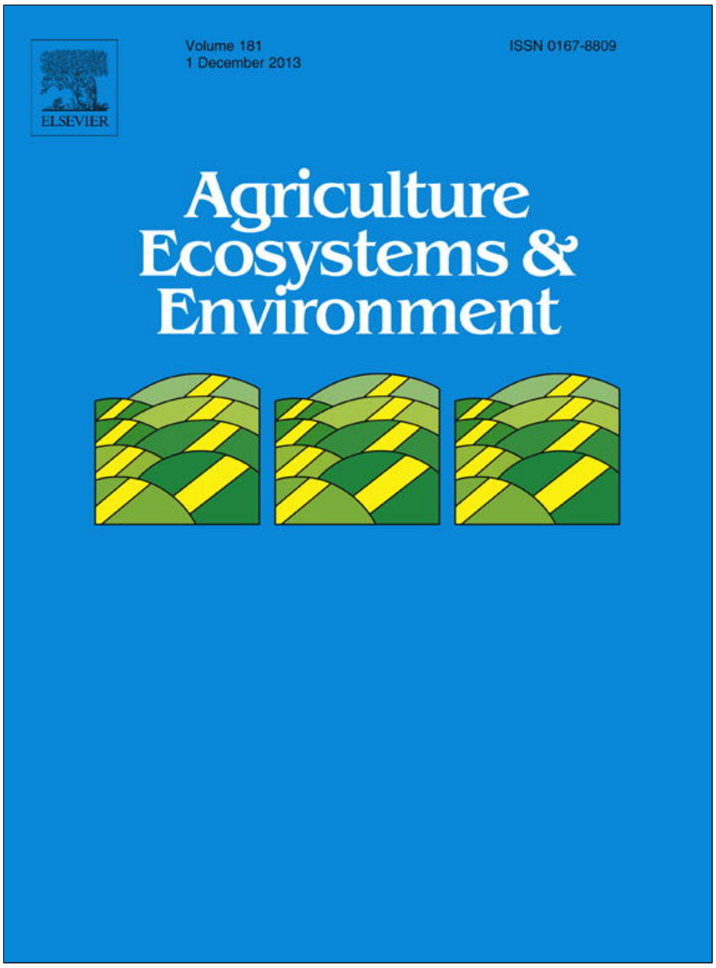
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Grass buffer strips benefit invertebrate and breeding skylark numbers in a heterogeneous agricultural landscape

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ABSTRACT

The loss of non-crop habitat is often suggested to be a key driver of biodiversity decline on arable land. Grass buffer strips on cereal field edges, to reduce erosion and agro-chemical runoff into surface water, could be useful to mitigate this diversity loss as they are often assumed to provide refuge and food for invertebrates, small mammals and birds. Evidence for this idea is, however, scarce and it remains unclear whether densely vegetated buffer strips benefit biodiversity in structurally complex landscapes of Northern Europe. Here, we examined whether buffer strips affected breeding skylark *Alauda avensis* numbers and its main food supply (i.e. beetles *Coleoptera* and spiders *Arachnida*) on cereal fields in a heterogeneous agricultural landscape of south-central Sweden. We also examined whether buffer strip effects on skylark density depended on seasonal sward height differences between sowing regimes (spring- vs. autumn-sown) as they presumably influence seasonal invertebrate accessibility. Fields with buffer strips supported on average 0.51 ± 0.26 more skylark territories per hectare up to 100 m into the field and boosted invertebrate activity densities compared to fields without buffer strips. These effects were most apparent early in spring, but persisted throughout the sampling period, and were similar among spring and autumn sown fields. Thus, our results provide evidence to suggest that buffer strips target multiple environmental objectives on cereal fields in heterogeneous farmland. Future research should work to identify buffer strip management practices that further increase their value to biodiversity at the local scale, and investigate how they affect farmland biodiversity in different landscape types at larger spatial scales for more efficient implementation across Europe.

1. Introduction

Across Europe and North America, increased size of arable fields together with simplified crop rotation has resulted in loss of non-crop habitat and a simplification of agricultural landscapes (Smith et al., 1993; Stoate et al., 2001, 2009). Increased pesticide and fertilizer use has further boosted agricultural productivity, but also imposes a negative impact on surface water quality (Watson, 2004), biodiversity (Fuller et al., 1995; Chamberlain et al., 2000a,b; Donald et al., 2001; Power, 2010), and biological control potential (Straub et al., 2008; Geiger et al., 2010).

Multi-purpose buffer strips have been established on a large scale to mitigate these negative effects of intensified agriculture (Muscutt et al., 1993; Marshall and Moonen, 2002). These densely vegetated strips are typically established on field edges by sowing a mixture of perennial grass species adjacent to streams and larger ditches to avoid soil erosion (Vought et al., 1995), reduce leaching of agro-chemicals from agricultural land (Uusi-Kämppä and Jauhiainen, 2010), benefit invertebrates for pest suppression (Bianchi et al., 2006), and provide habitat for ground-foraging farmland birds (Vickery et al., 2002). However, evidence for positive effects of buffer strips on farmland birds is scarce, as studies on biodiversity effects of field margins often comprise of a variety of margin types that are managed mainly for the conservation of arable plants and pollinators, or provision of food and protection for birds and small mammals (Perkins et al., 2002; Vickery et al., 2002; Marshall et al., 2006; Conover et al., 2009; Douglas et al., 2009).

Without active management buffer strips form tall, dense and species-poor swards throughout the year that limit food accessibility (Blake et al., 2013) for ground-foraging farmland birds such as skylarks *Alauda arvensis* (Weibel, 1998), wheatears *Oenanthe oenanthe* (Low et al., 2010), and yellowhammers *Emberiza citrinella* (Douglas et al., 2009). In the same way that has been shown for field edges, buffer strips may also attract predators and increase nest predation risk (Morris and Gilroy, 2008; Schneider et al., 2012), and may thus be avoided by farmland birds (Vickery et al., 2002; Piha et al., 2003; see also Lima and Dill, 2013; Eggers et al., 2006). Compared to cereal fields, however, buffer strips can provide refuges

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and overwintering habitat for invertebrates (Thomas and Marshall, 1999; Barker and Reynolds, 1999), and relatively more shelter against nest predators (Morris and Gilroy, 2008). Hence, crop fields with buffer strips could still be a preferred option on intensively farmed land (Kuiper et al., 2013).

We assessed how buffer strips affect breeding skylark numbers and activity densities of their invertebrate food in a heterogeneous agricultural landscape of south-central Sweden. Explicitly, we examined whether (1) breeding skylark densities are higher in fields adjacent to buffer strips compared to control fields without buffer strips and if (2) this difference is associated with increased activity densities of their main food supply; namely ground-living beetles *Coleoptera* and spiders *Arachnida* spreading from buffer strips into adjacent cereal fields. Further, as grass strips on spring-sown fields can be assumed to provide relatively more shelter against predators and bad weather in early spring compared to strips on autumn-sown fields (Eggers et al., 2011), we examined if (3) the anticipated positive effect of buffer strips is more pronounced in spring- than in autumn-sown fields.

2. Methods

2.1. Survey area and field selection

The fieldwork was carried out in Uppsala county in the south-central Swedish plain (59°40′ N; 17°15′ E), where the landscape is dominated by crop fields interspersed by forests, small areas of semi-natural grasslands and wetlands (see Fig. S1, Supplementary data). We selected cereal crop fields with ($N = 12$; treatment) and without ($N = 12$; control) buffer strips in 2011 ($N = 6$) and 2012 ($N = 18$). Of the 24 cereal fields, 10 were sown with spring barley *Hordeum vulgare* and 14 with winter wheat *Triticum aestivum*. Fields with and without buffer strips were matched pairwise across multiple criteria to account for potentially confounding effects of year, sowing regime (spring/autumn-sown), field size, ditch size and other landscape elements (see below) affecting skylark breeding numbers and invertebrate abundance. Field pairs consisted of the same crop and were always inventoried the same year. Field size and the distance between landscape elements (i.e. forest edge, semi-natural grassland and farmstead) and the center point of each study plot (see below) did not differ between fields with and without buffer strips (paired *t*-tests, all p-values > 0.4).

To avoid potentially confounding effects of buffer strips and crop management on skylark numbers and invertebrate activity we selected only fields under conventional management. All fields were treated with both fertilisers and herbicides (once), and were accessed through tramlines (i.e. tracks where the tractors drive through the crop parallel to buffer strips). To the best of our knowledge insecticides and fungicides were not applied during the study period. Wheat and barley are sown with a row space of 12 cm with no difference in seed density. Thus, the only difference between crop types (during May–June) was a difference in sward height and leaf density caused by different sowing time.

2.2. Inventory methods

2.2.1. Skylark counts

We counted skylarks with point counts (five visits) in intervals of one week between May 22nd and June 21st. Study plots extended into fields as an arc with a radius of 100 m (approx. 1.57 ha). To define the border of study plots and estimate the location of skylarks we used landmarks (e.g. fence posts, bushes and other structures) and bamboo sticks as reference points. Visits were made in good weather between 8 a.m. and 3 p.m. and the timing of visits to different fields was randomized to avoid biases due to temporal variation in bird activity. To minimize observer effects on skylark activity we waited 5 min after arrival at the study plot before the 5-min bird counts were conducted (Bonthoux and Balent, 2011). The location of all singing skylarks observed within the study plot was recorded on field observation maps.

2.2.2. Invertebrate sampling

In 2012, we placed three pitfall traps (diameter 9 cm) each in the 18 cereal fields: one in the field border, and at 15 and 30 m into the field. Traps were placed in the ground with the rim at the ground level. The pitfall traps were filled with water, and detergent added to reduce surface tension. Plastic roofs prevented rain from filling the traps. Traps were set at the date of the first skylark count (May 22nd) and were emptied each week concurrent with skylark counts. After each bird count we approached traps using tramlines and row spaces (see above) to avoid irreversible changes of crop swards through trampling that could influence invertebrate sampling. After collection, all samples were kept in 70% ethanol until further analysis. From the samples, we counted the number of all beetle and spider individuals larger than 0.5 cm (>approx. 90% of the spider sample). We focused on beetles and spiders since these two orders constitute the majority of the diet of skylark chicks (Holland et al., 2006).

2.3. Statistical analyses

The effect of buffer strips on skylark and invertebrate abundance was assessed with Generalized Linear Mixed Models (GLMMs) using the lme4 package in R (R Development Core Team, 2011). Explanatory variables included presence of buffer strip (presence/absence), sowing regime (spring/autumn-sown) and time (visit number), which were included as fixed effects together with the two-way interactions sowing regime × buffer strip, sowing regime × time and buffer strip × time and the three way interaction buffer strip × sowing regime × time. We also included a squared term for time in season to account for possible non-linearity in seasonal trends, but this parameter was only found to improve the invertebrate models (i.e. lower AIC_c) and was hence dropped from the skylark models. The invertebrate models also included distance to trap from field border and the interaction term trap distance × buffer strip as fixed effects to test whether the within-field distribution of individuals differed between margin types. To account for effects of geographic location of field pairs, we included field identity nested in pairs as random effect. We used an observation-level random effect in our models to account for overdispersion (Poisson-lognormal model).

To compare candidate models, we used an information theoretical approach based on Akaike's Information Criterion with a second-order correction for small sample size (AIC_c) to prevent overfitting. Candidate models were derived using the dredge function in the MuMIn package for multimodel inference (Barton, 2010). Parameter estimates were compiled using model averaging with AIC_c relative importance weights to rank variable importance (Burnham and Andersson, 2002), and included models that had ΔAIC_c values of <4.

3. Results

In total, we made 154 observations of territorial skylarks (including repeated visits from the same field) from 24 fields and we collected 8400 beetle individuals and 2318 spider individuals from 18 fields.

3.1. Buffer strips and breeding skylark numbers

Average density of singing skylarks across all study plots was 0.86 ± 0.06 per hectare. As hypothesized, there was a positive effect of buffer strips on abundance of skylarks (1.05 ± 0.09 and 0.68 ± 0.08 per hectare for plots with and without buffer strips respectively; Fig. 1; Table 1). Further, spring-sown fields had a lower

Table 1
Model average parameter estimates, standard errors (SE), 95% confidence and relative variable importance of models with $\Delta AIC_c < 4$ demonstrating the effects of vegetated buffer strip, sowing regime (autumn/spring) and time in season (visit) on abundance of singing skylarks. Bold, confidence intervals do not include zero.

Model average parameters	Estimate	SE	95% CI		Relative variable importance
			Lower	Upper	
Sowreg	**−1.094**	**0.511**	**−2.096**	**−0.092**	**0.89**
Strip	**0.508**	**0.257**	**0.004**	**1.012**	**1.00**
Visit	−0.084	0.081	−0.243	0.075	0.82
Sowreg × strip	−0.344	0.345	−1.020	0.332	0.28
Sowreg × visit	**0.333**	**0.120**	**0.098**	**0.569**	**0.82**
Strip × visit	−0.060	0.115	−0.286	0.165	0.22
Intercept	0.306	0.278	−0.240	0.851	

Sowreg, sowing regime (spring sown); strip, vegetated buffer strip (present).

abundance of singing skylarks compared to autumn-sown fields (Table 1). However, as the breeding season progressed, the number of singing skylarks increased in spring-sown fields and approached those observed in autumn-sown fields (Fig. S2).

3.2. *Buffer strips and activity densities of ground-living invertebrates*

Activity densities for both beetles and spiders varied over time, with distance to field border, between sowing regimes and with the presence of buffer strip (Fig. 2; Table 2). Generally, activity densities declined over time in a logarithmic fashion and the overall effect of buffer strips seemed to weaken later during the sampling period, although the 95% CI for the parameter estimate of the interaction term time × buffer strip included zero (Fig. 2). In fields with buffer strips, beetle densities were higher in traps at 30 m from the field border compared to the corresponding traps in control fields (with no difference at the field border) and for spiders the densities were higher at 15 and 30 m (Fig. 3). Further, while activity densities were higher in field borders than within fields overall, invertebrates were more evenly distributed in crop fields adjacent to buffer strips. Beetles and spiders showed reversed density patterns between sowing regimes. Beetles were more abundant on spring-sown than on autumn-sown fields and spiders were more abundant on autumn-sown than on spring-sown fields, but the difference between regimes declined during the season for both groups (Table 2).

4. Discussion

Our study provides strong evidence to suggest that densely vegetated buffer strips increase activity densities of ground-living invertebrates and skylark breeding numbers on adjacent cereal fields irrespective of sowing regimes. This effect was most apparent early in spring but persisted throughout the sampling period. Thus, our results indicate that buffer strips contribute to mitigate negative environmental impacts of farming through provisioning of multiple ecosystem services in structurally complex agricultural landscapes. They not only contribute to reduce erosion (Vought et al., 1995), and agro-chemical runoff from arable fields into surface water (Uusi-Kämppä and Jauhiainen, 2010), but can also benefit invertebrates for biological control (Bianchi et al., 2006) and food supplementation of farmland birds (such as skylarks) that rely on the cropped area of fields for both foraging and breeding.

4.1. *Buffer strips and breeding skylark numbers*

Buffer strips in our study region appear to boost breeding skylark numbers on average by more than 30%, from 0.68 ± 0.08 (control)

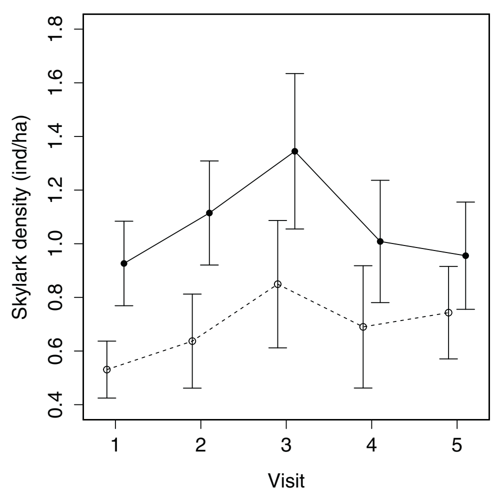

Fig. 1. Abundance of territorial skylarks (count/ha ±SE) in relation to presence of vegetated buffer strip and time in season (visit). Continuous line and closed circle, buffer strip present; dashed line and open circle, buffer strip absent.

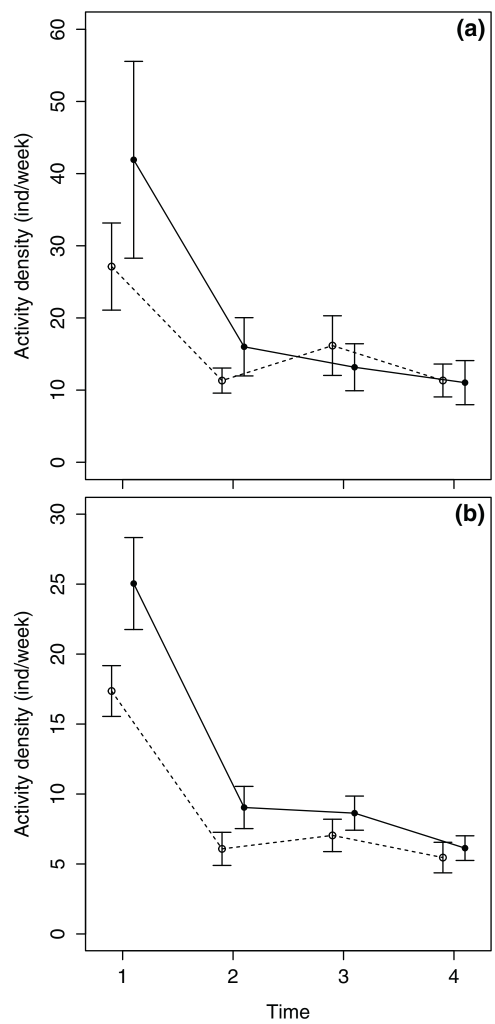

Fig. 2. Beetle (a) and spider (b) mean field abundance/activity density (±SE) in relation to presence of vegetated buffer strip and time in season. Continuous line and closed circle, buffer strip present; dashed line and open circle, buffer strip absent.

Table 2
Model average parameter estimates, standard errors (SE), 95% confidence and relative variable importance of models with $\Delta AIC_c < 4$ demonstrating the effects of vegetated buffer strips, sowing regime (autumn/spring), distance into field and time in season (visit) on abundance of invertebrates. Bold, confidence intervals do not include zero.

Model average parameters	Estimate	SE	95% CI		Relative variable importance
			Lower	Upper	
(a) Beetles					
Time	**−0.520**	**0.210**	**−0.932**	**−0.108**	**1.00**
Time^2	**0.124**	**0.040**	**0.045**	**0.203**	**1.00**
Sowreg	**1.515**	**0.446**	**0.642**	**2.389**	**1.00**
Strip	−0.248	0.342	−0.918	0.421	0.93
Trap 15 m	−0.216	0.138	−0.487	0.055	0.88
Trap 30 m	**−0.407**	**0.137**	**−0.676**	**−0.139**	**0.88**
Time × sowreg	**−0.364**	**0.081**	**−0.523**	**−0.204**	**1.00**
Time × strip	−0.131	0.074	−0.277	0.015	0.63
Sowreg × strip	0.677	0.399	−0.106	1.459	0.58
Strip × trap 15 m	0.278	0.197	−0.108	0.664	0.88
Strip × trap 30 m	**0.674**	**0.195**	**0.291**	**1.057**	**0.88**
Time × sowtype × strip	−0.031	0.155	−0.333	0.272	0.09
Intercept	**3.478**	**0.345**	**2.802**	**4.155**	
(b) Spiders					
Time	**−1.563**	**0.235**	**−2.024**	**−1.102**	**1.00**
Time^2	**0.219**	**0.047**	**0.013**	**0.310**	**1.00**
Sowreg	**−1.184**	**0.325**	**−1.821**	**−0.548**	**1.00**
Strip	−0.235	0.265	−0.754	0.283	1.00
Trap 15 m	**−0.766**	**0.161**	**−1.082**	**−0.450**	**1.00**
Trap 30 m	**−0.794**	**0.159**	**−1.106**	**−0.483**	**1.00**
Time × sowreg	**0.380**	**0.091**	**0.203**	**0.558**	**1.00**
Time × strip	−0.100	0.082	−0.260	0.060	0.40
Sowreg × strip	0.010	0.330	−0.638	0.657	0.24
Strip × trap 15 m	**0.795**	**0.225**	**0.354**	**1.236**	**1.00**
Strip × trap 30 m	**0.623**	**0.225**	**0.182**	**1.064**	**1.00**
Intercept	**4.706**	**0.310**	**4.098**	**5.314**	

Abbreviations as in Table 1.

to 1.05 ± 0.09 (treatment) territories per hectare within 100 m from field margins. This notable effect was not a result of unusually low breeding numbers on control fields. In fact, skylark densities in our study were similar or considerably higher compared to those reported for cereal fields (without buffer strips) from other study regions both in Sweden (e.g. 0.26 territories/ha, Berg and Pärt, 1994; 0.35 territories/ha, Eggers et al., 2011; 0.8 individuals/ha, Hiron et al., 2012) and across Central and Western Europe (e.g. 0.11 territories/ha, Wilson et al., 1997; 0.15 territories/ha, Poulsen et al., 1998; 0.37 territories/ha, Eraud and Boutin, 2002; 0.38 territories/ha, Suárez et al., 2003; 0.2 territories/ha, Copland et al., 2012).

The apparent preference of skylarks for cropped areas adjacent to buffer strips was linked to high activity densities of ground-living invertebrates, and particularly so early during the season (Figs. 1 and 2). This confirms the idea that skylarks select habitat (territory) quality based on good food availability (see Chalfoun and Martin, 2007) and may therefore be less likely to settle in more homogeneous arable landscapes with low food availability (Wilson et al., 1997; Benton et al., 2003; Eggers et al., 2011). This is important, as it has been frequently suggested that food shortage on crop fields is a key factor limiting ground-foraging farmland birds (Potts, 1986; Morris et al., 2004; Butler et al., 2007). However, higher arthropod abundance in dense swards of cereal fields (Douglas et al., 2010) and buffer strips (Vickery et al., 2002) may not necessarily increase food availability as dense swards can reduce the access for foraging and constrain farmland bird productivity (Morris et al., 2004, 2007; Low et al., 2010; Eggers et al., 2011). Accordingly, our results indicate that increased food supplies on crop fields do not fundamentally change the temporal shift of skylark preferences in relation to crop sward height due to differences in sowing regime in heterogeneous agricultural landscapes (Fig. S2; see also Piha et al., 2003; Eggers et al., 2011; Hiron et al., 2012).

In Northern Europe, skylarks seem to prefer autumn-sown cereals early during the season when these crops provide more protection against inclement weather, (nest) predators and farming disturbance (e.g. drilling; Evans, 2004) than spring-sown crop fields. As crop swards in autumn-sown fields grow tall (>40 cm) and dense skylark densities decline whereas they increase in spring-sown fields offering shorter vegetation (Fig. S2, Table 1; see also Eggers et al., 2011). This is in contrast to some studies from the UK where skylarks seem to prefer spring-sown cereals throughout the season (e.g. Wilson et al., 1997; Poulsen et al., 1998; Chamberlain et al., 2000a; Donald, 2004). This contrasting preference of sowing regimes between Northern and Western Europe is likely explained by the skylark's preference for vegetation of intermediate height and the temporal variation in crop development between the two regions (Hiron et al., 2012). Still, overall higher levels of breeding skylark numbers in cereal fields with buffer strips indicate that buffer strips may be a sufficiently powerful conservation tool to mitigate possible negative effects of crop management (e.g. pesticide use; Geiger et al., 2010) on breeding skylark numbers irrespective sowing regime. This might be particularly relevant for arable regions in Northern Europe where the autumn-sown crops are rarely taller than a few centimeters in April (Eggers et al., 2011). Also, the proportion of spring-sown crops is higher in Northern Europe (Wretenberg et al., 2006) compared to Central and Western Europe (e.g. data for UK reviewed in Chamberlain et al., 2000b). This results in more bare ground early in spring and sparser vegetation later during the season in northern regions, which might extend the positive effect of buffer strips on food accessibility further.

4.2. Buffer strips and invertebrate activity densities

The role of buffer strips for beetles and spiders has been acknowledged previously (e.g. Woodcock et al., 2005; Smith et al., 2008; Hof and Bright, 2010). In our study, the effect of buffer strips was present only within the cropped area and not in field borders for both beetles and spiders (Figs. 2 and 3; Table 2). Thus, both groups were more evenly distributed in fields with buffer strips

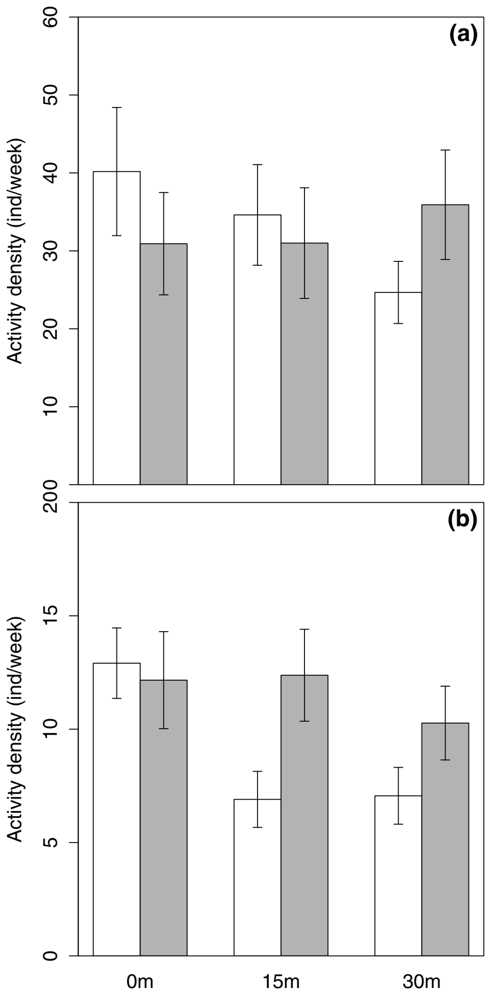

Fig. 3. (a) Beetle and (b) spider activity density (±SE) for different trap distances into the field. Shaded, buffer strip present; hollow, buffer strip absent.

compared to control fields, where activity densities were concentrated in field borders. This matches the pattern found for carabids in other studies (Saska et al., 2007; Hof and Bright, 2010) and might indicate that some invertebrates concentrate their activity in field edges, but spread out into fields when resource availability in field edges with buffer strips are high.

The seasonal decrease in the effect of buffer strips on skylark numbers appeared to correspond to a similar decrease in the effect on activity densities of invertebrates (Fig. 2). This could be explained by improved conditions (i.e. microclimate, food supply) in developing crop swards that reduce the dissimilarity between strip vegetation and crop allowing ground-living invertebrates to spread into fields to a greater extent (Douglas et al., 2010). The overall reduced activity across the season may have been influenced by colder and wetter weather during the second half of the study period (Saska et al., 2012). As pitfall catches are composite measures of activity and abundance they are, in addition to weather, influenced by e.g. sampling methodology, species composition and differential responses to habitat structure, which makes it difficult to make direct comparisons of abundance between studies (Topping and Sunderland, 1992).

4.3. Implications

Field boundary habitats have been shown to provide important foraging and nesting opportunities for many farmland birds (Perkins et al., 2002; Vickery et al., 2002), However, it is important to acknowledge that they also have the potential to reduce productivity through increased predation risk (i.e. edge effects). For instance, buffer strips can act as important foraging habitat and movement corridors of predators such as rodents *Rodentia*, badgers *Meles meles* and foxes *Vulpes vulpes*, (Morris and Gilroy, 2008; Schneider et al., 2012). These predators have been shown to pose a serious threat to ground nesting farmland birds such as wheatears and yellowhammers in proximity to cereal fields throughout our study region (Söderström et al., 1998; Low et al., 2010; Schneider et al., 2012). Yet, actual nest failure rates depend not only on predator activity but also on interactive effects between predator behavior, structural habitat complexity (e.g. prey density; Chalfoun and Martin, 2009) and species life history strategies (Evans, 2004; Eggers et al., 2005).

While the results of this study suggest that buffer strips have positive effects on biodiversity at field-scale, it is important to determine whether implementation of buffer strips on larger spatial scales have any positive effects at the population level (see Kuiper et al., 2013). Increased skylark abundances in cereal crops adjacent to buffer strips may *de facto* only be an aggregation effect reducing numbers further away from these preferred field boundaries with little or no impact on skylark numbers at a larger (i.e. landscape) scale. However, a recent study by Guerrero et al. (2012) indicates that buffer strips may exert a strong positive effect on skylark densities in simple landscapes dominated by agriculture. Further, optimal implementation of buffer strips requires more studies on the effects of landscape heterogeneity, different types of field margins and novel management options feasible to farmers. For instance, managing dense swards through selective cutting of buffer strips may improve food accessibility for ground-foraging birds, while still maintaining vegetation adjacent to water courses to sustain invertebrate populations and reduce agro-chemical runoff (Vickery and Fuller, 1998; Douglas et al., 2009). Since 2011, the establishment of buffer strips adjacent to surface waters is mandatory when using certain pesticides in the EU, a regulation that will increase the total area of agricultural land enrolled in this measure (EU Regulation 1107/09). In Sweden, buffer strips currently cover only between 5 and 9000 ha of arable land while the potential has been estimated to 100 000 ha (Rabinowicz, 2010). Hence, buffer strips represent a potentially important conservation tool to facilitate biodiversity in some arable regions and determining how these strips interact with field biodiversity is key to determine the best establishment and management practices that gain the greatest benefits.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2013.09.018.

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