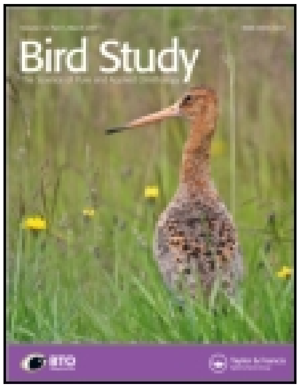

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Woodlarks *Lullula arborea* and landscape heterogeneity created by land abandonment

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Woodlarks *Lullula arborea* and landscape heterogeneity created by land abandonment

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Capsule Fine-grained landscape heterogeneity may be a major factor in the recent expansion of Woodlark populations.

Aim To determine the factors which may have led to the increase in Woodlark populations in the Mediterranean region.

Methods Woodlark habitat selection was determined using territory mapping in an area that had undergone widespread land abandonment during the past 50 years. Remote sensing data were used to study landscape changes within the study area between 1978 and 2003.

Results Most Woodlark territories included a combination of farmland and shrubland patches. These fulfilled the birds' requirements for territorial display and for foraging. Land abandonment has increased the availability of open shrubland, the dominant land-cover type selected by Woodlarks.

Conclusions Increased fine-grained landscape heterogeneity following farm abandonment has created opportunities for habitat use by Woodlarks and may be a major factor in the Woodlark population expansion observed between 1978 and 2003.

INTRODUCTION

Landscape heterogeneity has been recognized as a key feature in bird habitat selection, especially in farmland (Benton *et al.* 2003). It has been shown to be essential for grassland birds that often require different habitat features for foraging and breeding (Soderstrom & Part 2000). Dunning *et al.* (1992) have developed several hypotheses to explain species' responses to landscape heterogeneity in relation to the need for or availability of distinct landscape elements. For example, the Little Bustard *Tetrax tetrax* in the south of France provides an example of habitat complementation: although this species is primarily associated with natural steppes, it occurs at higher densities when steppes are associated with cultivated patches (Wolff *et al.* 2001). Understanding the effect of landscape heterogeneity on species abundance and distribution can, therefore, be essential to understand and predict species' responses to land-use changes, especially in farmland.

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In European farmlands, land-use changes through intensification or land abandonment have caused major modifications in landscape composition, quality and heterogeneity (Benton *et al.* 2003) and have been identified as a likely cause for the general decline of farmland birds (Donald *et al.* 2001). However, some species associated with farmland have shown a significant population recovery since the 1980s (Birdlife International 2004). Woodlark *Lullula arborea* are one such species of conservation concern which, after a period of decline in population size and range contraction (Wright *et al.* 2009), are now increasing at the European (Birdlife International 2004), national (e.g. in the UK [Wotton & Gillings 2000] and France [Julliard *et al.* 2004]) and local levels (e.g. Pic Saint Loup 1978–2003 [Sirami *et al.* 2007]). In the Mediterranean region, this species is associated primarily with open farmland and grazing land (Pons *et al.* 2003). Despite a major decrease in the spatial extent of these habitats because of land abandonment, this species has increased in abundance during the last decades throughout the northwest

Mediterranean (based on a meta-analysis of species trends in eight independent studies [Sirami *et al.* 2008]).

Our aim was to explore the apparent contradiction between land abandonment and Woodlark increase in the Mediterranean by studying this species' habitat selection and vegetation changes at the landscape scale. First, we hypothesized from previous knowledge of the species resource needs (Sitters *et al.* 1996; Mallord *et al.* 2007a,b) that Woodlarks will select landscape locations where different habitats fulfilling such needs coexist. Woodlarks have been described as associated with well-drained soils with bare ground or short grass, scattered trees, and some areas or tufts of taller vegetation cover (Sitters *et al.* 1996). Our prediction was that fine-grained heterogeneity of Mediterranean landscapes is playing a role in Woodlark selection of breeding territories. Finally, we hypothesized that the combination of Woodlark habitat selection in the Mediterranean and the recent changes in Mediterranean landscape heterogeneity contribute to the recent increase in Woodlark occurrence in this region. We tested these hypotheses in a landscape in southern France where Woodlarks have increased between 1978 and 2003 (Sirami *et al.* 2007). We combined data on Woodlark habitat selection at the territory level and information on temporal changes in landscape structure and composition between 1978 and 2003. We tested three predictions: (1) Woodlark territories contain multiple patches of different habitat types, in particular a mix of farmland and shrubland patches; (2) individuals within these territories use different landscape patches to fulfil different needs (territorial display, foraging, nesting), and (3) these components of landscape heterogeneity have increased between 1978 and 2003, providing the species with better opportunities to fulfil its needs.

METHODS

Study area

The study area was situated 20 km north of Montpellier (southern France; 43° 47′ N, 03° 50′ E). It covered 238 ha on a karstic limestone plateau with an average altitude of 270 m. The climate is Mediterranean, with moist and cool winters. The annual average rainfall ranges from 950 to 1350 mm, average maximum temperature during the warmest month is 28°C and average minimum temperature during the coldest month is −1°C (Debussche & Escarre 1983).

The study area is a typical Mediterranean mosaic of grasslands and croplands embedded within a matrix of shrublands and woodlands (Preiss *et al.* 1997). Grasslands were maintained by extensive sheep grazing until the middle of the 20th century. Shrublands were also used for grazing sheep and for the production of juniper oil (Debussche *et al.* 1987). Around the 1960s, a period of rapid land abandonment started with a strong decrease in sheep grazing. After the 1980s, new grazing systems appeared: horse grazing for leisure and cattle breeding (e.g. Camargue bulls). Their impact on the vegetation differs dramatically from those of extensive sheep grazing. Horses cause over-trampling in small enclosures near houses and bulls create a patchwork of grassland, over-grazed patches around water points, and clumps of thorny species such as Blackberry *Rubus fructicosus* L. At the same time, the focus of wine production gradually changed from high-yield to high-quality systems, resulting in the creation of new vineyards with new grape varieties on the well-drained slopes that provide the required water stress.

Territory mapping and behavioural monitoring

To study the fine-scale habitat selection by Woodlarks, we mapped the territories of ten singing males within our study area (Bibby *et al.* 1992). We focused only on singing males because of time constraints, and aimed to determine home range and foraging habitat use in detail. Five two-hour visits took place in each of the areas where a singing male had been located. These five visits were spread over the breeding season, from 12 April to 9 June 2005. Territory mapping was restricted to days without marked rainfall or wind and during the period of peak vocal activity (four hours after sunrise, around 06:00–10:00). Geographical locations were recorded using a global positioning system. Behaviour (singing or foraging) and position (e.g. on the ground, on top of tree, height) were recorded for each location. Each individual was observed in a number of different locations ranging from 12 to 29 (Table 1). Territory boundaries were built using convex polygons (Fig. 1). As there was little or no overlap between neighbouring territories, locations were easily associated with an individual male. In the particular context of our study, observations of individuals singing in flight were not taken into consideration for territory mapping as they could not be associated with fine-scale habitat use.

Table 1. Vegetation characteristics of the Woodlark territories.

Territory	Vegetation cover (%)						Land cover (%)					
	Area (ha)	Obs no.	Tree	Shrub	Herb	Bare ground	Crop	Grass	OShrub	CShrub	OWood	CWood
1	8.3	24	6	40	45	9	0	16	67	0	17	0
2	3.5	29	1	16	74	8	0	56	44	0	0	0
3	1.1	12	2	18	70	10	0	86	14	0	0	0
4	3.5	13	16	29	52	3	0	0	89	10	1	0
5	5.9	16	11	26	58	5	0	13	87	0	0	0
6	1.7	14	14	23	56	7	0	4	42	49	0	6
7	2.5	21	4	12	51	33	60	1	38	0	0	0
8	3.2	17	3	14	56	27	47	0	50	1	0	2
9	0.9	13	3	40	56	1	0	98	1	0	0	1
10	3.6	18	2	25	69	4	0	1	99	0	0	0
Average	3.42	17.7	6.2	24.3	58.7	10.7	10.8	27.4	53.1	6	1.8	0.9
Study area	238		12.5	31.2	48.7	7.6	4.6	10.6	64.7	10.1	5.2	2.9

Obs no., number of locations where the males have been observed; Crop, cropland; Grass, grassland; OShrub, open shrubland; CShrub, closed shrubland; OWood, open woodland; CWood, closed woodland.

Land-cover data

We used a land-cover map to quantify landscape composition and structure at the scale of the territory and assess temporal changes in landscape heterogeneity. We used infrared aerial photographs taken in 1981 and 2002. The main vegetation dynamic in the study area since 1981 was the increase of shrub cover as a result of land abandonment. There had been very little change in landscape composition between 2002 and 2005. We thus considered maps based on 2002 to represent accurately the situation in 2005. We might only have slightly underestimated shrub cover increase. Photographs were ortho-rectified and geo-referenced to the Lambert Conformal Conic system with a spatial resolution of 0.7 m in ENVI 4.0 (RSI Research Systems 1996). We used ARCGIS 8.3 (Environmental Systems Research Institute, Inc.) complemented by field observation to obtain land-cover maps for each year. We identified land-cover polygons (minimum polygon size was approximately 0.05 ha, average polygon size = 2 ha) on the aerial photographs. We assigned these polygons to seven land-cover types. Two land-cover types corresponded to farmland: grassland (grasses with other annuals and few short shrubs dominated by two species of grass: Mediterranean False-brome *Brachypodium retusum* (Pers.) P. Beauv. and Erect Brome *Bromus erectus* Hudson) and cropland (1–2-ha plots of wine grapes or cereals). Four land-cover types consisted of spontaneous vegetation: open shrubland (shrubs ranging from 0.5 to 2.5 m in height with a grass/bare ground cover higher than 30%, dominated by Prickly Juniper *Juniperus oxycedrus* L., European Box *Buxus sempervirens* L. and Rosemary *Rosmarinus officinalis* L); closed shrubland (associations of shrubs and of scattered trees, representing a total cover of more than 30%, dominated by Prickly Juniper, European Box and Rosemary); open woodland (trees taller than 3m with a grass/bare ground cover higher than 30%, dominated by Holm Oak *Quercus ilex* L. or Downy Oak *Quercus pubescens* Willd.) and closed woodland (dense trees taller than 3 m with few shrubs and less than 30% covered by grass/bare ground, dominated by Holm Oak or Downy Oak). The last land-cover type consisted of built-up areas (clustered or isolated buildings and associated gardens).

Vegetation mapping

We used a pixel classification of the same aerial photographs (pixel size = 0.7 × 0.7 m) for fine-grained quantification of vegetation at the scale of the observation plot. We used four pixel classes: Bare ground (little or no vegetation), Herb (herbaceous vegetation), Shrub (woody vegetation 0.5–2.5 m) and Tree (woody vegetation >3 m). We used a maximum-likelihood supervised method (Campbell 1996) in ENVI to assign each pixel in the study area to one of the four pixel classes. We tested the accuracy of classifications with a confusion matrix comparing ground truth pixel classification to photographic-based pixel classification for a test data set (around 5000 pixels). The overall accuracy (kappa coefficient 0.83) for all pixel classes legitimated the study of fine-scale vegetation cover.

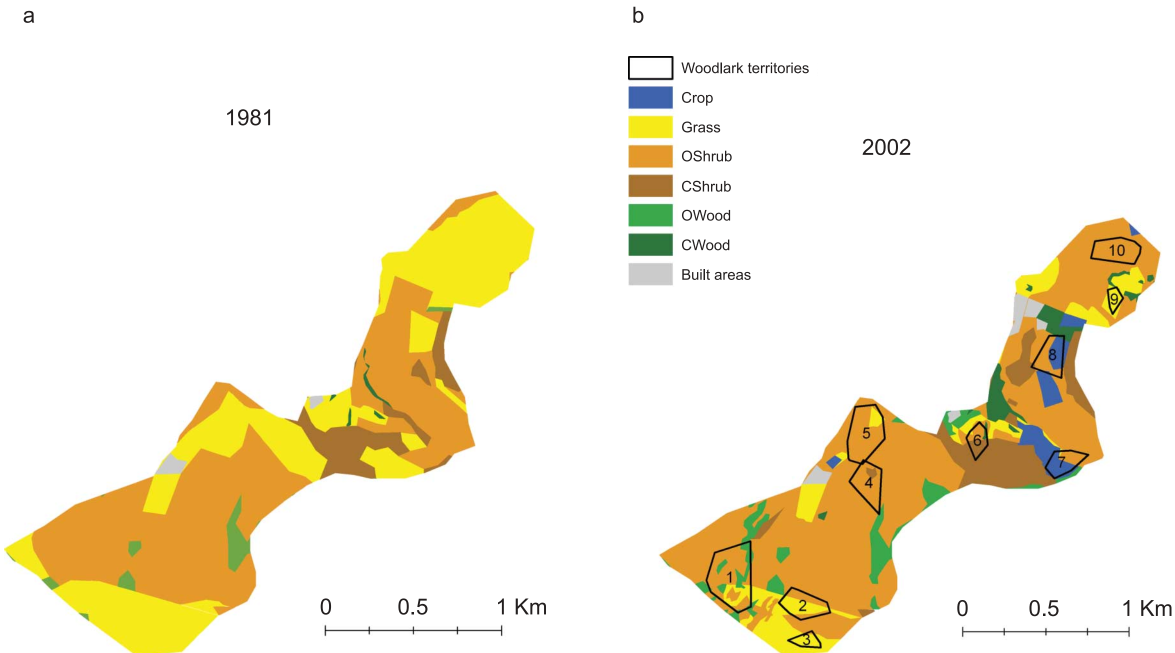

Figure 1. Map of the study area showing the land-cover types in (a) 1981 and (b) 2002. Crop, cropland; Grass, grassland; OShrub, open shrubland; CShrub, closed shrubland; OWood, open woodland; CWood, closed woodland; the map of 2002 shows the ten territories obtained using the convex polygons method based on observations made in 2005.

Data analysis

We analysed Woodlark habitat selection at two scales: the scale of the territory and the scale of each individual observation. At the territory scale, we calculated territory area and the number of locations recorded within each territory. In order to verify that Woodlarks are primarily associated with open habitat, we calculated, for each territory, the percentage of the four pixel classes (vegetation composition). To test prediction (1), whether heterogeneity is important for Woodlarks, we calculated, for each territory, the percentage cover of each of the seven land-cover types identified (landscape composition). We compared the vegetation and landscape composition in Woodlarks' territories and in the study area using a Chi-square test.

At the scale of the individual observation, we calculated the percentage cover for the four pixel classes within 5 m around each observation. In order to test prediction (2), whether individuals use different vegetation types for singing and foraging, we produced a GLMM using the LMER function from the R-package LME4 (Bates and Sarkar 2007). We used individual Woodlarks as a random term, behaviour (singing/foraging) as the dependent variable and tree, shrub and bare ground cover as the explanatory variables (we included three of the four vegetation variables in order to avoid correlation between explanatory variables). Independent factors were added sequentially to the model, and the final model was selected based on the minimum AIC.

To test prediction (3), whether landscape heterogeneity increased and became more favourable for Woodlarks during 1978–2003, we calculated the proportion of each land-cover type as well as the number of patches in the study area in 1981 and 2002. We compared patch size between 1981 and 2002 using a Mann–Whitney *U*-test (non-parametric).

RESULTS

We identified 10 woodlark territories and made 178 observations of singing or foraging males. Territory area ranged from 0.9 to 8.3 ha (mean = 3.4 ± 2.3 se; Table 1). At the pixel scale, the vegetation was dominated by herb in all territories – 58.7% on average compared with 48.7% in the study area (χ^2 = 0.44,

P = 0.21; Table 1). At the patch scale, territories were associated with two to four land-cover types and all territories but one (Territory 4) included one of the farmland land covers (grassland or cropland). The composition of territories was significantly different from the average composition of the study area (χ^2 = 14.79, P = 0.11). Most territories were associated both with crops/grassland and open shrubland (except Territory 4: open and closed shrubland and open woodland). Open shrubland was the dominant land-cover type, on average 53.1% of territories. Males were observed mainly on the ground (33% of 178 locations in total) and on the top of Prickly Juniper shrubs (35% of 178 locations). Locations where Woodlarks were observed on the ground showed high grass and bare ground cover, on average 66% herb cover and 12% bare ground cover. All birds that were singing (66% of the observations) were recorded on shrubs, trees or poles and were located at an average height of 3.1 m when singing. All of the birds recorded on the ground were silent and most of them were observed foraging. Concerning the role of vegetation cover in Woodlark behaviour patterns, the best model included shrub cover (Table 2). Woodlarks were singing in areas with a significantly higher shrub cover, 26% on average. The proportion of open shrubland, the dominant land-cover type in Woodlark territories, increased from 51% to 66% of the whole study area between 1981 and 2002 (Table 3). The proportion of farmland land cover (grassland and cropland) decreased from 39.7 to 15.5%, whereas the proportion of closed shrubland and woodland increased from 9.4% to 18.5% between 1981 and 2002. The number of patches doubled and their average size decreased between 1981 and 2002 (P = 0.06).

Table 2. GLMMs for the relationship of Woodlark behaviour (response variable: singing/foraging) with vegetation cover (explanatory variables: tree, shrub and bare ground cover).

Response variable	Explanatory variables	Coefficient (± se)	z	Residual deviance	AIC
Behaviour	Intercept	0.587 (± 0.19)	2.98**	146	150
	Shrub	0.023 (± 0.01)	1.91*	142	148
	Tree	0.025 (± 0.02)	1.04	140.6	148.6
	Bare ground	−0.006 (± 0.01)	−0.50	140.3	150.3

*P < 0.05; **P < 0.01.

Table 3. Landscape composition and structure in the study area in 1981 and 2002, showing proportions of each land-cover type, total number of patches and median patch size (range in parentheses) in hectares.

Land-cover type	1981	2002
Crop	0.0	4.6
Grass	39.7	10.9
OShrub	50.8	66.0
CShrub	6.9	10.3
OWood	2.1	5.3
CWood	0.4	2.9
n patches	32	64
Patch size (ha)	1.01 (0.01–113)	0.57 (0.03–97)

Crop, cropland; Grass, grassland; OShrub, open shrubland; CShrub, closed shrubland; OWood, open woodland; CWood, closed woodland.

DISCUSSION

Habitat selection by Mediterranean Woodlarks

Woodlarks breeding in our Mediterranean habitat study sites showed habitat requirements similar to those described in other parts of the species range. The birds foraged in areas containing a high percentage of bare ground, similar to those previously described by Bowden (1990) and Mallord *et al.* (2007b) in Britain. Although individuals were often singing from the air, our study suggests that Woodlarks in the Mediterranean also heavily use areas with high shrub cover for singing, and most often the tops of Prickly Juniper were used as singing posts. This differs from Woodlark behaviour observed in Britain, where territorial signalling was primarily done in the air and secondarily associated with trees (Sitters *et al.* 1996). This difference might be because of the higher density of shrubs in Mediterranean landscapes. Moreover, landscape composition within Woodlarks' territories was different from the average conditions in the whole study area, suggesting a positive selection of territories. These results confirmed our first prediction that landscape heterogeneity is important for Woodlarks; all territories but one contained both patches of farmland (managed grassland and cropland) and patches of shrubland. Territories contained, on average, 53% of open shrubland and 27% of grassland. This study focuses on singing males, which could have resulted in an over-estimation of the proportion of shrubland, thus the proportion of grassland and crops used by Woodlarks might be higher than 27%. Moreover, singing males could have been either paired or single and there may be a significant difference in habitat selection between single and paired males. This question would require further investigation with larger sample sizes. Woodlarks used patches with contrasting vegetation structure available in their territories for distinct activities. This pattern of habitat selection and behaviour is consistent with the process of complementation as hypothesized by (Dunning *et al.* 1992), i.e. a given individual will need different types of habitat patches within the landscape to meet its vital needs (Delettre *et al.* 1992). The process of complementation found in the present study is also likely to explain the previously reported preference of Woodlarks for regions with a mix of farmland and shrubland in Spain (Vallecillo *et al.* 2008). Complementation has already been shown in several other bird species in Mediterranean landscapes (Brotons *et al.* 2005). These findings emphasize the need to consider vegetation and landscape heterogeneity in habitat selection studies, particularly in agricultural landscapes.

Fine-scale dynamics of Mediterranean landscape

Land-use changes have caused significant changes in landscape composition and structure between 1981 and 2002. Land abandonment resulted in an increase in open shrublands, i.e. an increase in the land-cover types that dominate in Woodlark territories. Moreover, we observed an increase in the number of patches and a decrease in their size, i.e. an increase in fine-grained landscape heterogeneity. The abandonment of pastoral practices, which included shrub removal and burning, resulted in a rapid encroachment of grasslands by shrubs.

The few patches of farmland that remained in 2002 were mostly of recent origin and the result of recent changes in the local socio-economic context. First, the shift from traditional vineyards to quality vineyards resulted in the abandonment of vineyards in the plains and in the creation of new vineyards on the slopes and the dry plateau. Second, the increasing influence of the nearby city of Montpellier promoted new types of grazing by cattle raised for bull races and horses, both kept in small enclosures characterized by severe browsing of the ground vegetation. These two new land-uses created patches with a high proportion of bare ground attractive to foraging Woodlarks.

Although open habitats have been decreasing overall, the combination of fine-scale landscape changes and Woodlarks' need for complementary habitat patches has certainly appeared to contribute to the increase in their occurrence between 1978 and 2003 within our study area. Based on bird and vegetation surveys conducted in 24 census-plots (Sirami *et al.* 2007), Woodlark were observed in 12 plots in 1978 and 20 plots in 2003. The mean number of habitat patches increased from 2.21 ± 0.78 se to 3.29 ± 0.99 se within these 24 plots over the same period. These new patches were mainly woodland, open shrubland and cropland. New patches of open or closed woodland appeared in ten plots; new patches of open shrubland appeared in six plots and new patches of crops appeared in four plots. More globally, we suggest that land abandonment and complementation processes are some of the factors explaining Woodlark population increases in several north Mediterranean study sites (Sirami *et al.* 2007, 2008). Moreover, the increase of open-shrubland boundaries may favour predator avoidance (Schaefer & Vogel 2000) and may provide natural boundaries between neighbouring territories, which may result in higher Woodlark densities.

Factors other than vegetation changes might also have contributed to Woodlark increases. For example, Woodlark occurrence could have been affected by changes in food supply; in particular caterpillars, beetles and spiders, which form an important component of the diet of Woodlarks during the breeding season (Langston *et al.* 2007). Improved weather conditions during winter might have affected demographic components such as survival. Climate changes may have affected Woodlarks, but the nature of these effects is considered equivocal in Britain (Langston *et al.* 2007).

In other parts of the Woodlark's range, such as Britain, other factors might have played a role in its recovery. There, improved forest management and restoration of traditional heathlands have greatly benefited Woodlarks through the reinstatement of grazing and the clearance of dense scrub and trees to create better conditions for foraging (Wotton & Gillings 2000; Conway *et al.* 2009). Over most of Europe, however, Woodlarks predominantly use farmland (Schaefer & Vogel 2000), and we believe that our findings could help explain their overall recovery at the European scale. The present study also emphasizes how integrating behaviour and landscape heterogeneity in studies on habitat selection allows a better understanding of how species respond to land-use changes and underlines the need that some species have for landscape heterogeneity, especially in farmland birds with a high conservation profile (Blondel & Farre 1988).

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