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

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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.

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

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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 Nuttle, 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 microhabitat (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 km^2 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