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Effect of field margins on moths depends on species mobility: Field-based evidence for landscape-scale conservation

Thomas Merckx [a,*], Ruth E. Feber [a], Rebecca L. Dulieu [b], Martin C. Townsend [a], Mark S. Parsons [c], Nigel A.D. Bourn [c], Philip Riordan [a], David W. Macdonald [a]

[a] *Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Tubney House, Abingdon Road, Tubney, Abingdon OX13 5QL, UK*
[b] *Centre for Wildlife Assessment and Conservation, University of Reading, School of Biological Sciences, Environmental Biology, Whiteknights, Reading RG6 6AS, UK*
[c] *Butterfly Conservation, Manor Yard, East Lulworth, Wareham BH20 5QP, UK*

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ABSTRACT

Agri-environment schemes (AES) are widely used policy instruments intended to combat widespread biodiversity declines across agricultural landscapes. Here, using a light trapping and mark-release-recapture study at a field-scale on nine common and widespread larger moth species, we investigate the effect of wide field margins (a popular current scheme option) and the presence of hedgerow trees (a potential scheme option in England) on moth abundance. Of these, we show that wide field margins positively affected abundances, although species did not all respond in the same way. We demonstrate that this variation can be attributed to species-specific mobility characteristics. Those species for which the effect of wide margins was strongest covered shorter distances, and were more frequently recaptured at their site of first capture. This demonstrates that the standard, field-scale uptake of AES may be effective only for less mobile species. We discuss that a landscape-scale approach, in contrast, could deliver significant biodiversity gains, as our results indicate that such an approach (perhaps delivered through targeting farmers to join AES) would be effective for the majority of wider countryside species, irrespective of their mobility level.

1. Introduction

Agri-environment schemes (AES) provide financial support to farmers who agree to adopt a more environment-friendly style of land management. AES receive 20% of the total European CAP budget of 350 billion euros between 2007 and 2013 (Europe, 2008) and their implementation is currently considered the most important and only realistic policy instrument within Europe for reversing widespread biodiversity declines across agricultural landscapes (Donald and Evans, 2006). However, considerable opportunities remain to improve their cost-effectiveness and delivery in this respect (Wätzold and Schwerdtner, 2005; Kleijn et al., 2006; Sutherland et al., 2006).

Since species-specific meta-population processes take place on a landscape-scale within the agricultural mosaic of semi-natural habitats, and since a number of environmental functions may exhibit cumulative or threshold effects, it has recently been argued that in contrast to the appeal of the often used field-scale and 'one-size-fits-all' approach, a complementary, targeted, landscape-scale approach for AES-uptake could substantially enhance the ecological and environmental benefits of AES (Whittingham, 2007; Warren et al., 2008; Merckx et al., submitted). Hence, a targeted, landscape-scale approach has the potential to significantly increase the effectiveness (meeting policy objectives) and the cost-efficiency of AES. However, so far very little empirical evidence exists that a targeted approach will work (Dutton et al., 2008).

Larger moths are an ecologically diverse and species-rich group, occurring often abundantly in farmed landscapes, and constitute an important food resource for bats, birds, small mammals and invertebrates (e.g. Vaughan, 1997; Wilson et al., 1999). Rapid and significant declines have been recorded for the majority of common and widespread moth species that inhabit farmland in the UK, and it seems likely that a similar trend is occurring in other temperate-zone industrialised countries (Conrad et al., 2006). Partly because of their ecological diversity and species richness, they are considered a sensitive indicator group for biodiversity in terrestrial ecosystems (Luff and Woiwod, 1995; New, 2004; Thomas, 2005). Findings from a study of macro-moths are thus likely to be representative of other terrestrial insect groups that occur in this ubiquitous type of environment.

* Corresponding author. Tel.: +44 1865 393104; fax: +44 1865 393101.
E-mail address: thomas.merckx@zoo.ox.ac.uk (T. Merckx).

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At a field-scale, we assessed the effects of an AES option, wide (6 m) field margins, and a key landscape feature, hedgerow trees, within arable land, on the abundance of nine species of common and widespread larger moth, in a multi-site mark-release-recapture (MRR) experiment using light traps. MRR is a well-established method to assess mobility levels of butterfly populations, and hence the mobility and population structure of many butterfly species are well known (Warren, 1992). There is however very little information on the relative mobility of the majority of night-active Lepidopteran species, apart from a few well established long-range migrants and some species with very restricted ranges (Woiwod and Stewart, 1990). We know of only one published MRR study on moths captured in light traps (i.e. Nieminen, 1996), and we hence consider this method to be a novel approach. Furthermore, our study is the first to apply MRR of moths with light traps on farmland, since Nieminen's study was performed in a small group of Finnish islands mostly covered by rock with either a few small patches of woodland or a few small trees. In contrast to MRR studies on day-flying Lepidoptera, where the observer actively patrols through a study site, light traps are fixed sampling points. This probably results in lower recapture rates compared to 'standard' butterfly studies. Nieminen's study was characterized by 10% and 15% overall recapture rates (two years). Studies on both White Ermine *Spilosoma lubricipeda* L. (M. Young, pers. comm.) and Sussex Emerald *Thalera fimbrialis* Scop. (Parsons and Kirby, 1993) resulted in recapture rates of less than 5%. In another study ca. 700 individuals of Large Yellow Underwing *Noctua pronuba* L. were marked and only one was recaptured (M. Young, pers. comm.).

Six metre wide grassy field margins are an important conservation tool (Feber et al., 1996; Macdonald et al., 2000). Their restoration and management is financially rewarded under current AES, and widely taken up by farmers [grass/buffer strips on arable land covered over 47,000 ha in English AES by autumn 2006 (DEFRA, 2005; Butler et al., 2007)]. By early February 2008 more than 51% of agricultural land in England was under AES, and grass/buffer strips on arable land were one of the popular scheme options (DEFRA/NE, 2008). Hedgerow trees are prominent landscape features. In the UK, their abundance has dramatically declined since the late 18th century to a currently estimated 1.8 million isolated hedgerow trees, of which nearly a third are over a century old and may hence disappear from the landscape at any time over the next 25 years (Stokes and Hand, 2002). Although proactive conservation management of hedgerow trees is not currently rewarded financially under English AES, the recent review of progress of these schemes includes a recommendation for new options for the establishment of new hedgerow trees and the protection of existing hedgerow trees (DEFRA/NE, 2008). Both landscape features provide resources for the nine moth species in this study. Wide field margins provide (i) relatively undisturbed larval habitat, (ii) adult food resources (i.e. nectar), and (iii) buffer zones against the impact of agricultural chemicals on larvae and host plants (Longley and Sotherton, 1997; Pywell et al., 2004). In the study, hedgerow trees (predominantly Pedunculate oak *Quercus robur* L.) did not directly provide larval or adult food resources to the selected species, but will have created a further level of structural diversity (Maudsley, 2000), increased shelter and hence a warmer microclimate. These are important for insects, which are prone to convective cooling in agricultural landscapes (Dover and Sparks, 2000; Pywell et al., 2004).

We selected nine common species of larger moths (see Section 2) that were not shrub or tree feeders, but for which field margins provide larval and/or adult food resources. We first tested whether wide field margins and hedgerow trees were useful in increasing the abundance of these species. We hypothesized that if they were, abundance would be lowest at field centres, higher at standard field margins, and highest at wide field margins (hypothesis 1a). Accordingly, moths would have the highest abundance at sites where a hedgerow tree was present (hypothesis 1b). Our second hypothesis was that the more mobile a species, the less it would be affected at a field-scale by the presence of wide field margins and hedgerow trees. Hence, we would expect to detect the strongest statistical evidence for effects of the presence of wide field margins and hedgerow trees on the least mobile species (hypothesis 2).

2. Materials and methods

2.1. Study sites and design

We conducted a MRR-experiment in four adjacent arable fields (Stonesfield, Oxfordshire, UK, SP3917). All fields were bordered with average-sized hedgerows (2–3 m high; 1.5–2.5 m wide), with hedgerow trees scattered throughout, and with no banks or ditches. Fields had dimensions typical of the lowland agricultural Upper Thames Tributaries area of southern England, UK [average area (ha) $\pm$ S.E.: 10 ± 2], and either had surrounding wide (6 m) perennial grass margins (current AES-option, Environmental Stewardship, DEFRA, 2005) or standard grass margins (ca. 1 m, Cross-compliance). Within each of the four fields, we sampled five sites (twenty sites in total): one site at the centre of the field, and four sites at the field margins (one site at each margin). Two of these field margin sites were positioned at a distance of ca. 5 m from the trunk of an open-grown hedgerow tree (minimum height: 15 m; predominantly *Q. robur*). There were thus six different experimental groups: (i) centre + wide margin, (ii) tree + wide margin, (iii) no tree + wide margin, (iv) centre + standard margin, (v) tree + standard margin, (vi) no tree + standard margin (Fig. 1).

Sampling sites were carefully selected so that the variation in hedgerow tree and margin characteristics other than the subject variables was minimal throughout. All sites were >100 m apart in order to minimize possible action radius interference between light traps, and all sites were fixed for the duration of the experiment. All sites were more than 50 m from hedgerow intersections, to reduce bias due to local aggregation of individuals that use hedgerows as flight corridors (Maudsley, 2000). Sampling sites in margins were always located 1 m from hedgerows.

2.2. Sampling

The MRR-experiment ran from 5th June until 14th July 2007 on 32 nights (i.e. all nights with suitable weather conditions; see below) out of a possible 40 nights. The biggest gaps in trapping effort were two periods of two nights each. Since traps were operated from dusk to dawn, we alternated trapping between fields (i.e. individual trap sites were not run on consecutive nights). This permits normal movement, greatly reducing the likelihood of recaptures at the same site. Every night ten sites of both a field with wide margins and a field with standard margins were sampled. Heath pattern actinic light traps (6 W) were used for sampling (Heath, 1965). These operate on the 'lobster-pot principle', whereby moths are drawn to an actinic tube held vertically between baffles, fall unharmed down a funnel, and rest on the inside of the trap or on pieces of egg-tray provided.

Based upon a concurrent light trap experiment (Merckx et al., submitted) in the same agricultural area (see above), we selected nine species of larger moths (i) for which field margins provide larval and/or adult food resources; (ii) that were not shrub or tree feeders; and (iii) that were caught abundantly the year before during the same period (June–mid-July) at the same sites (Table 1). All nine species are common in the wider countryside, but national populations of the majority of common moth species are in decline

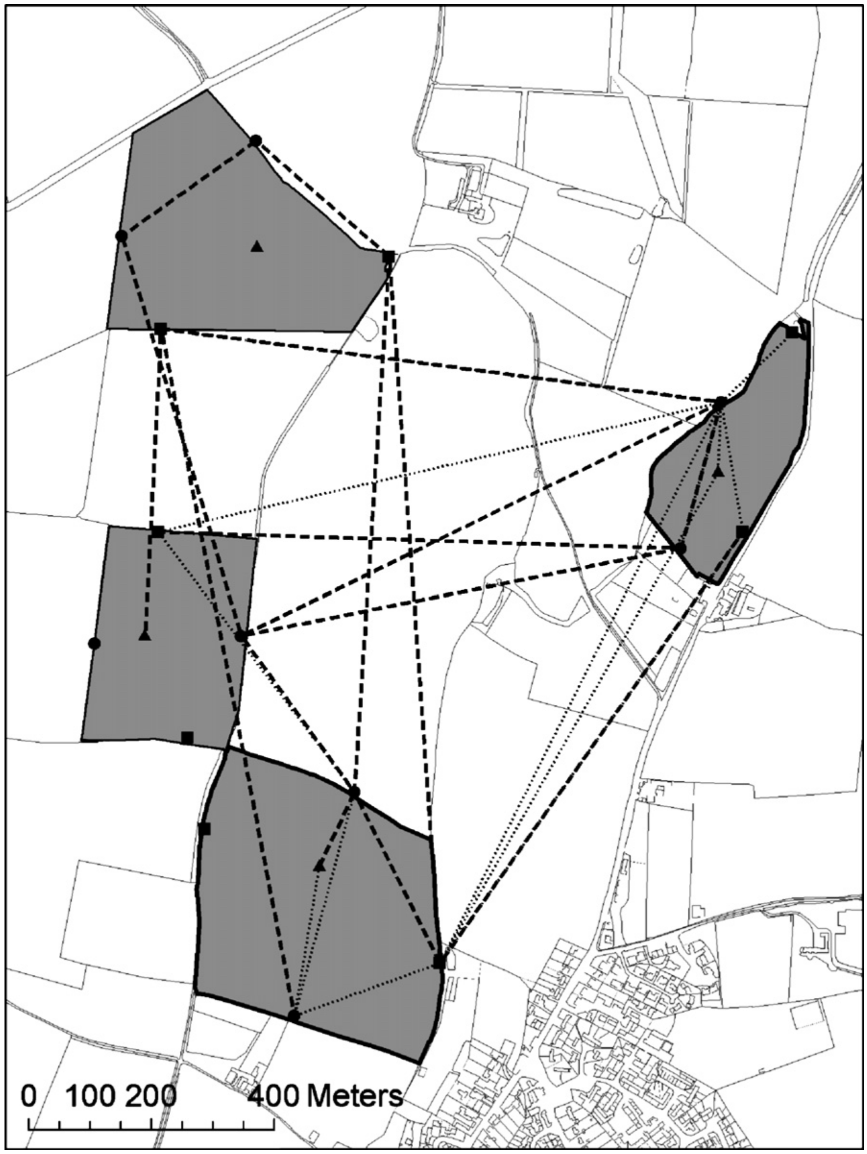

Fig. 1. Map showing the four study fields (grey); the two fields with wide field margins are outlined in bold. Sampling sites near a hedgerow tree are indicated with a square; sites lacking hedgerow trees are indicated with a circle. Observed individual movements (>0 m) are contrasted between the species groups with opposite effects for the variable 'margin'. Individuals within the group of species where the statistical evidence for an effect of 'margin' was absent covered longer distances and were less frequently recaptured at the site of first capture than the group of species where the effect of 'margin' was stronger (bold dashed lines; Large Nutmeg *Apamea anceps*, Setaceous Hebrew Character *Xestia c-nigrum*; N_{total} = 21; $N_{recaptured\ at\ site\ of\ first\ capture}$ = 4 versus slim dashed lines; Treble Lines *Charanyca trigrammica*, Brown-line Bright-eye *Mythimna conigera*, Heart and Dart *Agrotis exclamationis*, Common Footman *Eilema lurideola*, Common Swift *Hepialus lupulinus*; N_{total} = 43; $N_{recaptured\ at\ site\ of\ first\ capture}$ = 29; respectively). One of the bold dashed lines and one of the slim dashed lines cover the movements of two individuals each.

Table 1
Comparison of selected nine species of common and widespread larger moths.

Species	Scientific name	Family	*N*	*R*	Adult nectar	Larval food	Annual change rate
Common Swift	*Hepialus lupulinus*	Hepialidae	320	13	No	Grass herbs	−0.005
Common Footman	*Eilema lurideola*	Arctiidae	56	3	Yes	Lichens	0.010
White Ermine	*Spilosoma lubricipeda*	Arctiidae	18	2	No	Herbs	−0.041
Heart and Dart	*Agrotis exclamationis*	Noctuidae	597	11	Yes	Herbs	−0.031
Setaceous Hebrew Character	*Xestia c-nigrum*	Noctuidae	112	5	Yes	Herbs	0.004
Brown-line Bright-eye	*Mythimna conigera*	Noctuidae	89	13	Yes	Grass	−0.023
Dark Arches	*Apamea monoglypha*	Noctuidae	90	0	Yes	Grass	−0.009
Large Nutmeg	*Apamea anceps*	Noctuidae	329	16	Yes	Grass	−0.058
Treble Lines	*Charanyca trigrammica*	Noctuidae	88	3	Yes	Herbs	0.007

'*N*' = number of captured individuals. '*R*' = number of all recaptured individuals. The table shows whether or not the adults require nectar, and whether the larvae feed on grass, low-growing plants and/or lichens (Waring and Townsend, 2003). The 'annual change rate' is the annual rate of national population change in Britain estimated from 35-year time series (data from Conrad et al., 2006). Rates >0 indicate species are on the increase; rates <0 indicate species are in decline. Note that two of these common and widespread species have decline rates of 30–50% 10 year^{-1}, which labels them as vulnerable when applying the IUCN criteria (White Ermine and Large Nutmeg had a 77% and 88% decline over 35 years, respectively).

(Conrad et al., 2006; Table 1). This selection was done before the start of the experiment so as to ensure that the marking effort was only focused on those species–with a similar ecological niche and a high probability for obtaining large sample sizes–that would enable us to test the hypotheses (see Section 1). At dawn, all trapped individuals of the selected species were cooled down for a short period within a cool box. They were then marked (at first capture) *in situ* by writing a unique number on the upper side of the left forewing with a fine, non-toxic, permanent waterproof marker (Staedtler Lumocolor 313-5) and were released immediately into nearby tall vegetation. For each capture we recorded (i) species, (ii) date, (iii) site, and (iv) individual mark number. Locations of trap sites were obtained via a handheld GPS receiver. Distances of movements between captures were measured via a GIS (ArcGIS 9.0) and were $\log_{10}$-transformed prior to analyses. The average distance among all pair-wise combinations of all trap sites is 663 ± 27 m (mean $\pm$ S.E.; $N = 210$). The furthest distance between any two traps is 1444 ± 7 m (combined error on GPS positions).

Sampling followed a strict protocol to control for confounding factors between sites and between sampling events. Activity levels of nocturnal flying insects are affected by a number of variables. Warm, cloudy nights with light or no wind are the most productive in terms of sample size and cold, clear nights the least productive (Fry and Waring, 2001). Wind speed, heavy rain and moon brightness also have negative effects, although light to moderate rain appears to have little or no effect (Holyoak et al., 1997). Therefore, the protocol was designed to ensure that sampling was conducted in similar, sufficiently favourable conditions to minimize bias. Sampling occurred under pre-defined weather forecast criteria of minimum night temperature (10 °C), maximum wind speed (20 km/h) and maximum precipitation risk (50%), derived from variables as predicted for the nearest town (Chipping Norton, Oxfordshire) between sunset and sunrise on http://uk.weather.com (in practice the minimum night temperature was in most cases considerably higher and maximum wind speed considerably lower).

2.3. Nectar availability and hedge composition

As an indication of the abundance of nectar sources available for adult moths, we assessed nectar availability. At each trap site, and approximately in the middle of the experiment (25th June), we counted the number of flowerheads present on field margins 10 m either side of the trap locations. Every flowerhead was identified to species level. We then calculated (i) the total number of flowerheads by lumping all species, and (ii) the total number of flowerheads of a restricted group of plant species known to be visited by adult moths (i.e. Clover *Trifolium*, Bramble *Rubus fruticosus* agg., Bladder Campion *Silene vulgaris* (Moench) Garcke, St. John's Wort *Hypericum perforatum* L., Field Scabious *Knautia arvensis* (L.) Coult., and Ragwort *Senecio jacobaea* L.).

For every hedge bordering the sampled fields we estimated the percentage cover of each woody plant species (trees, shrubs and climbing plants), excluding trees, in 10 m sections. We then, separately for every hedge, calculated the percentage cover for each of these species over the whole length of the hedge. These values (relative abundances) were used to calculate the Shannon Index (H') for each hedge as a measure of plant species diversity. We also recorded the species richness of woody plant species for every hedge.

2.4. Analyses

2.4.1. Habitat use

For each moth species we totalled the number of individuals (excluding any recaptures) sampled at each of the twenty sites, the number of visits being constant ($N = 16$) across sites. Using a generalized linear model (Proc Mixed, SAS 9.1) we contrasted the effects of the independent class variables (i.e. fixed effects): 'species' (9 classes); 'margin' (standard versus wide); 'position' (centre, no tree, tree); and all possible two-way interactions on these abundances. We included 'site' as a random effect as the analysis includes both 'within-site' and 'between-site' effects. Abundances were $\log_{10}$-transformed as they are multiplicative. Model residuals were normally distributed (Shapiro-Wilk). Degrees of freedom were calculated using the Satterthwaite option. Differences of least squares means were calculated.

2.4.2. Mobility, nectar availability and hedge composition

Distances covered by individuals at first recapture were $\log_{10}$-transformed prior to analyses. In case of multiple recaptures, only the first movement was taken into account, so that all data points are independent (i.e. different individuals). Species groups were contrasted using student *t*-tests (Proc Ttest, SAS 9.1). Equality of variances was tested for. Species groups were contrasted in (i) overall recapture percentage, and (ii) proportion of recaptures at site of first capture out of the total number of recaptures via χ^2 and Fisher's Exact tests (Proc Freq, SAS 9.1), excluding recaptures after the first recapture (data independence). The number of days between first capture and recapture was not taken into account in these analyses, since it was not correlated with the distance moved ($F_{1,69} = 0.55$; $p = 0.46$; $R^2 = 0.0081$). Additionally, Pearson correlation coefficients (r) were calculated between the species-specific model estimates for the parameter 'wide field margin' and these three mobility measures: (i) covered distance, (ii) percentage of recaptures at site of first capture, and (iii) overall recapture percentage (Proc Corr, SAS 9.1).

Flower abundance, hedge species richness and hedge species diversity were independently contrasted between sites with wide field margins and sites with standard field margins using student *t*-tests (Proc Ttest, SAS 9.1). Equality of variances was tested for.

3. Results

A total of 1699 individuals were captured throughout the trapping period. Numbers varied greatly among the nine species studied (Table 1).

3.1. Habitat use

Overall, there was no difference in moth abundance between field margin sites with or without hedgerow trees ($F_{1,13} = 0.43$; $p = 0.52$). The generalized linear regression model showed that, overall, there were highly significantly more (+91.7%) individuals in the field margins than in the centre of the arable fields (Table 2). The difference in abundance between the centres and the margins

Table 2
Results of a generalized linear regression model for the abundance of larger moths.

Effect	F	p
Species × margin	$F_{8,128} = 2.71$	<0.01
Species × position	$F_{16,128} = 1.44$	0.13
Species	$F_{8,128} = 35.35$	<0.0001
Margin	$F_{1,16} = 4.61$	<0.05
Position	$F_{2,16} = 7.09$	<0.01

Abundance was analyzed in relation to species ($N = 9$), field margin width (wide or standard) and position of the sampling site (in a margin nearby a hedgerow tree, in a margin away from hedgerow trees, or in the centre of a field) (see Section 2). The Mixed procedure was applied (SAS 9.1) using type III sums of squares. We excluded the non-significant interaction 'margin × position' ($F_{2,14} = 0.66$; $p = 0.53$). This resulted in a final model with a better fit (judged by the AIC).

of the fields applied to all nine species studied ('species × position' non-significant: Table 2).

We detected a significant effect of margin width on moth abundance. Overall, sites with wide margins were characterized by more individuals (+40%) than sites with standard margins (Table 2). The absence of an interaction between the parameters 'margin' and 'position' (see above) demonstrates that the effect of 'margin' applied not only to the sites located in the field margins, but also to sites located at the field centres; moth numbers in the field centres were indeed higher (+58%) in fields with wide margins. However, the statistical significance of the effect of 'margin' varied strongly among the nine species, with most species not showing a significant effect (Table 2). Model estimates for the parameter 'margin' were obtained by running separate models for all nine species (Table 3). These parameter estimates (species) could be grouped into negative and positive values. The former contribute to the overall effect of 'margin' (N in wide margins $>N$ in standard margins), whereas the latter do not (Fig. 2a; Table 3). Model estimates were significant only for two species (Treble Lines *Charanyca trigrammica* Hufn. and Brown-line Bright-eye *Mythimna conigera* D. & Schif.), although Heart and Dart *Agrotis exclamationis* L. showed a trend towards having a higher abundance at fields with wide compared to standard margins (Fig. 2a; Table 3). Whereas overall, the species with negative model estimates had 62% higher abundances at fields with wide margins than at fields with standard field margins, the three species with positive model estimates had overall slightly fewer (−3%) individuals at fields with wide margins.

Table 3
Model estimates for the parameter 'margin'.

Species	Parameter estimate ± S.E.	F	p
Charanyca trigrammica	−0.47 ± 0.149	$F_{1,16}$ = 9.99	<0.01
Mythimna conigera	−0.43 ± 0.178	$F_{1,16}$ = 5.88	0.03
Agrotis exclamationis	−0.17 ± 0.088	$F_{1,16}$ = 3.74	0.07
Eilema lurideola	−0.15 ± 0.121	$F_{1,16}$ = 1.47	0.24
Apamea monoglypha	−0.11 ± 0.130	$F_{1,16}$ = 0.76	0.40
Hepialus lupulinus	−0.031 ± 0.160	$F_{1,16}$ = 0.04	0.85
Apamea anceps	0.068 ± 0.146	$F_{1,16}$ = 0.22	0.65
Spilosoma lubricipeda	0.082 ± 0.108	$F_{1,16}$ = 0.58	0.46
Xestia c-nigrum	0.14 ± 0.119	$F_{1,16}$ = 1.31	0.27

Estimates [(i) differences of least squares means ± S.E. between standard and wide field margin estimates; (ii) F-values] result from generalized linear models for the abundance of larger moths in relation to field margin width (wide or standard) and position of the sampling site (see Section 2). The Mixed procedure was applied (SAS 9.1) separately for all nine species using type III sums of squares. Parameter estimates are sorted and grouped into species with negative values (more individuals at wide than at standard margins) and species with positive values (less individuals at wide than at standard margins).

3.2. Mobility

During the course of the experiment a total of 66 individuals were recaptured (Table 1), three of which were recaptured twice. Second recaptures occurred at the same sites as the first capture and they are not included into the analyses so that all data points are independent (see Section 2). No Dark Arches *Apamea monoglypha* Hufn. were recaptured, and so this species could

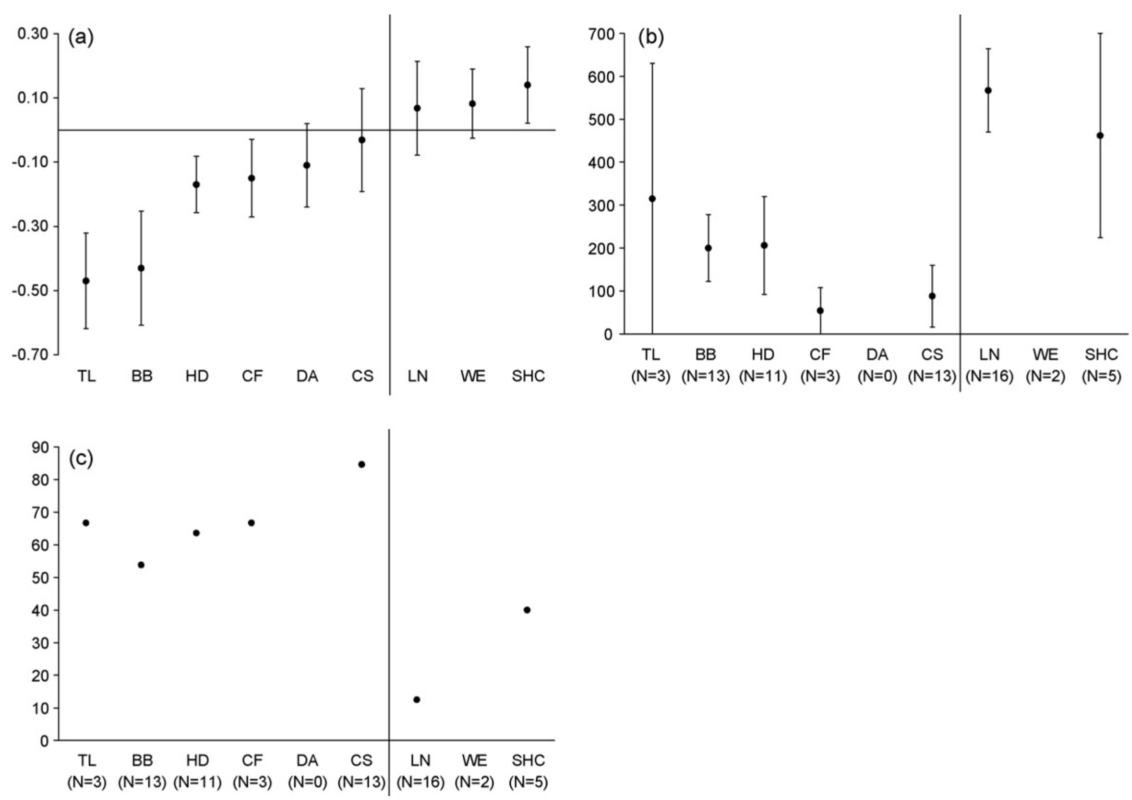

Fig. 2. (a) Model estimates (differences of least squares means ± S.E.) of the parameter 'field margin width' ('wide' versus 'standard') sorted in ascending order for all nine species. We demarcated species with positive estimates from species with negative estimates. The former had more individuals at standard margins than at wide margins, whereas the latter contribute to the overall effect of 'margin'. (b) Distances covered [average (m) ± S.E.] by individuals in between first capture and first recapture. Species with negative model estimates moved significantly smaller distances than species with positive estimates (see Section 3). (c) Percentage of recaptures at site of first capture out of the total number of recaptures. Only first recaptures were taken into account. Species with negative model estimates were to a significantly larger degree recaptured at the site of first capture than species with positive estimates (see Section 3). TL = Treble Lines *Charanyca trigrammica*; BB = Brown-line Bright-eye *Mythimna conigera*; HD = Heart and Dart *Agrotis exclamationis*; CF = Common Footman *Eilema lurideola*; DA = Dark Arches *Apamea monoglypha*; CS = Common Swift *Hepialus lupulinus*; LN = Large Nutmeg *Apamea anceps*; WE = White Ermine *Spilosoma lubricipeda*; SHC = Setaceous Hebrew Character *Xestia c-nigrum*. Species in panels (b), and (c) are sorted in the same order as in panel (a). Sample sizes are given below the species labels. DA and WE are not represented in panel (b) and (c) due to an insufficient number of recaptures (DA: 0; WE: 2).

not always be included in tests. We used three different measures as proxies to contrast the mobility of the two groups of species with opposite model estimates for the variable 'margin': (i) average distance moved between capture and recapture (high value = high mobility); (ii) percentage of recaptures at the site of first capture (relative to the total number of recaptures) (low value = high mobility); and (iii) recapture percentage (relative to the total number of first captures) (low value = high mobility).

Species with positive estimates moved further than species with negative estimates (means $\pm$ S.E.: 542 $\pm$ 91 m (N = 21) versus 166 $\pm$ 47 m (N = 43), respectively; $t_{62} = -4.28$; $p < 0.0001$). These tests excluded the one species where $N < 3$ (White Ermine *S. lubricipeda*). Similar tests where we did include this species, or excluded the three species with $N < 5$ (White Ermine *S. lubricipeda*, Common Footman *Eilema lurideola* Zinc. and Treble Lines *C. trigrammica*), also resulted in significant differences ($t_{64} = -3.67$; $p < 0.001$; $t_{56} = -4.19$; $p = 0.0001$, respectively) (Fig. 1; Fig. 2b).

The difference in percentage of recaptures at the site of first capture between the group of species with positive estimates (19.0%) and the one with negative estimates (67.4%) was highly significant ($\chi^2_1 = 13.23$; $p < 0.001$; Fisher's Exact: $p < 0.001$) (Fig. 2c). Similarly, this test excluded the one species where $N < 3$, though similar tests where we included this species, or excluded the three species with $N < 5$ (see above), resulted in significant differences as well ($\chi^2_1 = 10.29$; $p = 0.001$; Fisher's Exact: $p < 0.01$; $\chi^2_1 = 12.62$; $p < 0.001$; Fisher's Exact: $p < 0.001$, respectively).

The overall recapture percentage for all nine species combined was 3.9%. The recapture percentage for the group of three species with positive estimates (5.0%) did not differ significantly from the one for the group of six species with negative estimates (3.5%) ($\chi^2_1 = 1.37$; $p = 0.24$).

Tests for correlations between the species-specific estimates for the parameter 'wide field margin' and the same three measures of mobility gave similar results as above: (i) a positive correlation with the distance covered (excluding the species where $N < 3$: $r = 0.24$; $p = 0.05$; including all species: $r = 0.22$; $p = 0.08$; excluding the species where $N < 5$: $r = 0.28$; $p < 0.05$); (ii) a negative correlation with the percentage of recaptures at the site of first capture (excluding the species where $N < 3$: $r = -0.38$; $p < 0.01$; including all species: $r = -0.30$; $p < 0.05$; excluding the species where $N < 5$: $r = -0.36$; $p < 0.01$); (iii) no correlation with the overall recapture percentage ($r = -0.17$; $p = 0.66$).

3.3. Nectar availability and hedge composition

Nectar abundance differed significantly between wide and standard margins. The sites at the wide margins had more flowerheads, both overall (means $\pm$ S.E.: 409 $\pm$ 88 versus 163 $\pm$ 32; $t_{8.83} = -2.62$; $p < 0.05$) and when the comparison was restricted to those species known to be frequently visited by larger moths (means $\pm$ S.E.: 243 $\pm$ 66 versus 80 $\pm$ 17; $t_{7.89} = -2.38$; $p < 0.05$). Hedgerows bordering the wide field margins had plant species richness (S) and species diversity (H') similar to the hedgerows bordering the standard margins ($S = 10.83$ versus $S = 11.57$; $t_{11} = 0.48$; $p = 0.64$; $H' = 1.85$ versus $H' = 1.71$; $t_{11} = -0.56$; $p = 0.59$, respectively).

4. Discussion and conclusions

The presence of hedgerow trees did not significantly increase numbers of the nine species studied. Although these trees may provide shelter additional to that already provided by hedgerows in the exposed agricultural landscape, none of the selected nine species were directly dependent on trees as a larval or, as far as is known, adult food resource. In an earlier landscape-scale study, the effect of hedgerow tree presence was sevenfold larger for tree-feeders than for other guilds (Merckx et al., submitted). Additionally, in the earlier study, hedgerow trees increased moth abundance by 60% and species diversity by 38% only in areas where farmers were targeted to take up AES options, while their presence in non-targeted areas had no positive effect on abundance and diversity (Merckx et al., submitted). In the current study, the area sampled was not targeted for AES uptake, supporting these results.

Overall, moth abundance on field margins was almost double that found in the centres of fields. Moreover, wide field margins, financially rewarded under AES in England and other European countries (Kleijn and Sutherland, 2003; DEFRA, 2005), resulted in significantly higher levels of overall moth abundance (+40%) compared to standard field margins. This may be attributed to more abundant nectar sources [flowerheads were significantly more abundant (250%–300%) on wide versus standard field margins] and greater area and better quality of breeding habitat (increased larval food resources, better buffered from agrochemicals). Nectar sources were absent at field centres. Plant species richness and diversity of the hedgerows were not likely to be confounding factors as they did not differ between hedgerows bordering standard and wide field margins. The higher moth abundance at wide field margins could explain the observed 'source' effect, increasing moth numbers with almost 60% at the field centres compared to the centres of fields with standard margins. Some individuals captured at the field centres had indeed been captured before in a nearby field margin (Fig. 1), which indicates explorative movements out of the margin habitat (Van Dyck and Baguette, 2005). Improvements to the breeding habitat quality of wide field margins could be made by: (i) improving the floristic quality of commercial seed mixes; and (ii) modifying their management from annual cutting (the current regime) to cutting once every two–three years (Erhardt, 1985; Munguira and Thomas, 1992; Kuussaari et al., 2007; Valtonen et al., 2007). Annual cutting, particularly in high summer, in contrast to rotational cutting, makes it difficult for moths to complete a full life cycle, especially for uni-voltine species.

Wide field margins resulted in a significantly higher (40%) abundance overall compared to standard margins. However, the statistical evidence of this (main) effect varied significantly and strongly among the nine common and widespread species. Some species occurred as frequently in standard as in wide field margins, and had relatively high abundances in the field centres. For instance, the relatively mobile Setaceous Hebrew Character *X. c-nigrum* was 27% more abundant in field centres than in field margins, and Large Nutmeg *Apamea anceps* D. & Schif. was only 27% less abundant in the centres than in margins, whereas overall, numbers in the centres were almost half those in margins. In line with our prediction, we showed that the species-specific statistical strength of the effect of 'margin' was correlated with the mobility of the species. The stronger the effect of 'margin', the less mobile the species appeared to be. They covered shorter distances, and were more frequently recaptured at their site of first capture. However, although Dark Arches *A. monoglypha* contributed to the overall effect of 'margin' (Table 3), it might be unwise to label this species as relatively sedentary for a variety of reasons: (i) the species-specific effect of 'margin' is not significant, (ii) there is the risk that we have underestimated its mobility due to the spatial limits of this MRR-study (Schneider, 2003), (iii) Dark Arches *A. monoglypha* was only 48% less abundant in the field centres than in the field margins, and (iv) the absence of any recaptures points towards a high level of mobility (Table 1). We were unable though to link the effect of margin with a third measure of mobility–recapture percentage–but we believe this is merely due to the low overall rate of recapture (3.9%), as this measure is intrinsically more likely to be biased by low recapture rates than the two other measures.

Our finding that the variation in response to the presence of wide field margins can be attributed to species-specific mobility characteristics shows an effect of scale, as all nine species studied are common and widespread species that use field margins for larval and/or adult resources (Table 1). The apparent lack of response of the most mobile of these species to field margins may simply reflect that they use the agricultural habitat on a larger, landscape-scale, rather than a field- or farm-scale. Consequently, the popular AES-option of wide field margins may only benefit a relatively small proportion of all wider countryside species, at least when it is applied at the farm-scale (as in our study). The effect of differential mobility may explain why some widely applied measures within AES currently fail to deliver significant biodiversity gains.

To be effective, AES need to take account of the spatial scales at which populations of wider countryside species use the agricultural matrix and the mosaic of semi-natural habitat within this matrix. We hence believe that a significant improvement to this scheme option, and indeed to any future 'hedgerow trees' scheme option, could be made by applying it in a targeted way, and over a larger, landscape-scale, rather than the current field- or farm-scale approach. This would be effective for the majority of wider countryside species, irrespective of their mobility level. It might involve, for example, pro-actively encouraging contiguous farms to take up AES field margin options, in order to reduce habitat fragmentation and maximize habitat linkages across a landscape. This approach has been successfully used across the Chichester Plain, UK, where pro-active targeting of farms created a landscape-scale network of managed buffer strips along water courses, resulting in significant increases of the endangered Water Vole *Arvicola terrestris* (Macdonald et al., 2007). In the UK, ca. 95% of AES consists of conventional and organic Entry Level Stewardship (ELS and OELS), which are non-targeted schemes (DEFRA/NE, 2008). On the other hand, the Higher Level Stewardship (HLS and OHLS) schemes aim to deliver significant environmental benefits in targeted, high priority situations and areas, but these are a small minority of the total uptake of AES, remain discretionary, and may be less appealing to farmers because of the commitment to more complex management. We suggest that encouraging and facilitating the implementation of simple AES options over large (landscape-scale) areas would result in significant biodiversity gain.

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