df = 4, p < 0.05$). Recent agricultural activities tended to be more common in southern Spain, the area with the greatest amount of suitable habitat per plot, and the greatest proportion of steppe fragments that decreased in extent between 1991 and 1999 (Fig. 4).

Steppe cover tended to increase in plots with PPI values < 200 , while plots with PPI values > 300 on average declined in extent (differences among four classes of plant productivity: Kruskal-Wallis ANOVA $H_{3,47} = 43.6, p < 0.01$; Fig. 5).

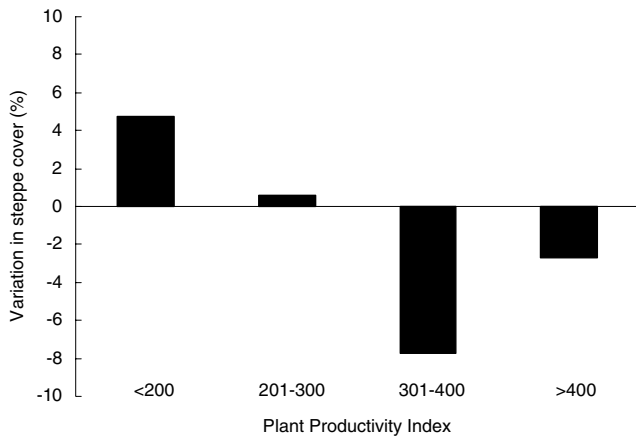


Figure 5 Variation in steppe cover (%) between 1991 and 1999 in each Plant Productivity Index class.

Table 2 Relative frequency of occurrence of garbage dumps, quarries, wind farms and anemometers in steppe plots of the five geographic areas.

Area	Relative frequency of occurrence (%)			
	Rubbish dumps	Quarries	Wind farms	Anemometers
Southern Plateau	38	0	0	50
Northern Plateau	40	40	0	20
Ebro Valley	50	35	10	30
Iberian Mountains	15	8	0	54
Southern Spain	50	25	0	25
Total	26	22	4	38

Industrial activities

Rubbish dumps were found in 26% of the study plots, mostly occurring in the steppelands of southern Spain, the Ebro Valley and the Northern Plateau (Table 2). Quarries were located in 22% of plots (Table 2). Wind turbines rarely occurred in the sampled steppes, but the repeated occurrence of anemometers (38% of the fragments; Table 2) suggests that the impact of wind farms is likely to increase in future. Anemometers tended to be located in the less disturbed steppes; the amount of suitable habitat in plots with anemometers was significantly greater than that of plots without anemometers (1999 data: 46% versus 37% steppe cover, respectively, $t = 1.8, n = 50$ plots, $p = 0.04$). Plots with rubbish dumps, wind farms and quarries tended to have lower PPI values (314 on average) than plots unaffected by industry (348 on average, $t = 1.7, n = 50$ plots, $p = 0.052$).

In a 230 × 3 km transect crossing the Iberian Mountains and Ebro Valley, we recorded the occurrence of 20 items (dumps, quarries, wind farms and anemometers), 80% of these in steppe-like habitat, and 10% each in farmland and woodland. This distribution was significantly different

Table 3 Results of a generalised linear model highlighting predictors of Dupont’s lark male density.

Predictor	Coefficient	SE	Wald statistics	p
Intercept	-1.895	6.271	0.091	0.763
Steppe availability	-0.062	0.029	4.566	0.033
Length of the least cost path to the nearest occupied patch	0.257	0.131	3.865	0.049
Straight line distance to the nearest occupied patch	-0.237	0.137	2.977	0.084
Plant Productivity Index	0.049	0.117	0.179	0.672
Latitude	0.126	0.155	0.657	0.418
Longitude	0.209	0.932	0.050	0.822

from that expected on the basis of the actual availability of steppe (19% cover), farmland (57%) and woodland (20%) (χ^2 goodness-of-fit = 39, $df = 2, p < 0.001$).

Four out of the 50 sample study areas were the only Spanish steppes at least partially protected in natural preserves and SEO-BirdLife (Sociedad Española de Ornitología) reserves.

Determinants of Dupont’s lark male density and co-occurrence with threatened steppe birds

The GLM showed that Dupont’s lark male density was negatively related to steppe availability and positively related to the length of the least cost path, suggesting that male density was greatest in isolated and small steppe fragments. Plant productivity and geographical location had no significant effect (Table 3).

An average Dupont’s lark plot hosted a high proportion (71%) of threatened species associated with natural shrub-steppe vegetation. The highest percentages of birds with an unfavourable status occurred in Ebro Valley plots (87%), followed by the Iberian Mountains (67%), Northern Plateau (65%), Southern Spain (50%) and Southern Plateau (50%) (Table 1). The number of threatened steppe bird species was higher the lower the productivity of the steppe ($r_S = -0.70, n = 50, p < 0.001$; Fig. 6).

DISCUSSION

This study shows that the area occupied by Iberian shrub-steppes has been greatly reduced by agricultural intensification and forestry, while becoming a favoured target of industrial activities, largely forgotten by conservation plans. The general public tends to value arboreal, steep or water-rich habitats over arid landscapes (Bernaldez *et al.* 1989; Suárez *et al.* 1992), suggesting that the aesthetic and conservation values of habitats do not always coincide. Knowledge about the basic

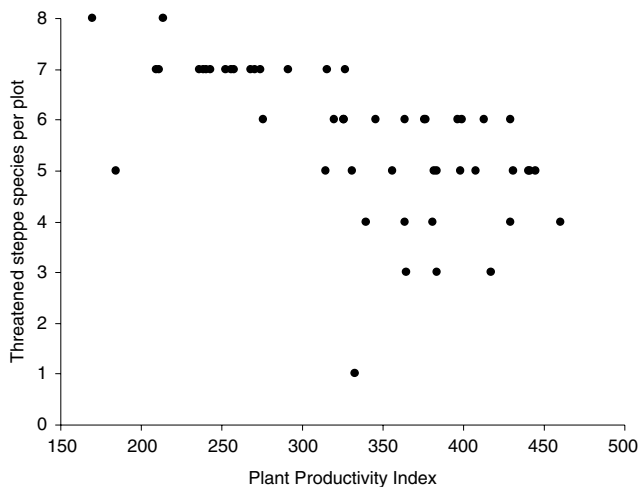


Figure 6 Number of threatened bird species per plot versus plot Plant Productivity Index.

ecology of shrub-steppe birds is sparse, suggesting this fauna is relatively ignored by the scientific community. A clear example of the scarce attention given to steppe avifauna is the late discovery (mid-1980s) of Dupont's lark among the breeding birds of Spain (Aragües 1992).

Agricultural development in Spanish steppes

The steppe remnants are largely affected by agricultural exploitation and are embedded in a heterogeneous habitat matrix, where farmland on average covers > 50% of the area. Agricultural intensification is the main factor historically responsible for the loss and fragmentation of Iberian steppes, which induced declines in the populations of several bird species that depended on it (Suárez *et al.* 1997a; De Juana 2004). This study shows that steppe cover has continued to decrease in several patches in recent years as a result of conversion to arable land, confirming that the flat steppe areas are susceptible to large farm management practices that can rapidly alter landscape composition (Serrano & Astrain 2005). We did not take into account the extreme loss undergone by patches where Dupont's lark was driven to extinction in the last two decades (Tella *et al.* 2005), as we only focused on the plots that are still occupied by the species. These remnants are considered the best preserved natural shrub steppes in Spain (De Juana *et al.* 1988; Pedrocchi 1998; Suárez *et al.* 1992).

At the national level, overall changes in land cover in the last decade have not been significant, but this can be ascribed to the disproportionate sample size of the two geographic areas with the greatest steppe availability and lower human pressure levels (Iberian Mountains and Ebro Valley); conversely, the contribution of the threatened and declining southern Spain, and Southern and Northern Plateau steppes was limited to a few fragments. This was not owing to sampling bias, but to the large-scale destruction that has reduced the steppe to a limited number of patches. At the plot level, it appears

that Southern Spain, Northern and Southern Plateau steppes have been significantly diminishing in extent in the last decade (Fig. 3). Those fragments that were precluded from excessive agricultural exploitation in the past seem to be the favourite sites for new agro-forestry practices.

Ploughing in the study areas has been indirectly promoted by EU subsidies under the European Common Agricultural Policy (CAP) since the late 1980s, given that farmers ploughed numerous fragments of natural steppes, often illegally, to increase the area of their farmland properties and thus the amount of subsidy paid. However, farming in several of the sample fragments was economically unviable given their low productivity, which is among the lowest recorded in Spain. Without external inputs such as irrigation, these areas have a cereal production that is three times lower than the European average (Suárez *et al.* 1997a). In the light of this, the CAP reform of 1992 promoted the abandonment of marginal low-productivity areas and the intensive cultivation of the rest, often with the help of irrigation measures (Tella *et al.* 1998). This would explain why low-productivity steppes have been slightly increasing in extent, whereas the most productive areas have decreased (Fig. 5).

The great proportion of conifer plantation and woodland cover in the study sites is another consequence of changes in the subsidy policies of the EU, which has supported afforestation in unproductive areas to reduce food production and restore the environmental diversity lost through agricultural intensification. Plantations also provided revenue from wood extraction. However, pine forestation of former arable or degraded land has had a generally negative impact on the bird community of the Spanish plateau (Diaz *et al.* 1998). Plantations did not increase the species richness of forest avifauna, and at the same time were detrimental to threatened birds depending on traditional farming or dry open lands. Moreover, *matorral* (shrub vegetation) seems to be as effective as pine plantations in slowing water and soil loss in seasonally arid areas with highly erodible soils (Williams *et al.* 1995).

Industrial exploitation of Spanish steppes

The low productivity of Spanish steppes opens the way to industrial development, which guarantees alternative incomes to landowners and local administrations. Mining activities, rubbish dumps and wind industry are by far more common in steppes than in any other habitat of the study area. All these activities reduce steppe cover, but can also create new disturbances to the ecosystem. Rubbish dumps, for instance, can attract large numbers of opportunistic predators (such as foxes, corvids and raptors; Mendelsohn & Yom-Tov 1999), which might increase breeding failure of steppe birds (Yanes & Suárez 1996), which are mostly ground-nesters (De Juana *et al.* 2004).

In the case of wind farms, the risk of bird collisions with turbines and cables can be considerable, including reported casualties of Dupont's larks and other steppe birds (Pelayo

& Sampietro 2000; Johnson *et al.* 2002; Lekuona 2004; Barrios & Rodriguez 2004). In many European countries the planning and establishment of wind farms (Instituto Nacional de Meteorología 1988; Leddy *et al.* 1999; De Lucas *et al.* 2004; Garthe & Hüppop 2004) is giving rise to much controversy relating to bird conservation issues (Percival 1999; Larsen & Madsen 2000). Wind farms could be built in more than one-third of the study steppes in the near future, as indicated by the presence of anemometers. The wildest and least disturbed steppes are most likely to be affected, possibly reducing the noise and negative aesthetic impacts on the public, but affecting typical steppe wildlife to a large extent.

Effects of habitat loss on Dupont's lark densities

Habitat loss can influence the distribution, size and persistence (Driscoll 2004), and communication systems (Laiolo & Tella 2005) of natural populations. The availability of suitable habitat and patch isolation appear to influence the local density of Dupont's lark males, which seem to reduce inter-individual distances in small isolated patches. This finding can be explained by the dispersal dynamics of the species and its possible use of corridors for movements. When habitat connectivity is limited, the tendency of birds to leave the natal patch may be reduced, and this can lead to local territory saturation. In large steppe areas, the species distribution tends to be patchy rather than continuous, with empty gaps of apparently suitable habitat. Conversely, when steppe area is reduced, birds may be forced to occupy the entire available habitat. The low male densities recorded in Morocco, where large areas of steppe habitat still occur, corroborate this (densities estimated by the same procedure, average 0.59 males per 10 ha in Morocco, 0.98 males per 10 ha in Spain; P. Laiolo & J.L. Tella, unpublished data 2005).

The eventual reduction of natal dispersal and crowding in small and isolated fragments could have detrimental effects on long-term population viability, by favouring inbreeding, increasing resource competition, and reducing fecundity and/or survivorship (Wolff 1997; Newton 1998). The fact that Dupont's lark populations are more likely to be extirpated in fragments (area < 100 ha), and isolated nuclei do not appear to recover from population crashes (Tella *et al.* 2005; J. Manrique, personal observation 2004), suggest that extreme habitat loss can have dramatic consequences for population persistence.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Agriculture and forestry are driving loss of steppe habitat in Spain, even over very short time scales. Variability of Dupont's lark density in response to habitat availability and patch isolation indicate steppe loss might alter population dynamics of the avifauna. Impacts of agriculture intensification on steppeland are well recognized (Suárez *et al.* 1997a), but we found industrial activities affecting the

ecosystem in Spain as well. Steppe will be conserved only if all kinds of anthropogenic land uses are regulated appropriately. Conserving Dupont's lark habitat may serve to protect a larger community of threatened birds and this species may play an important role in steppe management planning.

Despite the high conservation concern for this habitat in Europe (Tucker & Heath 2004), only four of the study fragments were given some kind of protection in Spain, almost the sole reserves of natural shrub steppe vegetation in the country. Steppe habitat does not hold the public's interest like other habitats, and economic interests may be strong enough to prevent nature reserves from being set up (Suárez *et al.* 1992, 1997a; Beaufoy 1998). In Catalunya, future irrigation areas and current steppe bird distribution largely overlap (Brotons *et al.* 2004). Although we acknowledge that rural poverty is an issue, we also stress that conservation measures for the residual habitat should become a priority, to assure the long-term viability of steppe specialists and the continuity of a habitat that is unique in Western Europe.

Land abandonment may be unnecessary or even negatively impact steppe species that are adapted to live in traditional agro-ecosystems (such as the lesser kestrel; Tella *et al.* 1998; Ursua *et al.* 2005), however abandoning fields may become the only option to recover populations of specialists such as Dupont's lark. The abandonment of less productive areas may be the more economically viable option, also taking into account that the number of threatened steppe birds within the study range is negatively correlated with plant productivity, these species being mostly adapted to arid conditions and sparse low vegetation (De Juana 2004). Although the full recovery of steppe vegetation in abandoned fields could take a long time (Hutchings & Booth 1996; Römermann *et al.* 2005), steppe bird recolonization may be faster, provided that some requirements are met. First, abandoned fields should be located in the close proximity to large natural steppe areas and/or should be well connected to steppe fragments by corridors of suitable vegetation to facilitate dispersal. Second, the size of abandoned patches should be taken into account, given that large steppe areas represent more natural conditions and can assure the long-term viability of the avifauna. Third, wood or bush encroachment resulting from abandonment processes (Hibbard *et al.* 2003; Pons *et al.* 2003) should be slowed down by promoting grazing (Aragües 1992; Hibbard *et al.* 2003; Silva *et al.* 2004; Bartolome *et al.* 2005a, b), although this activity should be controlled to prevent the diffusion of grazing-resistant tall shrub or tree species (Bachelet *et al.* 2000; Dougill & Thomas 2004), excessive desertification and soil instability (Gintzburger *et al.* 2005; Oliva *et al.* 2005). The public consciousness of the ecological values of arid habitats also needs to change.

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