

Breeding habitat selection of Skylarks varies with crop heterogeneity, time and spatial scale, and reveals spatial and temporal crop complementation



Paul Miguet^{a,b,*}, Cédric Gaucherel^{a,c}, Vincent Bretagnolle^b

^a INRA, UMR AMAP, TA A51/PS2, Bd de la Lironde, 34398 Montpellier Cedex 5, France

^b CNRS, Centre d'Etudes Biologiques de Chizé (CEBC), 79360 Villiers-en-Bois, France

^c French Institute of Pondicherry (UMIFRE 21 CNRS-MAEE), 11 Saint Louis Street, Pondicherry 605001, India

ARTICLE INFO

Article history:

Received 11 January 2013

Received in revised form 15 June 2013

Accepted 24 June 2013

Available online 27 July 2013

Keywords:

Crop heterogeneity

Skylark

Habitat selection

Landscape complementation

Spatial ecology

Spatial scale

ABSTRACT

While many studies having investigated the effects of landscape complexity or heterogeneity on farmland biodiversity were focus on semi-natural habitats (e.g. forests, hedgerows), few have analyzed the consequences of local crop heterogeneity on species abundance. Here we quantify the effects of crop heterogeneity on the breeding habitat selection of the Skylark *Alauda arvensis* at spatial scales ranging from micro-habitat to landscape, in a western France farmland. We address the question of finding the processes behind the crop heterogeneity effect, usually never studied whatever the taxa. We first studied how crop composition at continuous spatial scales from within the breeding territory to the landscape (20–2000 m) affected Skylark habitat selection within a breeding season (i.e. the effect of each crop compared to the others), and how this selection changed with time. Second, we examined how the diversity of crops within areas of radius from 20 to 2000 m affected habitat selection by Skylarks. Third, we investigated for the processes behind the crop diversity, examining the detailed pattern of crop selection at the territory scale in presence of only two crops, to identify the synergetic effects of the simultaneous presence of two crops. Using an adequate spatial sampling of 200 m radius circular plots in which Skylarks positions were mapped twice the year, we observed a strong selection for grasslands, an intermediate selection for cereals and spring-sown crops (changing with scale and time), and an avoidance of oilseed rape. Selection for grasslands increased with the season, selection for spring-sown crops and oilseed rape was stable, while selection for cereals decreased but only at fine scale. Skylarks selected high crop diversity at the territory scale. Similarly, the synergetic effect of the presence of two crops was positive in most cases, and Skylarks preferred area with two crops rather than only one for some pairs of crops, indicative of landscape complementation (requirement for complementary resources located in different crop types). Our results suggest that smaller fields and crops well mixed in the landscape may benefit this farmland specialist, favouring the positive effects of the simultaneous presence of several crops. The study demonstrates the importance of considering simultaneously time and spatial scale dependencies, as well as the synergetic effects and the spatial arrangement of habitats in habitat selection studies, particularly in patchy dynamics environments such as farmlands.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Farmland is the most widespread human land use, covering about 38% of earth and 45% of the European Union (FAO, 2013). It supports a wide range of biodiversity (review in Marshall et al., 2003; Tucker, 1997), including threatened species as well as functional species that provide ecosystem services (Power, 2010). However, rapid agricultural changes in the second half of the 20th

century, associated with the replacement of natural and semi-natural habitats by crops and the intensification of the already used lands, are responsible for population declines of a range of species including plants, amphibians, reptiles, arthropods, mammals and birds (Krebs et al., 1999; Robinson and Sutherland, 2002; Stoate et al., 2001). Farmland specialist birds, even extremely common species such as the Skylark *Alauda arvensis* and the Corn Bunting *Miliaria calandra*, have therefore declined by more than 50% in the past 30 years (Donald et al., 2001b; Gregory et al., 2005; PECBMS, 2012; Vorisek et al., 2010).

In a review of biodiversity in farmlands, Benton et al. (2003) argued that habitat heterogeneity in farmlands is associated with higher biodiversity, and that the recent losses of farmland

* Corresponding author at: CEBC-CNRS, 79360 Villiers-en-Bois, France. Tel.: +33 5 49 09 35 13; fax: +33 5 49 09 65 26.

E-mail address: paul.miguet@gmail.com (P. Miguet).

biodiversity are therefore due to a homogenization of farmlands at multiple spatial and temporal scales. Landscape heterogeneity is defined by two components, composition and configuration (Fahrig and Nutton, 2005; Li and Reynolds, 1995): the former refers to the proportion of each cover type in a landscape, while the latter considers the spatial arrangement of these cover types and their neighbourhood relationships. In most previous studies, farmland landscape heterogeneity was measured by the quantity or diversity of semi-natural land uses only (e.g. Chiron et al., 2010 on birds), or with arable lands being considered as a single land use (e.g. Pickett and Siriwardena, 2011 on birds), or by the quantity of arable land or grasslands in the landscape used as a proxy of habitat-type diversity (Purtauf et al., 2005 on carabids; Roschewitz et al., 2005 on weeds; Rundlöf and Smith, 2006 on butterflies; Smith et al., 2010 on birds). However, due to both the rotation of crops, usually on an annual basis, as well as the variability in growth rates among crop types, crop heterogeneity in farmlands varies on a temporal scale as well as on a spatial scale, and therefore crop spatial organization and heterogeneity, in addition to semi-natural habitats, contribute to farmland landscape heterogeneity. Effect of crop heterogeneity on wildlife populations has received relatively little attention, and the few studies that investigated crop heterogeneity did not attempt to identify the processes responsible for its effects, limiting the heterogeneity to an index of crop diversity (e.g., Siriwardena et al., 2012 on birds).

Habitat selection is a hierarchical process that takes place from broader to finer spatial and temporal scales, by which individuals select the habitats they will use at those scales (Hutto, 1985; Johnson, 1980; Jones, 2001). In particular, when species require more than one resource to complete their life cycle, their abundance is predicted to be higher when those resources are both present (Dunning et al., 1992). This process is often referred to as “landscape complementation” and may have different origins. (i) Species may need these different resources spatially segregated at different periods of their life cycle (e.g. amphibians breed in ponds and winter in forests (Pope et al., 2000)). (ii) The quality of a habitat may change with time, so that several habitats are necessary to satisfy a given need for the species during the whole season (e.g. winter cereals are optimal for the nesting of Skylarks only early in the breeding season (Donald, 2004; Eggers et al., 2011)). (iii) Different resources found in different habitats may be necessary to fulfil the whole essential functions at a given time (e.g. birds need both a nesting site and a foraging area that are not necessarily in the same habitat (Barbaro et al., 2008; Ens et al., 1992)).

The Skylark, our model species, is a small passerine bird considered as a farmland specialist species, though it can be qualified as generalist within farmland landscapes with regard to the various crops used. These crops have different qualities and functions for the Skylark (Donald, 2004), since it prefers nesting and foraging in different crops during the breeding season (Eraud and Boutin, 2002; Wilson et al., 1997). Hence Skylarks are very likely to be positively affected by crop diversity, as suggested previously (Schläpfer, 1988). During the breeding season, the Skylark feeds mainly with invertebrates captured on the ground, while during winter the Skylark is mainly vegetarian (Donald, 2004). It lays several clutches per year (average 2.7: Delius, 1965), and therefore the breeding season is rather extended. We select Skylarks for study because (i) they are the most abundant passerine bird across European farmlands; (ii) they are strongly affected by land use decisions since they nest and forage directly in fields; (iii) their population has declined in Europe over the last 30 years (about 50%, PECBMS, 2012) consequently to agricultural changes, notably due to the replacement of spring-sown by autumn-sown cereals which offer a less favourable vegetation structure for breeding, and the disappearance of cereal stubbles, an important wintering habitat for the Skylark (Donald,

2004; PECBMS, 2012); and (iv) the species ecology (including habitat selection) has been well studied (see Donald, 2004 for a review).

In this study, we address the issue of the selection of a territory by Skylarks in a mosaic of crops during a breeding season, inspecting the individual effect of each crop and their synergies which are behind the heterogeneity effect. Our study is actually the first study attempting to both identify the effect of crop heterogeneity and the processes behind it, examining precisely the effect of each component of heterogeneity. Since Skylarks can move the limits of their territory between their two (or more) successive breeding attempts (Eggers et al., 2011; Schläpfer, 1988), we inspect scales above territory, and considered scales from micro-habitat (within territory) to the landscape, thus ranging from 20 m to 2000 m radius. Skylarks do not select crops randomly, i.e. according to their availability (see Boatman et al., 2010; Donald, 2004; Eraud and Boutin, 2002; Wilson et al., 1997 for previous study on crop preference). However, temporal changes in crop preferences in relation to spatial scale, or synergetic effects of crops behind a diversity effect have not been investigated so far in landscape ecology studies (but see Bissonette and Storch, 2007). In addition, although landscape complementation has been studied theoretically and empirically in relating population density to landscape composition using general linear modelling (e.g., Andren et al., 1997; Brotons et al., 2005; Stewart et al., 2010), here, we develop a finer method of analysis. In particular, our statistical unit is not a landscape, but the individual bird, a more adapted scale to detect significant synergetic patterns between crops. By using a same metric throughout all scales (Manly's standardized selection ratio) and bootstrap values to build a null model, we simultaneously investigate the following hypotheses: crop selection by Skylarks (i) varies with spatial scale, from territory to landscape scales and (ii) changes through the breeding season, due to variations in vegetation growth rates and harvesting dates among crops. We further study the hypothesis that, to fulfil these habitat requirements at multiple spatio-temporal scales, (iii) Skylarks will prefer areas of higher crop diversity since a mosaic of crop types can fulfil different functions (foraging, nesting) through the breeding season. The preference for crop diversity should be the strongest when the crops can fulfil different functions at a given time or the same function at different times. Therefore, we finally investigate the hypothesis that (iv) in a landscape composed of only two crops, Skylarks will not select area in direct proportion to its composition: areas where both crops are present simultaneously will be over-selected (positive synergetic effect), though depending on the identity of the pair of crops.

2. Methods

2.1. Study area and selection of plot location

The study area, “Zone Atelier Plaine & Val de Sèvre” (46°14' N, 0°24' W) in Poitou-Charentes, western France (Fig. 1), is a 430 km² farmland intensively cultivated, mainly with wheat and winter barley, but also sunflower, maize, oilseed rape, alfalfa and grasslands. Hedgerows and small forest fragments are still present but irregularly distributed. We selected a sample of 239 circular plots with a 200 m radius (Fig. 1). We favoured plots with no hedgerow or forest inside, since hedgerows are avoided by Skylarks and there is no Skylark in forest (Donald, 2004). We avoided the proximity of highly frequented roads, since it would have disturbed observations and added noise in our data. Plots were centred along tracks and small roads that separate fields to facilitate surveys. Our main purpose was to study crop effect on habitat selection; hence we chose plots in April on the basis of their current land use. Since

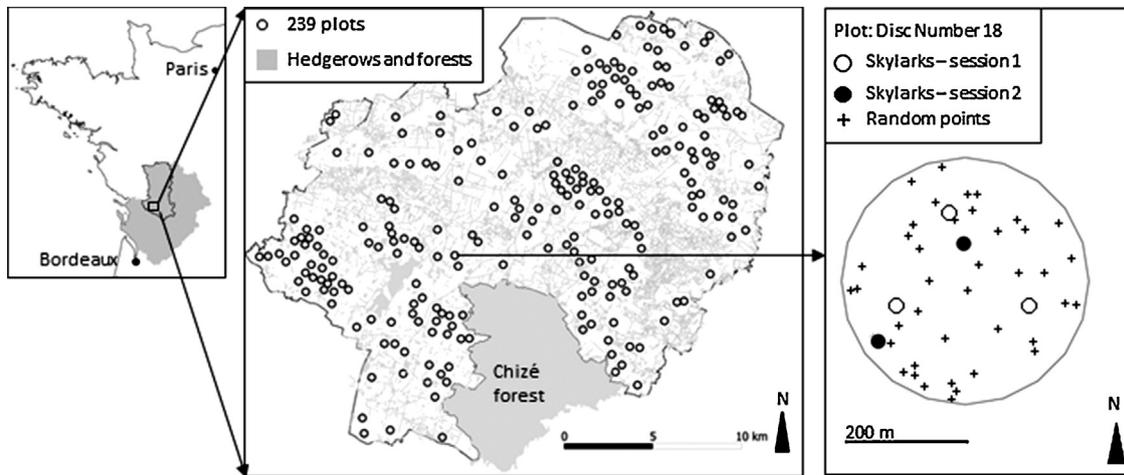


Fig. 1. Study area and sampling design. Situation of the study area “Zone Atelier Plaine & Val de Sèvre” in Poitou-Charentes, western France (left panel), spatial position of the 239 plots within the study area (middle panel), and an example of a specific plot (right panel), with the random points in this plot (crosses), and the position of the Skylarks observed in each session (white and black dots).

we could not study all crop types individually, that would have resulted in too many pairs of crops and not enough data for the most infrequent crops, we regrouped them in four crop categories, based on their abundance in the study area and their vegetation structure since this impacts crop’s functional role for Skylarks: (i) cereals (wheat and barley, which represent 44% of available crops, and 46% of the plot area), (ii) bare ground not yet sown or recently sown spring crops (29% of available crops, 24% of the plot area; mainly sunflower in the sample), (iii) oilseed rape (9% of available crops, 16% of the plot area) and (iv) artificial and temporary grasslands (18% of available crops, 14% of the plot area; mainly alfalfa was sampled). Plots were spatially chosen in order to show all possible combinations with 1, 2, 3 or 4 of the crop types. We aimed at obtaining similar sample sizes, but because of a lack of availability, the most infrequent crops were less present in the sample (e.g. alfalfa).

2.2. Bird surveys

Surveys were conducted in the spring of 2011, during two separate sessions included in the breeding season (Donald, 2004): 25th April to 14th May, and 28th May to 30th June. Surveys consisted in using a point-count method of 5 min (see Bonthoux and Balent, 2012 for a validation of this duration on the Skylark), points being located at the centres of the designated 239 plots (Fig. 1). Every singing Skylark detected within a 200 m range was counted and its position recorded each minute (i.e., individual birds were separated during the survey). The final position analyzed below is thus the average position (i.e. centroid) of each singing bird during the 5 min. The same plots were surveyed during both sessions. Surveys were conducted only during good weather conditions (no rain and no strong wind), since bird activity is reduced by bad weather conditions (pers. obs.). We assumed that the detection effort was constant during the observation period, as all detections were made aurally and with the help of 10×42 binoculars by the same observer to limit observer bias. Skylarks were all detected singing during their flight display, and there were no visual and sound obstacle to detection (no hedgerows or other vertical elements in the 200 m radius plots). Thus we assumed that all birds singing were detected with the same probability of detection, that the probability of detection did not change with the crops, that bird positions were correctly located on maps, and that the successive positions (five positions) were representative of the central area of the territory comprising the nest (Donald, 2004).

2.3. Habitat data

Crop data came from the annual land use survey of the study area: each field was visited twice during the year 2011 (April and June) and its land use was visually identified in the field and stored in a GIS. We used only four crop categories (cereals, spring-sown crops, oilseed rape and artificial grasslands) plus two non-crop categories (forest and village).

In addition to the points corresponding to the Skylarks’ positions, we generated 10,000 randomly positioned points in the 239 plots (compromise between precision and calculation duration). They were not generated in the whole study area since they were used to compare the observed positions of the Skylarks with random positions in the plots. Then, we computed the proportion of each of the four crop types (corrected by the total crop area) in circular buffers around the Skylarks positions and the 10,000 random points. This was calculated for 25 buffers with radii ranging from 20 m to 2000 m around each point (20, 30, 40, 50, 60, 70, 80, 90, 100, 120, 150, 200, 250, 300, 350, 400, 450, 500, 600, 700, 800, 900, 1000, 1500 and 2000 m). When a buffer’s surface laid outside the study area, i.e. where land use was not known, proportions of crops were computed using only data available within the study area, assuming that it was representative of the whole buffer. This however occurred rarely and so was expected to not affect the results (less than 6% of land use area was unknown for the 2000 m buffers, and this proportion decreased with buffer size decreasing up to less than 1% for buffers smaller than 600 m).

2.4. Quantifying crop selection

2.4.1. Index of crop selection

For each crop c_i and each buffer of radius b , the selection ratio ω_{b,c_i} (“used” to “available” ratio) was defined as the ratio of u_{b,c_i} , the proportion of crop c_i in the buffer b , averaged around all the observed Skylarks (“used”), to a_{b,c_i} , the proportion of crop c_i in the buffer b averaged around all the random points of the total surveyed area (“available”), i.e. the 239 plots. We quantified crop selection by birds using Manly’s standardized selection ratio α (Manly et al., 2002), defined as $\alpha_{b,c_i} = \omega_{b,c_i} / \sum_i \omega_{b,c_i} = (u_{b,c_i} / a_{b,c_i}) / \sum_i (u_{b,c_i} / a_{b,c_i})$, which can be interpreted as the probability that crop c_i is selected when all crops are equally available. With such standardization, the index is not influenced by the probability of detection of Skylarks at least if detectability is independent of crops.

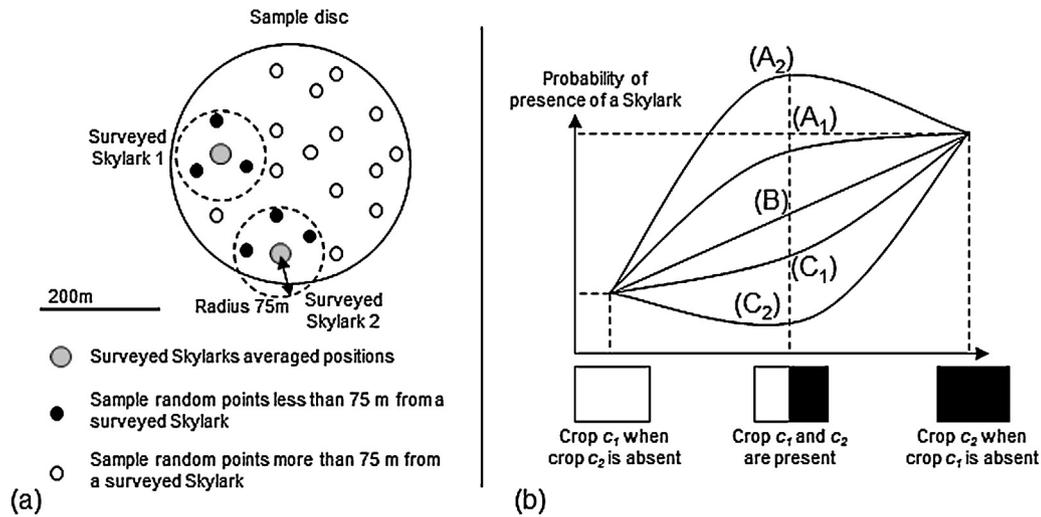


Fig. 2. Random point classification and different types of crop interaction. (a) Presentation of the classification of random points between presence and absence. Random points positioned less than 75 m from a Skylark were considered as presence points; random points positioned more than 75 m from a Skylark were considered as absence points. (b) Presentation of the three different types of crop interactions. The nature of the interaction was determined by the convexity of the curve. There were three cases: positive interaction (A_1 and A_2), no interaction (B), negative interaction (C_1 and C_2).

We computed four different versions of this index: during the first session (from the end of April to May), during the second session (June), during the whole breeding season (cumulating both sessions), and for each day for which data were available, i.e. when counts were performed ($N=40$ days). For the latter, the “available” random set used was only composed of the plots sampled that particular day. The values computed for each day were then used in a linear regression to test the effect of time on α . A positive slope would indicate that this crop is selected for more strongly compared to others as the breeding season progresses. We computed the value of the slope for each buffer radius and each crop.

We used 10,000 resamplings of Skylarks and random points to estimate bootstrapped confidence intervals of α for the whole breeding season, each session and each day; and bootstrapped values of selection ratios versus time slope (for each crop and each buffer radius). We used the same bootstrapped estimations to compare the values of α by pairs (calculating the two by two differences between values of α and comparing them to zero). P -values of these comparisons were computed for a two-sided test (null hypothesis: the two selection ratios are equal). Significances at the 5% level were adjusted using the Holm’s sequential Bonferonni correction for multiple tests (Holm, 1979).

2.4.2. Crop diversity selection

We computed Shannon crop diversity index around all Skylarks and random points, using the proportion of the four crops (cereals, spring-sown crops, oilseed rape and artificial grasslands). We then calculated the selection ratio for this index as the average Shannon index around Skylark locations to the average Shannon index around random points. This ratio was calculated for each buffer radius and each session. 95% bootstrapped confidence intervals were obtained using the method explained above.

2.4.3. Quantification of the synergetic effects of crops for pairs of crops

We next quantified the two by two interactive effects for each of the six possible pairs of crops to understand the causes of the crop heterogeneity effect. For each pair of crop (c_1, c_2) and buffer radius b , we selected from among the 10,000 random points mentioned above, those points that had more than 90% of cumulated proportion of c_1 and c_2 within a buffer b around them. We then sorted the points in two sets: the first set composed of points less than 75 m

from a Skylark and the second composed of points more than 75 m from a Skylark (Fig. 2a). This was done for the first session, the second session, and both cumulated. We chose a threshold distance of 75 m since it is the order of magnitude of a Skylark territory radius (Donald, 2004; Eraud and Boutin, 2002). For each pair of crops (c_1, c_2), and each buffer radius (b), we then computed the probability of a random point to be less than 75 m from a Skylark, $P_{b(c_1, c_2)} \sim 1 + X + X^2 + ID_{Plot}$, where $X = f_{b, c_1} / (f_{b, c_1} + f_{b, c_2})$ and f_{b, c_i} is the proportion of crop c_i in the buffer b , using spatial mixed effects logistic regressions with a quadratic term to detect non-linear relationships. X and X^2 are fixed effects. We added the identity of the plot ID_{Plot} as a random effect, and an exponential spatial correlation structure, to take into account the spatial structure of our data. We interpreted this probability as the probability of presence of a Skylark.

We plotted the estimated probabilities and their bootstrapped 95% confidence intervals for 100 m (this probability was also computed for buffer radii between 20 m and 200 m and we visually inspected that results were consistent with the 100 m results), and the estimates of the coefficient of the quadratic term of the logistic regressions for buffer radii between 20 m and 200 m. Then, according to the pattern of the curve and the sign of the estimated quadratic coefficient, several interpretations were possible. If the curve is linear or quasi-linear (i.e. quadratic coefficient non significantly different from 0), there is no synergetic effect of crop c_1 and c_2 and the probability of presence of a Skylark is only proportional to the composition of the studied buffer (Fig. 2b, curve B). It is the reference case. If the curve is concave (i.e. significantly negative quadratic coefficient), there is a positive effect of the synergy between crops and the probability of presence of a Skylark will be higher when both crops are present contiguously (Fig. 2b, curves A1 and A2) than in the reference case B. It can also be interpreted at broader scale: a positive effect of synergy means that, for a given composition of those two crops in a landscape, a configuration in which those crops are well mixed is better for Skylarks, as local conditions where both crops are simultaneously present occur more frequently. In the situation A1 (Fig. 2b), even a small quantity of the highest quality habitat is enough to ensure a high probability of presence. The situation A2 (Fig. 2b) is similar to A1 but when both habitats are present, the probability of presence is even higher than when the highest quality habitat is present alone, due to a positive edge effect or a complementation between both

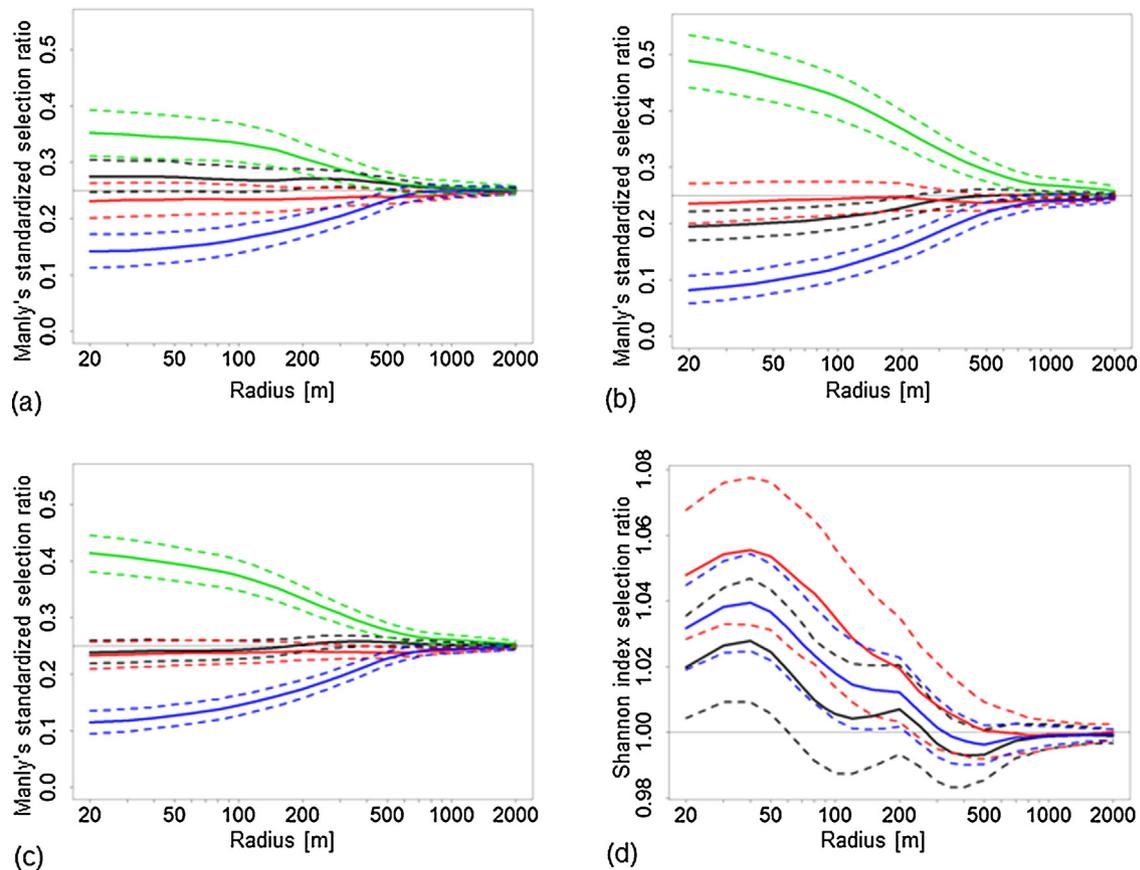


Fig. 3. Crop selection and crop diversity selection. (a)–(c) Manly's standardized selection ratio α for each of the four crop types (cereals in black, spring-sown crops in red, oilseed rape in blue, grasslands in green) during the first session only (a), the second session only (b), the whole census period (c). The continuous line is the mean Manly's standardized selection ratio and the discontinuous lines indicate its 95% confidence interval. (d) Selection ratio of the Shannon diversity index for each buffer radius. The Shannon index is calculated using the proportion of the four crops in each buffer: cereals, spring-sown crops, oilseed rape and grasslands. The solid line is the estimated selection ratio for each buffer radius (black curve: May; red curve: June; blue curve: both May and June). A value greater than 1 indicates that Skylarks select crop diversities higher than randomly. The discontinuous lines indicate the 95% confidence intervals estimated by 10,000 bootstraps. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

habitats. If the curve is convex (i.e. significantly positive quadratic coefficient), there is a negative effect of the synergy between crops and the probability of presence of a Skylark will be lower when both crops are present contiguously (Fig. 2b, curves C_1 and C_2) than in the reference case B. At broader scale, a configuration in which those two crops are more segregated is more appropriate for the species. In the situation C_1 (Fig. 2b), a high proportion of the highest quality habitat is needed to ensure a high probability of presence. The situation C_2 (Fig. 2b) is similar to C_1 but when both habitats are present, the probability of presence is even smaller than when the lowest quality habitat is present alone, due to a negative edge effect.

2.4.4. Softwares

All map manipulations and SIG calculations were carried out using ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA, USA, 2008). All other calculations were carried out using R 2.12.0 (R Development Core Team, 2010). Spatial generalized linear mixed models were adjusted using the function `glmmPQL` of the MASS package in R (Venables and Ripley, 2002).

3. Results

In total, we detected and positioned 1280 Skylarks (741 during the first session in May and 539 during the second session in June). The number of Skylarks detected declined continuously over the breeding season, with an average decrease of 0.85 Skylark per plot between the two sessions (standard error = 0.097,

$N = 239$, average interval between the two sessions = 41.2 days, range = 30–53), though we cannot know whether this decrease represents a decrease in the number of territorial birds, or a decrease in singing activity.

3.1. Comparison of selection between crops

Skylarks did not select crops randomly, significantly up to about 1500 m (Fig. 3c and Table 1). Grasslands were always more selected than any other crops, over 500 m in distance (Fig. 3c, Table 1). This latter value varied however during the breeding season, being 150 m early in breeding season (Fig. 3a, Table 1), and up to 600 m later (Fig. 3b, Table 1). Oilseed rape was the least selected crop, up to about 400 m, significantly avoided over larger buffers in June than in May (Fig. 3a, 3b, Table 1). Cereals and spring-sown crops presented intermediate situations, significantly more selected than oilseed rape over up to about 300–600 m (depending on the session) and less selected than grasslands, over a broader scale in June than in May.

However, the relative preference between cereals and spring-sown crops changed with scale as well as time (Fig. 3a–c, Table 1). During the breeding season, cereals were significantly more selected than spring-sown crops only at landscape scale between 300 m and 1500 m, but not at finer scales where both crops were equally selected (Fig. 3c, Table 1). In May, cereals were preferred to spring-sown crops at breeding territory and landscape scales, significantly over up to about 1000 m. However, later in the

Table 1
Comparison of the Manly's standardized selection ratios for each of the six pairs of crops (four crop types).

Crop 1	Crop 2	Session 1	Session 2	Sessions 1 and 2
Cereals (C)	Spring-sown crops (SS)	C > SS: (20) 150–1000	C < SS: 20–120	C > SS: (250) 300–1500
Cereals (C)	Oilseed rape (R)	C > R: 20–500	C > R: 20–500	C > R: 20–600
Cereals (C)	Grasslands (G)	C < G: 20–150 (200)	C < G: 20–600 (700)	C < G: 20–500 (600)
Spring-sown crops (SS)	Oilseed rape (R)	SS > R: 20–300	SS > R: 20–350 (400)	SS > R: 20–400 (450)
Spring-sown crops (SS)	Grasslands (G)	SS < G: 20–400 (450)	SS < G: 20–1500	SS < G: 20–1500
Oilseed rape (R)	Grasslands (G)	R < G: 20–450	R < G: 20–900 (1500)	R < G: 20–700

The sign < or > indicates the nature of the difference. Comparisons are tested using 10,000 bootstrapped simulations and two-sided tests with Bonferroni–Holm corrections (Holm, 1979). Capital letters refer to crop type (C: cereals, SS: spring-sown crop, R: oilseed rape, G: grasslands). The values indicate the interval where the difference of crop selection is significant at the 5% level. The values in bracket indicate the extension of the interval where the difference of selection ratio is almost significant, i.e. significant at the 10% level with the Bonferroni–Holm correction.

season, it was the reverse at territory scale, spring-sown crops being significantly preferred over up to 120 m (Fig. 3a, Table 1). But cereals were still more selected at landscape scale, beyond 300 m (Fig. 3b), though this was not significant anymore (Table 1).

Crop selection also varied with date (compare Fig. 3a and b; see Fig. 4 for statistical testing). Grasslands were more and more selected as the breeding season progressed, though this was significant over only up to 120 m (Fig. 4, green curve). Conversely, selection for cereals declined over the breeding season, significantly so over up to 300 m (Fig. 4, black curve). The trends in oilseed rape and spring-sown crops were not significant.

Finally, Skylarks selected preferentially areas of high crop diversity, more significantly so in June (over up to 200 m) than in May (Fig. 3d). Higher crop diversity was selected only at territory scale.

3.2. Selection for pairs of crops and synergetic effects

Interactions between crops were generally non-linear (Figs 5 and 6): curves looked generally concave, sometimes linear (concavity non significant) and only one curve was convex (Fig. 5). Estimated quadratic coefficients were either significantly negative (revealing a positive interaction, thus a concave relationship between the probability of presence and the crop composition) or not significantly different from zero (Fig. 6). These patterns were apparently unaffected by spatial scale over distances of 20 m–200 m (Fig. 6). The concave relationships were of type A1 or A2 (Fig. 2b).

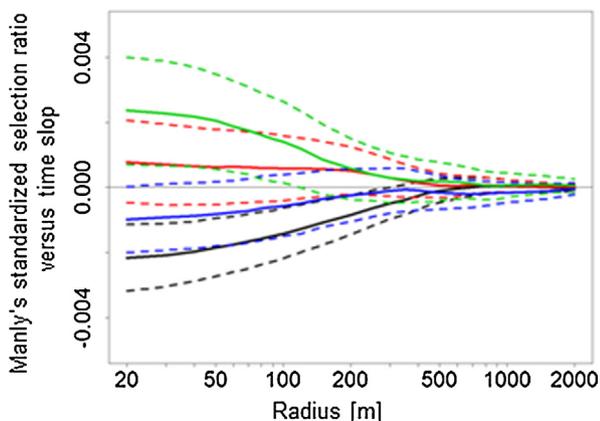


Fig. 4. Temporal trends in crop selection. Slope of the linear regression of the Manly's standardized selection ratio α versus time for each of the four crop types studied (cereals in black, spring-sown crops in red, oilseed rape in blue, grasslands in green) and for each buffer radius. The solid line is the estimated coefficient for each buffer radius. A positive slope indicates that this crop is more and more selected compared to other, as the breeding season progresses. A negative slope indicates that this crop is less and less selected along the breeding season. The discontinuous lines indicate the 95% confidence intervals estimated by 10,000 bootstraps. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The following relationships were concave in May and June: cereals – spring-sown crops (Fig. 5a and b, black curve), and cereals – oilseed rape (Fig. 5a and b, red curve). The cereals – grasslands relationship (Fig. 5a and b, blue curve) was concave in June, but linear in May. All other relationships (spring-sown crops – oilseed rape, spring-sown crops – grasslands, oilseed rape – grasslands) were not significantly different from linear (Fig. 6a–c, green, purple and grey curves). Cereals – spring-sown crops in May and June and on average during the whole breeding season (Fig. 5a–c, black curve) represented a concave interaction of type A2 (Fig. 2d), hence suggested complementation. Spring-sown crops – oilseed rape in May (Fig. 5a, green curve) was the only convex interaction (type C₁ Fig. 2d), though it was not a strong convex relationship, and the interaction was seldom significant (Fig. 6a, green curve), and rather positive at all studied scales in June (Figs 5b and 6b, green curve).

4. Discussion

4.1. Crop selection by Skylarks

As predicted, Skylarks did not select crops randomly, and their preferences changed with time as well as spatial scale. Artificial grasslands, which mainly consisted of alfalfa (73%) in our plots, were always the most preferred crops, while oilseed rape was mostly avoided, cereals and spring-sown crops occupying an intermediate position. Although grasslands were the most selected crop, cereals nevertheless supported more Skylarks than grasslands in our study area simply because they covered more area (44.4% vs. 17.6%), and grasslands outside our sampled plots were often associated with hedgerows (hence avoided by the Skylarks). Our results are fully consistent with the findings of previous studies that rank crops according to Skylark density (Boatman et al., 2010; Donald, 2004; Eraud and Boutin, 2002; Wilson et al., 1997): the highest nest or territory densities were observed in alfalfa, set-asides or grasslands, and then, lower down the scale, in cereals and spring-sown crops and, the least in oilseed rape, probably in relation to the structure of the crop vegetation.

Perhaps because our study area may not be enough contrasted, we could not detect habitat selection by Skylarks at distances greater than 1500 m. This may not, however, mean that land use at this scale had no more effect on Skylarks.

Cereals were preferred to spring-sown crops at the beginning of the season, but at the end of the season, cereals remained more selected at landscape scale (~300 m–1000 m) while spring-sown crops became more selected than cereals at local scale (i.e., the Skylark territory scale, ~20 m–100 m). This seasonal trend in selection is probably related to the fact that Skylarks prefer cereals of about 60 cm height (Donald et al., 2001a; Eggers et al., 2011), which are not anymore available late in season (see Gillis et al., 2012 for values of wheat height in this study site). Hence at local scale, Skylarks shift to spring-sown crops offering a more suitable vegetation structure. The absence of detectable shift at greater

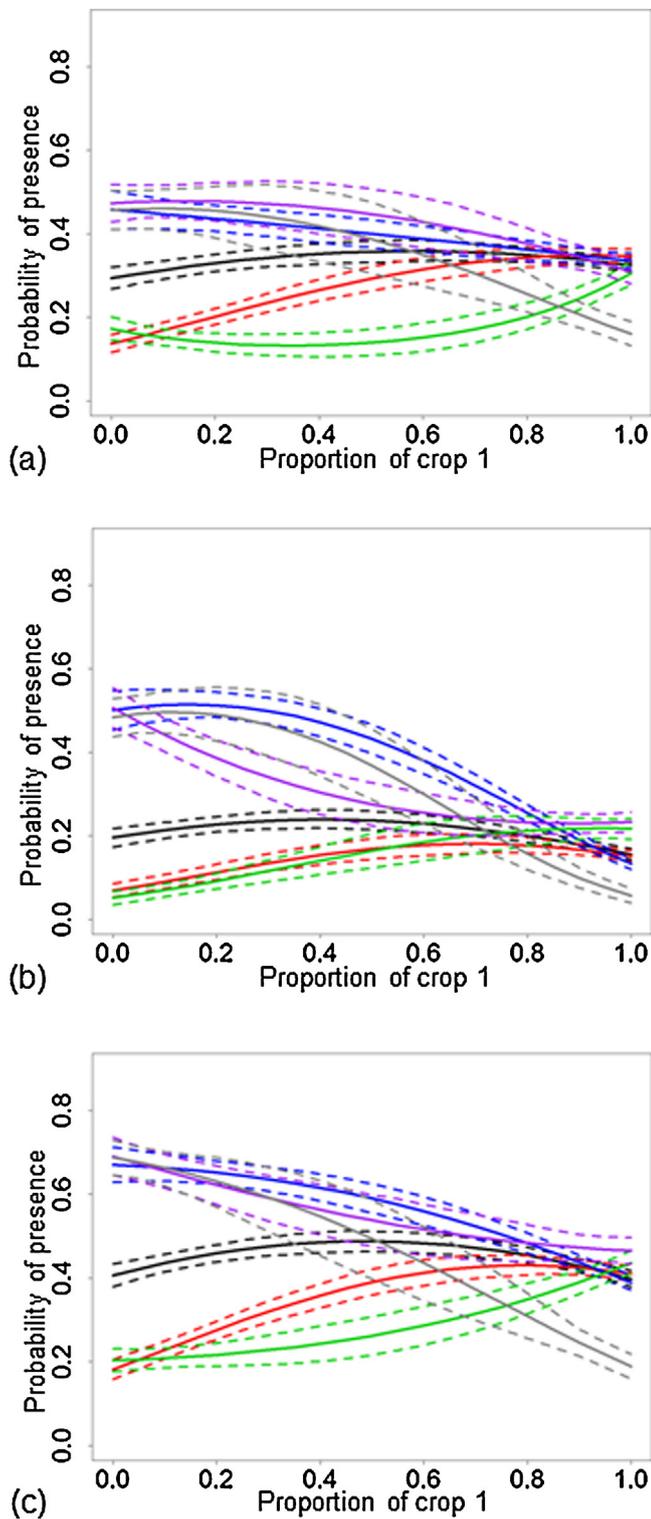


Fig. 5. Detailed pattern of crop selection for all pairs of crops. Probability that a random point, surrounded by two crops, is less than 75 m from a Skylark in (a) May, (b) June and (c) both. Curves are presented for crop composition computed in a buffer radius of 100 m. The continuous lines are predictions of a logistic regression (discontinuous lines are the 95% confidence intervals). Each colour refers to a combination of two crops. Black: cereals – spring-sown crops; red: cereals – oilseed rape; blue: cereals – grasslands; green: spring-sown crops – oilseed rape; purple: spring-sown crops – grasslands; grey: oilseed rape – grasslands. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

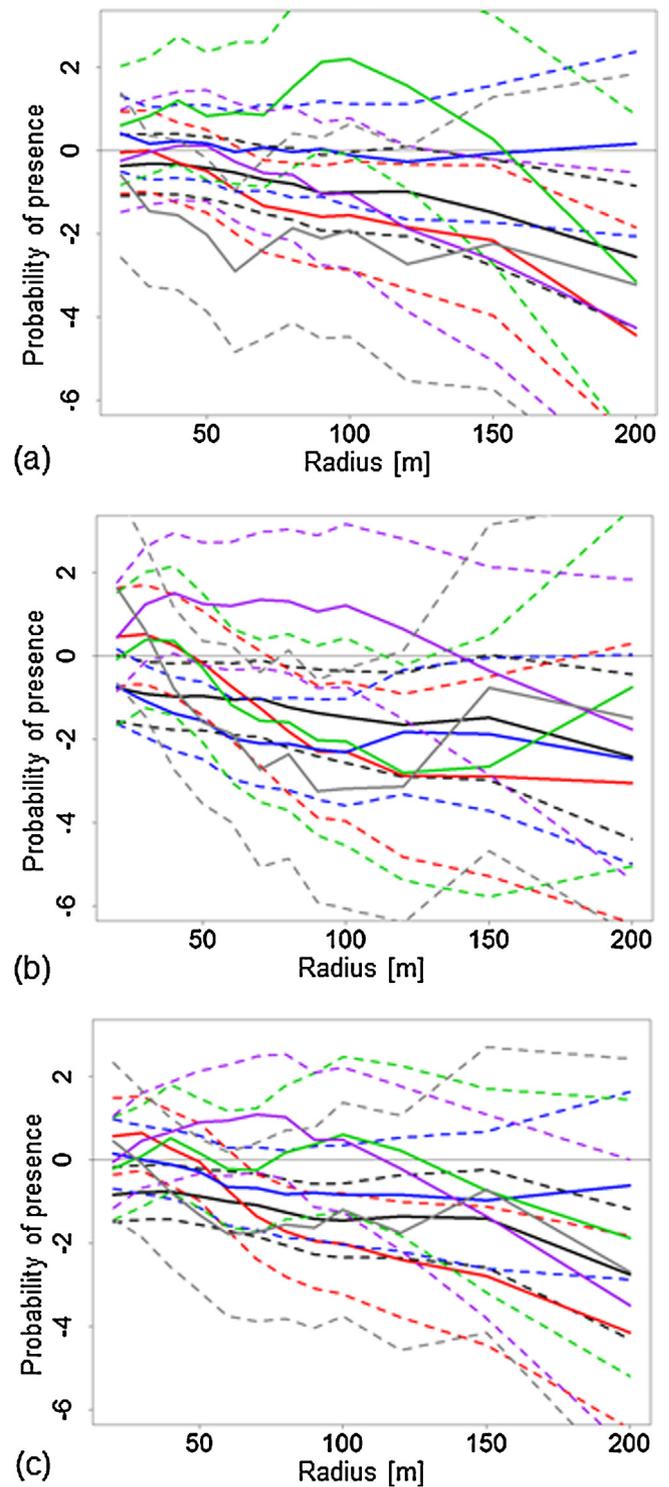


Fig. 6. Quadratic coefficients estimated by the logistic regression (continuous lines) with their 95% confidence interval (discontinuous lines), for each of the 6 pairs of crops, using May data (a), using June data (b), using both May and June data (c) for different scales from 20 m to 200 m. A negative coefficient indicates that the predicted curve is on the whole concave. Each colour refers to a combination of two crops. Black: cereals – spring-sown crops; red: cereals – oilseed rape; blue: cereals – grasslands; green: spring-sown crops – oilseed rape; purple: spring-sown crops – grasslands; grey: oilseed rape – grasslands. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

scale may be explained by the initial selection for cereals early in the season, and it suggests that Skylark breeding pairs tend to avoid large scale movements between consecutive breeding attempts. A shift of crop selection has already been demonstrated for Skylarks, essentially from winter cereals to spring-sown cereals (Eggers et al., 2011; Hiron et al., 2012), but none of the latter studies suggested that the shift could be scale-dependant. Our results therefore highlight that in species showing strong habitat preferences, these preferences may vary over time and spatial scale. Only a few other studies showed time-dependent selection (Boyce et al., 2003 for the Elk *Cervus canadensis*, Gilroy et al., 2010 for the yellow Wagtail *Motacilla flava* and Reid et al., 2010 for the Irish Hares *Lepus timidus hibernicus*) and scale-dependent selection (Orians and Wittenberger, 1991 for the yellow-headed Blackbird *Xanthocephalus xanthocephalus*, Boyce et al., 2003 for the Elk, Mayor et al., 2007 for the woodland Caribou *Rangifer tarandus caribou*). We hypothesize that time or scale dependent selections are actually a rather common pattern, given that the environment is temporally dynamic and many species use environmental resources at a limited spatial range (e.g. home range whose the size may change depending on the environmental context). Therefore a context dependent approach that considers all seasons and different spatial scales may be necessary to well understand habitat selection.

4.2. Synergetic effects of crops and landscape complementation

As predicted, Skylarks selected areas with higher crop diversity, but only at territory scale. This effect was stronger in June than in May. Synergetic effects of crops were generally positive, sometimes not significant, and negative for only one pair of crops in May. Skylarks prefer having two crops in their territory rather than only one. Other studies have already suggested that Skylarks prefer to encompass several crops in their territories and to nest close to field boundaries (Eraud and Boutin, 2002; Schläpfer, 1988). Schläpfer (1988) found that smaller territories tend to have higher crop richness, though Hiron et al. (2012) did not find higher Skylark density in presence of adjacent fields with contrasting vegetation height. For the first time to our knowledge however, our study is able to propose a mechanism by which crop diversity affects Skylark habitat selection. The simultaneous presence of cereals and spring-sown crops acts positively on the diversity effect, conversely to spring-sown crops and oilseed rape that act negatively on the diversity effect (mainly in May). This result highlights the need to understand individual roles of each component of the diversity. In this latter case, the presence of an avoided habitat decreased the positive effect of habitat diversity. Therefore, quantifying the synergies when different habitats are simultaneously present seems particularly relevant: in our case, we found that synergies can be positive, negative or neutral, even though a global positive effect of diversity was detected.

All positive synergies (type A1 or A2, Fig. 2b) mean that the highest quality crop of the pair improves significantly the attractiveness of an area even if it represents only a small proportion. For instance, if a crop can offer nesting sites, only a small quantity of this crop is necessary to fulfil the function. One of the strongest positive interactions observed (type A2, Fig. 2b) was between cereals and spring-sown crops. We suggest that these two crops are complementary: in May cereals are optimal for nesting (Eggers et al., 2011) and spring-sown crops allow higher food accessibility (large proportion of ploughed field), even though food abundance may not be as high as in cereals (Odderskaer et al., 1997). During the breeding season Skylark diet consists mainly in invertebrates. This is a case of spatial complementation, between nesting habitat and foraging habitat, as has been shown for other insectivorous farmland birds (Schaub et al., 2010; Barbaro et al., 2008). In addition, we

hypothesize that cereals and spring-sown crops represent a case of temporal complementation: in late spring, cereals are no longer suitable for nesting since vegetation has become too high and too dense, whereas spring-sown crops have grown and are suitable for nesting. Non-significant interactions (i.e. linear relations) concerned mainly pairs of crops very similar in quality, i.e. each crop does not add a significantly supplementary resource to the other.

All these positive interactions between pairs of crops may suggest that at broader scales farmlands where different crops are well mixed (over-dispersed) could have higher Skylark abundance than more homogenous landscapes. This situation is more likely to occur when fields are small. Hence even if configuration metrics were not explicitly included in our analyses, our results highlight the importance of crop configuration (field spatial arrangement) for Skylarks. Nevertheless, this has to be confirmed by studies at broader scales, or studies relating fitness to crop composition, to ensure that fitness is actually higher in the most selected configurations. The common assumption that observed density well reflects habitat quality may be misleading, e.g. in the case of ecological traps (see Vanhorne, 1983). Hence, only direct measurements of fitness (productivity and survival) can really quantify habitat quality.

4.3. Multi-scale habitat selection analysis in heterogeneous landscapes

Most habitat selection studies consider only one scale of analysis (typically the scale of individual territories in bird studies). However, the scale at which the studied species actually select their habitat is usually unknown, it may be context-dependant (e.g. the size of a territory may change in space and time), and it is well-recognized that habitat selection occurs at multiple spatial and temporal scales (Johnson, 1980). Hence, though commonly found in the literature, using an arbitrary scale may lead to erroneous conclusions if the chosen scale of analysis is not relevant. For instance, Orians and Wittenberger (1991) found that selection for a high density of food resource occurred only at the marsh scale but not at territory scale in yellow-headed Blackbirds, due to the unpredictability of food abundance at the territory scale at the time of territory selection. In addition, studies considering several spatial scales are generally limited to few discrete scales (Boyce et al., 2003; Orians and Wittenberger, 1991, but see Mayor et al., 2007). Here we have addressed habitat selection across a continuum of scales from territory to landscape (the whole extent of scales that our data allowed), and we found that selection, i.e. the preference between two crops, changed with scale. This result was explained by a shift in habitat selection due to a shift in crop quality, and seems like an unbalance habitat selection imposed by an initial choice more than a selection with positive effect on fitness.

Habitat selection occurs only in presence of heterogeneity (there can be no habitat selection in a completely uniform environment). Farmlands are very heterogeneous as a consequence of fields' spatial arrangement. However, it is because the heterogeneity is multi-scale that we observed this multi-scale habitat selection in our study. Indeed, a better mixing of cereals fields and spring-sown crops in the landscape (e.g. with smaller fields) would have made the initial selection by Skylarks at the territory scale consistent with their needs during the whole season. This result highlights that a study based only on landscape scale without considering crop synergetic interactions would have underestimated the positive effect of spring-sown crops. To conclude, our study demonstrates the importance of considering a continuum of scales, time-dependency, synergetic interactions and spatial arrangement of habitats in habitat selection studies and conservation planning.

Acknowledgements

Paul Miguet is funded by an INRA PhD grant (CJS, Institut National de la Recherche Agronomique, ED SIBAGHE Montpellier). We thank J. Girard, A. Bailur and S. Gaba for their critical reviews on a previous draft, two anonymous reviewers for their comments, as well as K. Le Rest for valuable discussions.

References

- Andren, H., Delin, A., Seiler, A., 1997. Population response to landscape changes depends on specialization to different landscape elements. *Oikos* 80, 193–196.
- Barbaro, L., Couzi, L., Bretagnolle, V., Nezan, J., Veillard, F., 2008. Multi-scale habitat selection and foraging ecology of the Eurasian Hoopoe (*Upupa epops*) in pine plantations. *Biodiversity and Conservation* 17, 1073–1087.
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution* 18, 182–188.
- Bissonette, J.A., Storch, I. (Eds.), 2007. *Temporal Dimensions of Landscape Ecology. Wildlife Response to Variable Resources*. Springer, New York.
- Boatman, N.D., Pietravalle, S., Parry, H.R., Crocker, J., Irving, P.V., Turley, D.B., Mills, J., Dwyer, J.C., 2010. Agricultural land use and Skylark *Alauda arvensis*: a case study linking a habitat association model to spatially explicit change scenarios. *IBIS* 152, 63–76.
- Bonthoux, S., Balent, G., 2012. Point count duration: five minutes are usually sufficient to model the distribution of bird species and to study the structure of communities for a French landscape. *Journal of Ornithology* 153, 491–504.
- Boyce, M.S., Mao, J.S., Merrill, E.H., Fortin, D., Turner, M.G., Fryxell, J., Turchin, P., 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* 10, 421–431.
- Brotons, L., Wolff, A., Paulus, G., Martin, J.L., 2005. Effect of adjacent agricultural habitat on the distribution of passerines in natural grasslands. *Biological Conservation* 124, 407–414.
- Chiron, F., Filippi-Codaccioni, O., Jiguet, F., Devictor, V., 2010. Effects of non-cropped landscape diversity on spatial dynamics of farmland birds in intensive farming systems. *Biological Conservation* 143, 2609–2616.
- Delius, J.D., 1965. A population study of Skylarks *Alauda arvensis*. *IBIS* 107, 466–492.
- Donald, P.F., 2004. The Skylark. T. & A. D. Poyser, London, 256 pp.
- Donald, P.F., Evans, A.D., Buckingham, D.L., Muirhead, L.B., Wilson, J.D., 2001a. Factors affecting the territory distribution of Skylarks *Alauda arvensis* breeding on lowland farmland. *Bird Study* 48, 271–278.
- Donald, P.F., Green, R.E., Heath, M.F., 2001b. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London Series B: Biological Sciences* 268, 25–29.
- Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65, 169–175.
- Eggers, S., Unell, M., Part, T., 2011. Autumn-sowing of cereals reduces breeding bird numbers in a heterogeneous agricultural landscape. *Biological Conservation* 144, 1137–1144.
- Ens, B.J., Kersten, M., Brenninkmeijer, A., Hulscher, J.B., 1992. Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology* 61, 703–715.
- Eraud, C., Boutin, J.M., 2002. Density and productivity of breeding Skylarks *Alauda arvensis* in relation to crop type on agricultural lands in western France. *Bird Study* 49, 287–296.
- Fahrig, L., Nutton, W.K., 2005. Population ecology in spatially heterogeneous environments. In: Lovett, G.M., Jones, C.G., Turner, M.G., Weathers, K.C. (Eds.), *Ecosystem Function in Heterogeneous Landscapes*. Springer, New York, pp. 95–118.
- FAO, 2013. FAOSTAT Statistics Database. Food and Agriculture Organization of the United Nations, Rome, Italy, Available from: <http://faostat.fao.org> (accessed 23.05.13).
- Gillis, H., Gauffre, B., Huot, R., Bretagnolle, V., 2012. Vegetation height and egg coloration differentially affect predation rate and overheating risk: an experimental test mimicking a ground-nesting bird. *Canadian Journal of Zoology* 90, 694–703.
- Gilroy, J.J., Anderson, G.Q.A., Grice, P.V., Vickery, J.A., Sutherland, W.J., 2010. Mid-season shifts in the habitat associations of Yellow Wagtails *Motacilla flava* breeding in arable farmland. *IBIS* 152, 90–104.
- Gregory, R.D., van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P.B., Gibbons, D.W., 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society B: Biological Science* 360, 269–288.
- Hiron, M., Berg, A., Part, T., 2012. Do Skylarks prefer autumn sown cereals? Effects of agricultural land use, region and time in the breeding season on density. *Agriculture, Ecosystems & Environment* 150, 82–90.
- Holm, S., 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6, 65–70.
- Hutto, R.L., 1985. Habitat selection by nonbreeding, migratory land birds. In: Cody, M.L. (Ed.), *Habitat Selection in Birds*. Academic Press, New York, pp. 455–476.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71.
- Jones, J., 2001. Habitat selection studies in avian ecology: a critical review. *Auk* 118, 557–562.
- Krebs, J.R., Wilson, J.D., Bradbury, R.B., Siriwardena, G.M., 1999. The second silent spring? *Nature* 400, 611–612.
- Li, H., Reynolds, J.F., 1995. On definition and quantification of heterogeneity. *Oikos* 73, 280–284.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, 2nd ed. Kluwer/Academic Publishers, New York/Boston/Dordrecht/London/Moscow, 240 pp.
- Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R., Ward, L.K., 2003. The role of weeds in supporting biological diversity within crop fields. *Weed Research* 43, 77–89.
- Mayor, S.J., Schaefer, J.A., Schneider, D.C., Mahoney, S.P., 2007. Spectrum of selection: New approaches to detecting the scale-dependent response to habitat. *Ecology* 88, 1634–1640.
- Odderskaer, P., Prang, A., Poulsen, J.G., Andersen, P.N., Elmegaard, N., 1997. Skylark (*Alauda arvensis*) utilisation of micro-habitats in spring barley fields. *Agriculture, Ecosystems & Environment* 62, 21–29.
- Orians, G.H., Wittenberger, J.F., 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137, S29–S49.
- PECBMS, 2012. Trends of common birds in Europe, 2012 update. Pan-European Common Bird Monitoring Scheme, Available from: <http://www.ebcc.info/index.php?ID=485> (accessed 13.06.13).
- Pickett, S.R.A., Siriwardena, G.M., 2011. The relationship between multi-scale habitat heterogeneity and farmland bird abundance. *Ecography* 34, 955–969.
- Pope, S.E., Fahrig, L., Merriam, N.G., 2000. Landscape complementation and metapopulation effects on leopard frog populations. *Ecology* 81, 2498–2508.
- Power, A.G., 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical Transactions of the Royal Society B: Biological Science* 365, 2959–2971.
- Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tscharnke, T., Wolters, V., 2005. Landscape context of organic and conventional farms: influences on carabid beetle diversity. *Agriculture, Ecosystems & Environment* 108, 165–174.
- R Development Core Team, 2010. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reid, N., McDonald, R.A., Montgomery, W.I., 2010. Homogeneous habitat can meet the discrete and varied resource requirements of hares but may set an ecological trap. *Biological Conservation* 143, 1701–1706.
- Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* 39, 157–176.
- Roschewitz, I., Gabriel, D., Tscharnke, T., Thies, C., 2005. The effects of landscape complexity on arable weed species diversity in organic and conventional farming. *Journal of Applied Ecology* 42, 873–882.
- Rundlof, M., Smith, H.G., 2006. The effect of organic farming on butterfly diversity depends on landscape context. *Journal of Applied Ecology* 43, 1121–1127.
- Schaub, M., Martinez, N., Tagmann-Isoset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F., Zbinden, N., Jenni, L., Arlettaz, R., 2010. Patches of bare ground as a staple commodity for declining ground-foraging insectivorous farmland birds. *PLoS ONE*, 5.
- Schläpfer, A., 1988. Populationsökologie der Feldlerche *Alauda arvensis* in der intensiv genutzten Agrarlandschaft. *Der ornithologische Beobachter* 85, 309–371.
- Siriwardena, G.M., Cooke, I.R., Sutherland, W.J., 2012. Landscape, cropping and field boundary influences on bird abundance. *Ecography* 35, 162–173.
- Smith, H.G., Danhardt, J., Lindstrom, A., Rundlof, M., 2010. Consequences of organic farming and landscape heterogeneity for species richness and abundance of farmland birds. *Oecologia* 162, 1071–1079.
- Stewart, A., Komers, P.E., Bender, D.J., 2010. Assessing landscape relationships for habitat generalists. *Ecoscience* 17, 28–36.
- Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., de Snoo, G.R., Eden, P., 2001. Ecological impacts of arable intensification in Europe. *Journal of Environmental Management* 63, 337–365.
- Tucker, G.M., 1997. Priorities for bird conservation in Europe: the importance of the farmed landscape. In: Pain, D.J., Pienkowski, M.W. (Eds.), *Farming and Birds in Europe: Common Agricultural Policy and Its Implications for Bird Conservation*. Academic Press, San Diego/London/Boston/New York/Sydney/Tokyo/Toronto, pp. 79–116.
- Vanhorne, B., 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47, 893–901.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, 4th ed. Springer, New York.
- Vorisek, P., Jiguet, F., Van Strien, A., Skorpilova, J., Klvanova, A., Gregory, R.D., 2010. Trends in abundance and biomass of widespread European farmland birds: how much have we lost? In: *BOU Proceedings – Lowland Farmland Birds III*, Available from <http://www.bou.org.uk/bouproc-net/1fb3/vorisek-etal.pdf> (accessed 07.01.13).
- Wilson, J.D., Evans, J., Browne, S.J., King, J.R., 1997. Territory distribution and breeding success of Skylarks *Alauda arvensis* on organic and intensive farmland in southern England. *Journal of Applied Ecology* 34, 1462–1478.