Habitat preference and mobility of *Polia bombycina*: are non-tailored agri-environment schemes any good for a rare and localised species?

Thomas Merckx · Ruth E. Feber · Mark S. Parsons · Nigel A. D. Bourn · Martin C. Townsend · Philip Riordan · David W. Macdonald

Abstract General agri-environment schemes (AES) have been shown to benefit widespread species, but there is little information on the extent to which rare, more localised, species may also benefit. We tested whether AES options aimed at increasing general biodiversity also benefit a highly endangered moth, *Polia bombycina*, without species-specific tailoring. We assessed effects on its abundance of two AES options, wide field margins and hedgerow trees, using light traps at the landscape-scale and for mark-release-recapture at the farm-scale. We hypothesized that abundance would be highest at wide field margins and at hedgerow trees, and that if hedgerow trees conferred a positive effect, individuals would be more likely to follow hedgerows than crossing exposed fields while on the move. The results showed that significantly more individuals were captured at sites with a hedgerow tree. Numbers were also higher at wide margins, but this was not statistically significant, and no individuals were caught at field centres. Our study suggests that general options within appropriately designed and implemented AES aimed at increasing overall biodiversity in intensive agricultural landscapes have the potential to not only benefit common, widespread habitat generalists, but some rare and more endangered species as well. *P. bombycina* serves as an example of how general AES options, existing and novel ones alike, might cater for the needs of rare and localised species. As the precise ecological requirements of most invertebrate species remain unknown, we urge scientists and governments to address the challenge to research and design truly general AES, which options should be able to deliver not only for widespread species but also for the less-widespread counterpart of farmland biodiversity.

Keywords Agricultural biodiversity · BAP species · Field margins · Hedgerow trees · Moths · Resource-based habitat concept · Shelter

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Introduction

Although the effectiveness of general agri-environment schemes (AES) has initially—and justifiably so—been questioned (Kleijn and Sutherland 2003), they are still considered the most important and only realistic policy instruments within Europe for reversing widespread biodiversity declines in agricultural landscapes (Donald and Evans 2006). It has become clear now that the key to their success is the manner in which these general AES are

implemented (Vickery et al. 2004). In order to improve their effectiveness, their design should strive to (1) optimize the choice of management options available to and optimise their uptake by farmers through providing personal and tailored advice (Dutton et al. 2008; Merckx et al. 2009a), (2) maximise scheme uptake, moving away from field-scale implementation of AES towards landscape-scale targeting (Holzschuh et al. 2008; Rundlöf et al. 2008a; Merckx et al. 2009a, b), and (3) prioritize scheme implementation near high-quality habitat (Kohler et al. 2008) and in low-intensity farming systems that still support high levels of biodiversity (Kleijn et al. 2009), although some AES have a larger effect in homogeneous landscapes (e.g. Rundlöf et al. 2008b). General AES should also take regional landscape context into account as this impacts on the biodiversity effects of AES (arthropods: Hendrickx et al. 2007—butterflies: Bergman et al. 2004; Öckinger and Smith 2006; Rundlöf and Smith 2006; Davis et al. 2007; Kivinen et al. 2007—(bumble) bees: Heard et al. 2007; Holzschuh et al. 2007; Rundlöf et al. 2008b—carabid beetles: Vanbergen et al. 2005—orthoptera: Marini et al. 2008—plants: Dufour et al. 2006).

However, whilst general AES often have been shown to benefit declining, though still common and widespread farmland species, what has hitherto not been thoroughly examined is the extent to which rarer and currently more endangered species within intensive agricultural landscapes (e.g. localised semi-natural habitat specialists, such as the butterfly *Lycaena tityrus* in Flanders/Belgium) may also benefit from these schemes that are not tailored to specific species. Kleijn et al. (2006) observed that uncommon species were known to benefit from AES in only two of five European countries, and that Red Data Book species rarely benefited from AES. As a result, it has been suggested that objectives of AES within intensively managed agricultural systems may have to be differentiated between general AES aiming to increase functional biodiversity, for example with the objective to improve ecosystem processes, and AES tailored to the autecology of particular endangered species still inhabiting these landscapes (Kleijn et al. 2006; Evans and Green 2007; Reid et al. 2007; Tscharntke et al. 2007; Verhulst et al. 2007; Wilson et al. 2007; but see Browne and Aebischer 2003). Such a two-tier approach may, in theory, be the best way to manage the trade-off between untargeted, and high volume measures to benefit more common and widespread species and targeted management to benefit rare and range restricted species (Evans and Green 2007).

Whilst we do not question the usefulness of such a two-tier approach when species-specific ecological requirements are known, we feel less at ease about the approach's implications in light of the strong research bias towards vertebrates (Clark and May 2002; Leather 2009). Indeed,

although we believe that it must be possible to design effective management prescriptions meeting the ecological needs of threatened bird species for instance, based upon sound ecological research on the species-specific reasons for their decline (Grice et al. 2004; Evans and Green 2007), the majority of threatened species will be invertebrates, lacking such data on ecological requirements. Hence, if the targeted tier is strongly biased towards a minority of taxa which may not be representative for other taxa, there is a clear risk that the current two-tier approach may neither cater for the needs of the majority of species nor improve general biodiversity. As we do not envisage this bias towards vertebrates disappearing, the best solution may be if general, non-tailored AES could be made more inclusive, not only catering for common, widespread species, but also for rarer and more localised species. We believe, indeed, that there exists a need to decrease the gap between the two tiers of the above-mentioned approach, by designing the general tier to be more 'general', in other words to cater for a larger number of species.

Here, we conduct an exploratory case study which tests whether possible AES options aimed at increasing biodiversity in general, also benefit a highly endangered noctuid moth, *Polia bombycina* (Hufnagel) (Lepidoptera: Noctuidae) the pale shining brown. Species-specific tailoring was not an option as the ecological requirements of this species are largely unknown (see "Materials and methods"). In 2006, an apparently strong population of *P. bombycina* was discovered during moth sampling in agricultural landscapes in Oxfordshire, UK (Townsend and Merckx 2007). The species was captured in large numbers in one of four landscapes under study, and was present on four farms (nine out of 12 sampling points) within this landscape (Fig. 1a). In 2007 and 2008 we repeated sampling at the same points, using an identical methodology, and also carried out a mark-release-recapture (MRR) study on one of the farms (Fig. 1b).

In this study we assessed the effects on the abundance of *P. bombycina* of two general AES options: 6 m wide grassy field margins (currently a popular option in many European countries) and hedgerow trees (a novel addition to the set of general AES options within England). This involved a multi-site, light trap study at a landscape-scale, and a multi-site, MRR light trap study at a farm-scale.

Six metres wide uncropped, grassy field margins are an important conservation tool (Macdonald et al. 2000). Their creation and management is financially rewarded under current AES in England, and widely taken up by farmers [grass/buffer strips on arable land covered over 47,000 ha by autumn 2006 (Butler et al. 2007; DEFRA/NE 2009)]. By early February 2008 more than 5 million ha (>51% of agricultural land) was under AES in England, and grass/buffer strips on arable land were one of the popular scheme
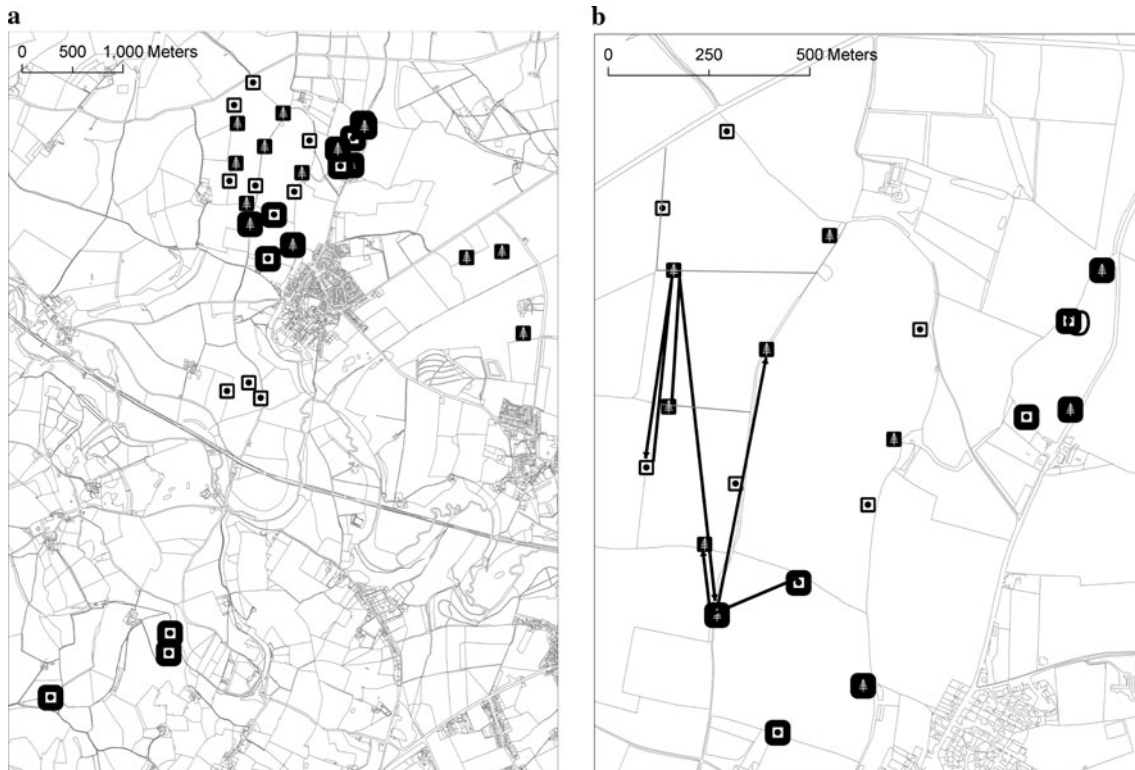
Fig. 1 a Study area and trap sites. Light trap sites ($N = 30$) in the study area of intensive agricultural land: sites with hedgerow trees are indicated with a *tree symbol*; sites without hedgerow trees are indicated with *dots*. Narrow and wide halos around the symbols indicate standard and wide field margins, respectively. The northerly clustered sites are part of the MRR study at a farm-scale (detailed view in Fig. 1b). Three of these sites and the other clusters are part of the habitat preference study at a landscape-scale (four farms; three sites per farm). *Note*: not all field boundaries are indicated. Base layer map: © Crown Copyright/database right 2008. An Ordnance Survey/EDINA supplied service. **b** MRR study trap sites and movements. Large-scale section of Fig. 1a (same symbology) showing 20 light trap sites from the MRR study at a farm-scale. *Light grey* lines indicate all field boundaries (i.e. hedgerows) and roads. *Black arrows* indicate movements of *P. bombycina* individuals ($N = 5$; 8 recaptures/movements). The central field was only sampled in one of the field seasons. Base layer map: © Crown Copyright/database right 2008. An Ordnance Survey/EDINA supplied service

options (DEFRA/NE 2008). They have been shown to increase overall diversity levels (e.g. invertebrates: Asteraki et al. 2004; butterflies: Feber et al. 1996; Field et al. 2005; bumblebees: Carvell et al. 2007; macro-moths: Merckx et al. 2009a). Wide field margins might provide *P. bombycina* with (1) relatively undisturbed larval habitat, (2) adult food resources (i.e. nectar), and (3) buffer zones against the impact of agricultural chemicals on larvae and host plants (Longley and Sotherton 1997; Pywell et al. 2004; de Jonga et al. 2008).

Hedgerow trees are prominent landscape features. In the UK, their abundance has dramatically declined since the late eighteenth century to an estimated 1.6 million isolated hedgerow trees, of which the annual recruitment is currently only half the level required to maintain a healthy population (Stokes and Hand 2002; DEFRA 2010). Conservation management of hedgerow trees is a very recent addition to the present set of general AES options within England (DEFRA/NE 2009). The presence of hedgerow trees increases overall diversity levels of macro-moths

(Merckx et al. 2009a), overall abundance of diptera (Peng et al. 1992), as well as temporal abundance and foraging activity of bats (Linton et al. unpubl. data). In order to minimize confounding variables, we almost exclusively selected pedunculate oak (*Quercus robur* L.) as hedgerow trees in this study. Although there is no evidence that they provide a larval food resource to *P. bombycina*, they increase shelter. Sheltered spots are important for insects, which are ectothermic, and hence prone to convective cooling in agricultural landscapes (Dover and Sparks 2000; Pywell et al. 2004).

We first tested whether wide field margins and hedgerow trees influence the abundance of *P. bombycina*. We hypothesized that, in the case of positive influence, abundance would be highest at wide field margins and where a hedgerow tree is present. Our second hypothesis was that, if hedgerow trees conferred a positive effect by providing shelter, *P. bombycina* would also be more likely to follow hedgerows while moving through the landscape, rather than crossing the more exposed field centres. Our

prediction was that we would not trap many individuals in the centre of the fields, irrespective of their mobility level. We sampled at fixed points in arable field margins characterised by four combinations of presence/absence of wide field margins and hedgerow trees. A MRR study provided complementary information on movement characteristics and activity.

Materials and methods

Study species

Since the mid-1970s *P. bombycina* has declined severely in Britain (Waring and Townsend 2009), and probably elsewhere in Europe (e.g. Sweden, Belgium: M. Parsons, pers. comm.; The Netherlands: De Vlinderstichting/Werkgroep Vlinderfaunistiek 2008). The reasons for this decline are not well understood. *P. bombycina* met the conservation status criteria for inclusion as one of 81 priority moth species in the UK government's Biodiversity Action Plan (BAP) (www.ukbap.org.uk) (UK Biodiversity Group 1999; Butterfly Conservation 2007). The BAP process has resulted in a much better understanding of the status and autecology of many of the moth species listed (Parsons et al. 2005). However, *P. bombycina*'s ecological requirements remain poorly known and, although its serious decline is beyond question, there is not enough focused monitoring data to assess the real extent of the remaining populations. For these reasons it is impossible to tailor specific measures or provide specific advice on habitat management. Thus, the response of this species to general AES provides a good case study to determine how AES options may benefit rare and localised species with relatively unknown resource requirements.

Until the mid-1970s *P. bombycina* was widely and well distributed in southern and southeast England (Waring and Townsend 2009), inhabiting downland and open country mainly on clay and light calcareous soils (Heath and Emmet 1979; Skinner 1998). A population at Salisbury Plain, Wiltshire, was regarded as the last stronghold between 2000 and 2005, as here the moth was recorded annually, albeit in low numbers (Thomas et al. 2006). By 2008, only nine record clusters were known, all within four 10 km squares. There are an additional seven sites, covering at least six additional 10 km squares, with single recent records, excluding those of immigrants of the silvery-grey continental form (The Action for Threatened Moths Project, undated). In Oxfordshire, *P. bombycina* was widespread, if local, up to at least 1979, but had last been seen in 1984 (Waring 2002). Single examples were again caught in a small area in the northwest of the county in 2005 and 2006 (Townsend and Merckx 2007). In 2006 we sampled large numbers (see below) on arable land in west Oxfordshire, and hence discovered the strongest population currently known in Britain (Townsend and Merckx 2007).

P. bombycina is a univoltine nocturnal species with a flight season from mid-June to mid-July. It almost certainly overwinters as a larva, and may sometimes complete its spring growth on the buds and leaves of deciduous trees and shrubs, like other members of the genus (Ronkay et al. 2002). However, the life cycle remains unconfirmed in the wild. Plants accepted in captivity include herbaceous species such as sow-thistles *Sonchus* spp., dandelion *Taraxacum officinale*, common restharrow *Ononis repens*, docks *Rumex* spp. and common broom *Cytisus scoparius*, as well as woody plants such as bilberry *Vaccinium myrtillus*, grey willow *Salix atrocinerea*, white willow *S. alba* and common hawthorn *Crataegus monogyna*.

We found that the larvae, in captivity, are highly negatively phototactic and are therefore likely to be active well after dark and perhaps only on darker nights (Townsend and Merckx 2007). It has also been observed that the larva is a poor climber (Waring and Townsend 2009). Pupation probably occurs underground. Adults visit flowers, including wood sage *Teucrium scorodonia*, white campion *Silene alba*, bladder campion *S. vulgaris*, woundworts *Stachys* spp. and viper's-bugloss *Echium vulgare* (BC/DEFRA 2005; Waring and Townsend 2009).

Sampling

We used Heath pattern actinic light traps (6 W) (Heath 1965). These operate on the 'lobster-pot principle', whereby moths are drawn from a relatively close distance to an actinic tube secured vertically between baffles, fall unharmed down a funnel, and rest on the inside of the trap or on pieces of egg-tray provided. Traps were operated from dusk until dawn, when the live sample was enumerated and released in situ.

We only sampled fields bordered by average-sized hedgerows (2–3 m high; 1.5–2.5 m wide) with hedgerow trees scattered throughout. Hedgerows had similar levels of woody plant species richness and diversity (Merckx et al. 2009b). We compared wide (6 m) perennial grass margins (current AES option; DEFRA/NE 2009) with standard (ca. 1–2 m; cross-compliance) margins in the fields sampled, and presence/absence of a hedgerow tree. Hedgerow tree sampling sites were positioned at a distance of 1 m from hedgerows and 5 m away from the trunk of a hedgerow tree (minimum height: 15 m; predominantly *Q. robur*). 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 more than 100 m apart in order to avoid interference between light traps, and all sites were fixed for the duration

of the study. 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 (Fry 1991; Dover 1996; Maudsley 2000). All sampling sites in margins were located 1 m from hedgerows.

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; therefore, the protocol was designed to ensure that sampling was conducted in similar, sufficiently favourable conditions to minimise 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 temperatures were in most cases considerably higher and maximum wind speeds considerably lower).

Studies

Landscape-scale study

We sampled twelve field margin sites spread over four predominantly arable farms (3 per farm) in an agricultural landscape (River Evenlode catchment, Oxfordshire, UK). Each farm was allocated to a different experimental group as follows: (1) hedgerow tree + wide margin; (2) hedgerow tree + standard margin; (3) no hedgerow tree + wide margin; (4) no hedgerow tree + standard margin (Fig 1a). The classification towards these experimental groups was representative for the whole farm as the three sampled margin sites per farm were representative of the majority of margins of a given farm. Sampling at each farm was carried out from mid-May to mid-October in discrete fortnightly periods, once in each period, in random order within the period. A maximum of three farms (i.e. nine sites) were sampled on any one night, and traps were collected in, and moved to a different site, after each sample. This was done during three consecutive years (2006/2007/2008), as part of a larger project (Merckx et al. 2009a; in prep.).

Farm-scale mark-release-recapture study

We conducted a MRR study across five adjacent arable fields (Stonesfield, Oxfordshire, UK). In 2007, five sites were sampled within each of four fields (central field was not sampled; twenty sites in total): one site at the centre of each field, and four sites at the field margins (one site at each margin). Two of these field margin sites were near a hedgerow tree (see above). Two fields had standard

margins, and the other two had wide margins (Fig. 1b). In 2008, we sampled four field margin sites within each of the five fields (twenty sites in total): two sites near a hedgerow tree and two sites without a hedgerow tree. Three fields had standard margins, and the remaining two had wide margins (Fig. 1b). We alternated trapping between fields (i.e. individual trap sites were not run on consecutive nights). This method avoids a bias towards recaptures at the same site, as individuals released in situ would otherwise be very likely to end up in the trap nearby when they get active at dusk. In 2007 we sampled every night ten sites of both a field with wide margins and a field with standard margins, whereas in 2008 we sampled every night eight sites of both a field with wide margins and a field with standard margins, as well as an additional two sites of the central field, so that all sites were covered equally within a given year. In both years the study covered the entire flight period of *P. bombycina*: in 2007 the study ran from 5th June until 14th July on 32 nights, and in 2008 from 9th June until 19th July on 33 nights (i.e. on all nights with suitable weather conditions; see above). The biggest gaps in trapping effort, due to the weather, were of periods of two consecutive nights, twice in 2007 and once in 2008.

At dawn, all trapped individuals of *P. bombycina* were 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) and were released immediately into nearby tall vegetation. For each capture we recorded (1) date, (2) site, and (3) individual mark number. Locations of trap sites were obtained via a handheld GPS receiver (Garmin/etrex). Distances of movements between captures were measured using a GIS (ArcGIS 9.0) and were $\log_{10}$-transformed prior to analyses in order to obtain normality of the residuals. The average distance among all possible, pair-wise combinations of all trap sites was 663 ± 27 m and 624 ± 25 m in 2007 and 2008, respectively (mean $\pm$ SE; $N_{\text{in both years}} = 210$). The furthest distance between any two traps was $1,444 \pm 7$ m (2007 and 2008; combined error on GPS positions).

MRR is a well-established method to assess mobility and population structure of butterfly populations (Warren 1992) and those of other species. There is, however, very little information on the relative mobility of the majority of nocturnal Lepidoptera 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 two published MRR studies on moths captured in light traps (Nieminen 1996; Merckx et al. 2009b), and we therefore consider this method to be a novel approach. In contrast to MRR studies on day-flying Lepidoptera, where the observer actively patrols through a study site, moth light traps are fixed sampling points.

This method thus results in lower recapture rates. Nieminen's study was characterized by 10 and 15% overall recapture rates (2 years). The overall recapture percentage in Merckx et al. (2009b) for all nine species combined was 3.9% (range: 0–14.6%). Studies on both white ermine *Spilosoma lubricipeda* (M. Young, University of Aberdeen, UK, pers. comm.) and sussex emerald *Thalera fimbrialis* (Parsons and Kirby 1993) resulted in recapture rates of less than 5%. In another study ca. 700 individuals of large yellow underwing *Noctua pronuba* were marked and only one was recaptured (i.e. 0.1%) (M. Young, pers. comm.). Presumably moths have a continuum of open-closed population structures and dispersal abilities in a similar way to butterflies, and open population structures will similarly result in lower recapture rates.

Analyses

Habitat preference

We totalled the number of individuals sampled at each of the 32 sites per year: 12 sites from the landscape-scale study during 2006, 2007 and 2008, and 20 sites from the MRR study, excluding the field centres, during 2007 and 2008. These abundances ($N = 72$) were $\log_{10}$-transformed. We used the Information Theoretic (IT) approach (Burnham and Anderson 2002; Richards 2005) to compare 15 alternative and biologically plausible models that capture key elements of the system under study. This IT approach aspires to find the best of a suite of models, with the fewest parameters absolutely necessary (Johnson and Omland 2004; Boyce et al. 2007). The additive models were generalized linear models (GLM) that contrast the effects of three independent class variables (i.e. fixed effects) on these abundances of *P. bombycina*: 'margin' (standard versus wide); 'hedgerow tree' (absent versus present); 'year' (2006, 2007, 2008); and all two- and three-way interactions of the three main effects. All possible combinations of these fixed effects give a total of 15 different models. 'Site' nested within 'farm' was included as a random effect in all models. Akaike's Information Criterion (AIC; Akaike 1974), corrected for small sample sizes (AICc), was used to determine Akaike's weights of evidence for each model given the other models considered. Using the COMPMIX macro (Russell D. Wolfinger; http://support.sas.com/kb/24/996.html; SAS 9.1), we selected the model with the lowest AICc. The Akaike's weight of this model (0.61) was much larger than the second best model (0.16), and the Akaike's difference between the top-ranked model and the second best model was larger than 2 ($\Delta = 2.7$). According to Burnham and Anderson (2002, 2004) this means that there is substantial evidence to support our top-ranked model, and that this best model has

considerably more support than the second-best and all other models tested. We therefore used this selected generalised linear model (Proc Mixed, SAS 9.1). Model residuals were normally distributed (Shapiro–Wilk). Degrees of freedom were calculated using the Satterthwaite option (Littell et al. 1996). Differences of least squares means (DLSM) were calculated.

Mobility

For every recaptured individual we calculated the distance covered between first capture and last recapture (i.e. sum of covered distances in case of multiple recaptures; 1 data point/individual; data independence). We used three different measures of mobility, combining the data of 2007 and 2008: (1) average ($\pm$ SE) of these total covered distances, (2) overall recapture percentage, and (3) proportion of first recaptures at site of first capture.

Weather

In order to correlate climatic data with the contrasting high numbers in 2006 versus low numbers in 2007/2008, the following climatic parameters for every sampling night were compared between 2006 (4th June—19th July; $N = 22$) and the combined data of 2007 and 2008 (2007: 5th June—14th July; 2008: 9th June—19th July; $N = 65$) using Student's t-tests (Proc Ttest; SAS 9.1): (1) temperature at dusk and dawn (°C); (2) maximum and minimum overnight wind speed (km/h); and (3) humidity at dusk and dawn (%). Equality of variances was tested for, and accordingly we used the Pooled or Satterthwaite method to calculate degrees of freedom.

Results

Habitat preference

Significantly more individuals were captured at sites where a hedgerow tree was present than at sites without a hedgerow tree, both at standard and wide field margins (tree: $F_{1,27} = 21.81$; $P < 0.0001$; tree x margin: non-significant) (Fig. 2). This main effect of hedgerow tree, however, was only present in 2006 (tree × year: $F_{2,42.1} = 13.86$; $P < 0.0001$; DLSM$_{06}$: $t_{64.7} = -5.98$; $P < 0.0001$). In 2007 and 2008 no effect of hedgerow tree could be detected, but the direction of the trend was the same in all years (DLSM$_{07}$: $t_{63.7} = -0.41$; $P = 0.68$; DLSM$_{08}$: $t_{63.1} = -0.81$; $P = 0.42$). The absence of a hedgerow tree effect in 2007 and 2008 was probably due to a lack of statistical power as numbers of *P. bombycina* were much lower in 2007 and 2008 than in 2006 (year: $F_{2,42.1} = 21.91$;
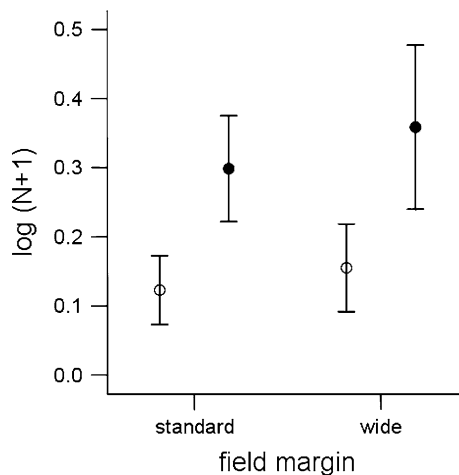
Fig. 2 *P. bombycina* counts. Abundances (mean ± SE; $\log_{10}$-transformed) of *P. bombycina* at standard and wide field margin sites with (*filled circle*) and without (*open circle*) a hedgerow tree (*Q. robur*). Abundance at sites with a hedgerow tree is significantly higher than at sites without a hedgerow tree, both at standard and wide field margins. *Numbers* are higher at wide compared to standard field margins, but not significantly so. Numbers were totalled over 3 years (2006–2008). Sampling occurred at a total of 30 light trap sites

$P < 0.0001$; $N_{06} = 86$; $N_{07} = 23$; $N_{08} = 18$; LSM_{06} ($\pm$ SE) $= 0.65 \pm 0.07$; LSM_{07} ($\pm$ SE) $= 0.18 \pm 0.05$; LSM_{08} ($\pm$ SE) $= 0.13 \pm 0.04$; $DLSM_{06-07}$: $t_{45.8} = 5.77$; $P < 0.0001$; $DLSM_{06-08}$: $t_{47.8} = 6.41$; $P < 0.0001$; $DLSM_{07-08}$: $t_{36.3} = 0.74$; $P = 0.46$). The abundance of *P. bombycina* did not differ significantly between wide and standard field margins, though numbers were higher in wide than in standard margins ($F_{1,22.7} = 0.30$; $P = 0.59$) (Fig. 2).

Mobility

As numbers of trapped *P. bombycina* individuals were low, we combined the data from 2007 and 2008. Overall, only five out of a total of 29 marked individuals were recaptured, of which three were recaptured twice, and two were recaptured once (i.e. eight recapture events; overall recapture percentage: 17.2%). Only one out of these five recaptured individuals was recaptured at the same spot of first capture (i.e. 20%). On average, individuals covered a total distance of 653 ± 214 m (range: 0–1157 m; $N = 5$) (Fig. 1b). Recapture events occurred shortly after first capture [mean ± SE: 1.63 ± 0.26 nights ($N = 8$); range: 1–3 nights]. No individuals were caught at the field centres (2007 MRR study), although 18, plus one recaptured individual, were trapped in the surrounding field margins of the same fields over the course of the study. Movements show that *P. bombycina* is a rather mobile species, likely to follow hedgerows while traversing the landscape.

Climate

Climatic data from 2006 were contrasted with pooled data from 2007 and 2008 in order to correlate these data with the contrasting high numbers in 2006 versus low numbers in 2007/2008 (see *Results Habitat preference*). Temperatures at dusk and dawn were higher in 2006 than in 2007/08 (dusk: 19.6 ± 0.7 vs. 16.4 ± 0.2°C; $t_{26.5} = 4.29$; $P = 0.0002$—dawn: 13.5 ± 0.5 vs. 12.0 ± 0.2°C; $t_{28.3} = 2.77$; $P = 0.01$). Maximum overnight wind speed was lower in 2006 than in 2007/08 (11.2 ± 0.9 vs. 14.0 ± 0.6 km/h; $t_{85} = -2.37$; $P = 0.02$). There was no difference in the minimum overnight wind speed (8.2 ± 0.8 vs. 9.3 ± 0.6 km/h; $t_{85} = -0.98$; $P = 0.33$). Humidity at dusk was lower in 2006 than in 2007/08 (61.8 ± 2.2 vs. 74.6 ± 1.4%; $t_{84} = -4.69$; $P < 0.0001$). There was no difference in humidity at dawn (89.2 ± 1.5 vs. 90.2 ± 1.3%; $t_{53} = -0.51$; $P = 0.61$).

Discussion

In line with our first hypothesis, the presence of hedgerow trees conferred a considerable positive effect on numbers of adult *P. bombycina*. No individuals were trapped in the field centres and numbers were higher in wide compared to standard field margins, but the effect of wide field margins was not statistically significant. Nevertheless, this AES option may benefit *P. bombycina*. In a field-scale study in the same study area on nine common macro-moth species for which field margins provide resources for the larval and adult stages, Merckx et al. (2009b) demonstrated that wide margins positively affected adult abundance, more so for less mobile species but not for the most mobile. Here, all three mobility measures we used indicate that *P. bombycina* would be at the mobile end of the gradient displayed by the nine species. In line with the conclusion of Merckx et al. (2009b), this may indicate that wide field margins would be more effective for *P. bombycina* if uptake of this AES option were implemented across a landscape, rather than the current field-scale uptake. Additionally, Merckx et al. (2009b) showed that wide field margins had significantly more nectar sources than standard margins, benefiting nectar-dependent species, such as *P. bombycina* (see also Pywell et al. 2004).

In line with our second hypothesis, we showed that *P. bombycina* adults are likely to be highly dependent on shelter-providing structures in the landscape. Although hedgerows alone provide some degree of shelter in exposed agricultural landscapes (Lewis and Stephenson 1966; Dover and Sparks 2000; Maudsley 2000), the large majority of individuals were trapped near hedgerow trees. In captivity, *P. bombycina* larvae are able to grow on a

variety of herbaceous and woody plant species, but it is not known whether they accept oak leaves. As the life cycle in the wild is still unknown, evidence is lacking as to whether oak trees are a larval foodplant for *P. bombycina*. Nevertheless, hedgerow trees are probably of benefit in providing a higher level of shelter than hedgerows without trees. This must especially be the case for insect species that routinely fly at levels above the average height of hedges where they cannot benefit from their shelter shadow. This is likely to be the case for *P. bombycina*, a typically built noctuid designed for powerful flight (Waring and Townsend 2009), as Taylor and French (1974) showed that relatively large numbers of noctuids are flying at varying heights up to 100 m (contrasting with numbers of Geometridae, another species-rich group but of smaller and less mobile moths, concentrated close to ground level). Furthermore, in a study on the whole macro-moth fauna in agricultural landscapes, Merckx et al. (2009a) showed that the positive effect of hedgerow trees on adult abundance applied both to oak-feeders and species that fed on other woody and herbaceous plant species in the margins and hedgerows, which also suggests that the effect was due to the shelter provided by the trees. In addition to this shelter effect, night air temperature may well be slightly higher beneath hedgerow tree canopies compared to surrounding temperatures in the open agricultural landscape, especially at clear and calm nights (see Langvall and Ottosson Löfvenius 2002; Merckx et al. 2008). Both effects of shelter and temperature mean that convective cooling of flying insects will be reduced at hedgerow tree sites. Hedgerow trees might also be expected to impact on water and nutrient levels of the soil, affecting sward structure and composition, with possible effects on nectar abundance. These related aspects need further research.

We argue from these observations that *P. bombycina* is dependent on large, shelter-providing structures to move through agricultural landscapes, and probably follows high hedgerows and hedgerow tree lines when searching for resources, at least in agricultural landscapes (see also Dover 1990). Consequently, the actual distances covered are probably considerably larger than the reported Euclidean distances between captures. Moreover, MRR studies generally underestimate mobility levels and are systematically biased by the spatial scale of the study (Schneider 2003). It is hence not surprising that the spatial resolution of our study may have influenced the estimated mobility: the average observed distance covered by *P. bombycina* (653 ± 214 m) resembles closely the average distance among all pair-wise combinations of all trap sites (2007: 663 ± 27 m; 2008: 624 ± 25 m).

Abundance of *P. bombycina* adults was much lower in 2007 and 2008 than in 2006. Adult Lepidoptera generally prefer higher ambient temperatures (within limits) and lower wind speeds, which make it easier to stay within the thoracic muscles' optimal thermal window for flight activity (Merckx et al. 2008). Hence, the higher temperatures ($\Delta 3.2°C$ at dusk and $\Delta 1.5°C$ at dawn) and the lower maximum overnight wind speeds ($\Delta 2.8$ km/h) in 2006 meant that conditions for flight were more favourable than in 2007 and 2008. Moreover, the summers of 2007 and 2008 were characterised by persistent and frequent heavy rain in lowland England [trapping nights in 2007/2008 had higher humidity percentages at dusk ($\Delta = 12.8\%$) than in 2006]. These conditions have been blamed for the generally low numbers of Lepidoptera during 2007 and 2008 (Waring 2008). For instance, overall macro-moth abundance in samples from the same region was 42% in 2007 and 46% in 2008 of values in 2006 (Merckx et al. in prep.). There were no obvious changes in habitat due to agricultural management in the study landscape, and the optimum conditions for larval survival of this species are not known. Therefore, variation in seasonal weather patterns is the most likely explanation for the differences between years.

General options within appropriately designed and implemented AES aimed at increasing overall biodiversity in intensive agricultural landscapes could not only benefit common and widespread habitat generalists, but here we show that they might also work for some more localised, rare and highly endangered species. AES management options focused on the establishment of new hedgerow trees and the retention of existing hedgerow trees are likely to be successful in increasing numbers of *P. bombycina*, at least in areas where the species still occurs, given the demonstrated positive effect of their presence on numbers of this endangered species. Although numbers of this species were not significantly higher in wide compared to standard grassy field margins, AES options for nectar-rich margins might well have a significant effect on this nectar-feeding insect species (see Pywell et al. 2004). Further studies are needed to test whether our finding on general AES options holds for other species of conservation concern, such as rare, locally distributed species and/or habitat specialist species for which detailed ecological requirements are lacking. It has already been shown that general AES can be successfully tailored to meet additionally the needs of a particular species or species group of conservation concern when their specific resource requirements are taken into account (e.g. seed-eating birds: Evans 1997). For example, Bayliss et al. (2005) applied a spatially explicit multi-species approach, targeting eight threatened bird species associated with rare neutral grasslands within a general AES. Another example is a general AES targeted at the cirl bunting *Emberiza cirlus*, amendments to which boosted local populations by 83% in just six years (Peach et al. 2001). A further example is a recent study of the impact of AES on the marsh fritillary butterfly on chalk

grassland in Dorset, southern England. This study showed a recovery from a low of 10–17 colonies between 1995 and 2007 following the introduction of a special extensive cattle grazing option to the general AES in 1993 (Bulman et al. in prep.). However, species-specific amendments to general AES are not feasible for every species of conservation concern, and are likely to create a bias towards high-profile species. Attention is already highly biased towards vertebrates, among which mammals and birds are substantially over-represented (Clark and May 2002; Macdonald et al. 2007; Leather 2009). Furthermore, species-specific conservation requires detailed autecological knowledge on resource use and mobility, and distribution data. Without such information, AES implementations may even have detrimental effects on species (Konvicka et al. 2008). Adequate information is often lacking for the large majority of species, even in the UK after centuries of published scientific research. There is a need for optimized general schemes that deliver gains for the large majority of currently declining species, still common and more localized alike, in intensive agricultural landscapes. Our work on *P. bombycina* shows this might be feasible, as general AES options (e.g. for the establishment of new and the protection of existing hedgerow trees) were likely to increase abundance without species-specific tailoring. Although the presence of wide grassy field margins did not result in significantly higher numbers of this endangered species, a general AES option for the establishment of nectar-rich wide margins might do so (see above).

Since policy reform is an important driver of changes in agricultural land-use (Mattison and Norris 2005), we are encouraged to see policy measures that specifically address biodiversity and landscape protection being implemented, at least in Europe and the US (e.g. 155 such measures as of December 2004 within the OECD: Herzog 2005). In order to be successful (i.e. meeting a pre-defined target of increased biodiversity overall), integrative approaches are key. AES that integrate multi-species conservation of whole landscapes, as well as the economic and social consequences of land-use change, are likely to meet such targets (see also Polasky et al. 2008), especially since we show here that they may not only benefit declining, though still common, generalist species but they might also benefit rare, more localised and more endangered species. Making the general tier of the two-tier approach to AES more inclusive, by including novel, effective options within general schemes, will make AES more powerful and will increase their likelihood to reverse negative biodiversity trends in the wider countryside. Additionally, benefits to non-target species will be gained from the multitude of juxtaposed conservation measures within the species-specific tier, targeted at those species where the ecological requirements are better understood. The next phase of the

English Higher Level AES (HLS), targeted within selected areas (NE 2008), is an example of a more integrated AES, and it is essential that this targeted approach be monitored to assess its impact to biodiversity. It should be clear that we are not advocating against species-specific conservation. Indeed, we believe that general integrative AES should be topped-up with species-specific prescriptions, where and when the precise ecological requirements of certain species of high conservation concern are known.

In practice, more integrated AES should be designed taking into account a number of general points (see also Grashof-Bokdam and van Langevelde 2005). For example, AES should be implemented over wide areas so that whole populations and, hence, whole agro-ecosystems can benefit (e.g. Tscharntke et al. 2005, 2007). Merckx et al. (2009a, b) show that targeting of entire landscapes is necessary to produce the largest effects from AES options, moving away from a field/farm-scale implementation of AES towards landscape-scale conservation by AES. Within-landscape heterogeneity also needs to be increased, so as to cater for as many species as possible, especially in the face of climate change (Dennis et al. 2007). It is thus important to preserve, restore and implement semi-natural elements (e.g. hedges, trees, woods) (Holland and Fahrig 2000; Fahrig 2001; Swift et al. 2004). A large-scale study covering 25 agricultural landscapes in seven EU countries showed that species richness of plants, birds and five arthropod groups increased with the area of semi-natural habitats in the landscape (Billeter et al. 2008).

A policy change towards the development of better AES would also have to be accompanied by a shift from a patch/matrix or habitat/non-habitat approach towards a resource-based approach to the whole agricultural landscape (see also Dennis 2004, 2010; Dennis et al. 2003, 2006). Fahrig (2001) enumerated the conditions of species survival in landscape mosaics and concluded that the habitat/non-habitat model should be avoided. Her simulations predicted that under certain circumstances up to 58% less habitat is required for population persistence, if a matrix of very low quality is converted to a matrix of very high quality. Matrix quality has a larger effect on population persistence than does habitat pattern (i.e. habitat fragmentation) (Fahrig 2001). Within the whole-landscape context, these findings emphasise the need to increase the amount and quality of resources within the 'matrix' so as to increase the suitability of the agricultural habitat, and to decrease the need for movements and its associated cost.

By showing that numbers of adult *P. bombycina*—a UK conservation priority species—are higher at hedgerow trees and wide field margins, at least when AES are sufficiently implemented and at a large enough spatial scale, our results indicate that there is scope to integrate such

widely applicable AES options within inventively designed AES aimed not only to benefit common and widespread, though declining species, but also to benefit rarer and more endangered species within agricultural landscapes. As it is not realistic to cater precisely for the needs of all species within agricultural landscapes, we believe there is a great urgency to invest strongly in ecological research to develop inclusive AES that manage for increased habitat quality (i.e. more habitat resources) for populations of low-profile species, which comprise the largest part of global biodiversity.

References

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Auto Contr 19:716–723

Asteraki EJ, Hart BJ, Ings TC, Manley WJ (2004) Factors influencing the plant and invertebrate diversity of arable field margins. Agric Ecosyst Environ 102:219–231

Bayliss JL, Simonite V, Thompson S (2005) The use of probabilistic habitat suitability models for biodiversity action planning. Agric Ecosyst Environ 108:228–250

BC/DEFRA (2005) Pale Shining Brown BAP species fact sheet. Butterfly Conservation—UK government Department for the Environment, Food and Rural Affairs http://www.butterfly-conservation.org/uploads/pale_shining_brown.pdf

Bergman KO, Askling J, Ekberg O, Ignell H, Wahlman H, Milberg P (2004) Landscape effects on butterfly assemblages in an agricultural region. Ecography 27:619–628

Billeter R, Liira J, Bailey D, Bugter R, Arens P, Augenstein I et al (2008) Indicators for biodiversity in agricultural landscapes: a pan-European study. J Appl Ecol 45:141–150

Biodiversity Group UK (1999) Tranche 2 action plans–Volume VI: Terrestrial and freshwater species and habitats. JNCC, Peterborough, UK

Boyce MS, Rushton SP, Lynam T (2007) Does modelling have a role in conservation? In: Macdonald DW, Service K (eds) Key topics in conservation biology. Blackwell, Oxford, UK, pp 134–144

Browne SJ, Aebischer NJ (2003) Arable Stewardship: Impact of the pilot scheme on the Brown hare and Grey partridge after five years. Report RMP1870vs3 to DEFRA. UK government Department for the Environment, Food and Rural Affairs, London

Burnham KP, Anderson DR (2002) Model selection and multimodel inferences. A practical Information-Theoretic approach, 2nd edn. Springer, New York

Burnham KP, Anderson DR (2004) Multimodel inference–Understanding AIC and BIC in model selection. Soc Meth Res 33:261–304

Butler SJ, Vickery JA, Norris K (2007) Farmland biodiversity and the footprint of agriculture. Science 315:381–384

Butterfly Conservation (2007) The UK Biodiversity Action Plan—moths http://www.butterfly-conservation.org/uploads/The%20UK%20Biodiversity%20Action%20Plan%20-%20BC%20website%20draft%2020071.pdf

Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M (2007) Comparing the efficacy of agri-environment schemes to enhance bumblebee abundance and diversity on arable field margins. J Appl Ecol 44:29–40

Clark JA, May RM (2002) Taxonomic bias in conservation research. Science 297:191–192

Davis JD, Debinski DM, Danielson BJ (2007) Local and landscape effects on the butterfly community in fragmented Midwest USA prairie habitats. Land Ecol 22:1341–1354

de Jonga FMW, de Snoo GR, van de Zandec JC (2008) Estimated nationwide effects of pesticide spray drift on terrestrial habitats in the Netherlands. J Environ Manag 86:721–730

De Vlinderstichting/Werkgroep Vlinderfaunistiek (2008) Vlindernet, version 2—http://www.vlindernet.nl/vlindersoort_verspreiding.php?vlinderid=583andvq=

DEFRA (2010) Trends, long term survival and ecological values of hedgerow trees: development of populations models to inform strategy. Forest Research, Forestry Commission, report to the UK government Department for the Environment, Food and Rural Affairs, London

DEFRA/NE (2008) Environmental Stewardship Review of Progress. UK government Department for the Environment, Food and Rural Affairs—Natural England. http://www.defra.gov.uk/erdp/schemes/es/es-report.pdf

DEFRA/NE (2009) Entry Level Stewardship: Environmental Stewardship handbook, third edition—February 2010. UK government Department for the Environment, Food and Rural Affairs—Natural England. http://naturalengland.etraderstores.com/NaturalEnglandShop/NE226

Dennis RLH (2004) Butterfly habitats, broad-scale biotope affiliations, and structural exploitation of vegetation at finer scales: the matrix revisited. Ecol Entomol 29:744–752

Dennis RLH (2010) A resource-based habitat view for conservation: Butterflies in the British landscape. Wiley-Blackwell, Oxford, UK

Dennis RLH, Shreeve TG, Van Dyck H (2003) Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102:417–426

Dennis RLH, Shreeve TG, Van Dyck H (2006) Habitats and resources: The need for a resource-based definition to conserve butterflies. Biodiv Cons 15:1943–1966

Dennis RLH, Shreeve TG, Sheppard DA (2007) Species conservation and landscape management: a habitat perspective. In: Stewart AJA, New TR, Lewis OT (eds) Insect conservation biology. CABI, Wallingford, UK, pp 92–126

Donald PF, Evans AD (2006) Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. J Appl Ecol 43:209–218

Dover JW (1990) Butterflies and wildlife corridors. The Game Conservancy review of 1989, 21. The Game Conservancy, Hants, UK, pp 62–64

Dover JW (1996) Factors affecting the distribution of satyrid butterflies on arable farmland. J Appl Ecol 33:723–734

Dover JW, Sparks T (2000) A review of the ecology of butterflies in British hedgerows. J Environ Manag 60:51–63

Dufour A, Gadallah F, Wagner HH, Guisan A, Buttler A (2006) Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. Ecography 29:573–584

Dutton A, Edwards-Jones G, Strachan R, Macdonald DW (2008) Ecological and social challenges to biodiversity conservation on

farmland: reconnecting habitats on a landscape scale. Mam Rev 38:205–219

Evans AD (1997) The importance of mixed farming for seed-eating birds in the UK. In: Pain DJ, Pienkowski MW (eds) Farming and birds in Europe: the Common Agricultural Policy and its implications for bird conservation. Academic Press, San Diego, pp 331–357

Evans AD, Green RE (2007) An example of a two-tiered agri-environment scheme designed to deliver effectively the ecological requirements of both localised and widespread bird species in England. J Ornithol 148:S279–S286

Fahrig L (2001) How much habitat is enough? Biol Cons 100:65–74

Feber RE, Smith HE, Macdonald DW (1996) The effects on butterfly abundance of the management of uncropped edges of arable fields. J Appl Ecol 33:1191–1205

Field RG, Gardiner T, Mason CF, Hill J (2005) Agri-environment schemes and butterflies: the utilisation of 6 m grass margins. Biodiv Cons 14:1969–1976

Fry GLA (1991) Conservation in agricultural ecosystems. In: Spellerberg IF, Goldsmith FB, Morris MG (eds) The scientific management of temperate communities for conservation. Blackwell, Oxford, UK, pp 415–443

Grashof-Bokdam CJ, van Langevelde F (2005) Green veining: landscape determinants of biodiversity in European agricultural landscapes. Land Ecol 20:417–439

Grice P, Evans A, Osmond J, Brand-Hardy R (2004) Science into policy: the role of research in the development of a recovery plan for farmland birds in England. Ibis 146(S2):239–249

Heard MS, Carvell C, Carreck NL, Rothery P, Osborne JL, Bourke AFG (2007) Landscape context not patch size determines bumblebee density on flower mixtures sown for agri-environment schemes. Biol Lett 3:638–641

Heath J (1965) A genuinely portable MV light trap. Entomol Rec J Var 77:236–238

Heath J, Emmet AM (1979) The moths and butterflies of Great Britain and Ireland, Vol. 9. Harley, Colchester, UK

Hendrickx F, Maelfait J, Van Wingerden W, Schweiger O, Speelmans M, Aviron S et al (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. J Appl Ecol 44:340–351

Herzog F (2005) Agri-environment schemes as landscape experiments–Preface. Agric Ecosyst Environ 108:175–177

Holland J, Fahrig L (2000) Effect of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. Agric Ecosyst Environ 78:115–122

Holzschuh A, Steffan-Dewenter I, Kleijn D, Tscharntke T (2007) Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. J Appl Ecol 44:41–49

Holzschuh A, Steffan-Dewenter I, Tscharntke T (2008) Agricultural landscapes with organic crops support higher pollinator diversity. Oikos 117:354–361

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. TREE 19:101–108

Kivinen S, Luoto M, Kuussaari M, Saarinen K (2007) Effects of land cover and climate on species richness of butterflies in boreal agricultural landscapes. Agric Ecosyst Environ 122:453–460

Kleijn D, Sutherland WJ (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? J Appl Ecol 40:947–969

Kleijn D, Baquero RA, Clough Y, Diaz M, De Esteban J, Fernandez F et al (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol Lett 9:243–254

Kleijn D, Kohler F, Báldi A, Batáry P, Concepción ED, Clough Y, Díaz M, Gabriel D, Holzschuh A, Knop E, Kovác A (2009) On the relationship between farmland biodiversity and land-use intensity in Europe. Proc R Soc Lond B 276:903–909

Kohler F, Verhulst J, van Klink R, Kleijn D (2008) At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? J Appl Ecol 45:753–762

Konvicka M, Benes J, Cizek O, Kopecek F, Konvicka O, Vitaz L (2008) How too much care kills species: grassland reserves, agri-environmental schemes and extinction of Colias myrmidone (Lepidoptera: Pieridae) from its former stronghold. J Insect Cons 12:519–525

Langvall O, Ottosson Löfvenius M (2002) Effect of shelterwood density on nocturnal near-ground temperature, frost injury risk and budburst date of Norway spruce. Forest Ecol Manag 168:149–161

Leather SR (2009) Institutional vertebratism threatens UK food security. TREE 24:413–414

Lewis T, Stephenson JW (1966) The permeability of artificial windbreaks and the distribution of flying insects in the leeward sheltered zone. Ann Appl Biol 58:355–363

Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) SAS system for mixed models. SAS Institute Inc., Cary, NC

Longley M, Sotherton NW (1997) Factors determining the effects of pesticides upon butterflies inhabiting arable farmland. Agric Ecosyst Environ 61:1–12

Macdonald DW, Feber RE, Tattersall FH, Johnson PJ (2000) Ecological experiments in farmland conservation. In: Hutchings MJ, John EA, Stewart AJA (eds) The ecological consequences of environmental heterogeneity. Blackwell, Oxford, UK, pp 357–378

Macdonald DW, Tattersall FH, Service KM, Firbank LG, Feber RE (2007) Mammals, agri-environment schemes and set-aside - what are the putative benefits? Mam Rev 37:259–277

Marini L, Fontana P, Scotton M, Klimek S (2008) Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. J Appl Ecol 45:361–370

Mattison EHA, Norris K (2005) Bridging the gaps between agricultural policy, land-use and biodiversity. TREE 20:610–616

Maudsley MJ (2000) A review of the ecology and conservation of hedgerow invertebrates in Britain. J Environ Manag 60:65–76

Merckx T, Van Dongen S, Matthysen E, Van Dyck H (2008) Thermal flight budget of a woodland butterfly in woodland versus agricultural landscapes: an experimental assessment. Basic Appl Ecol 9:433–442

Merckx T, Feber RE, Riordan P, Townsend MC, Bourn NAD, Parsons MS, Macdonald DW (2009a) Optimizing the biodiversity gain from agri-environment schemes. Agric Ecosyst Environ 130:177–182

Merckx T, Feber RE, Dulieu RL, Townsend MC, Parsons MS, Bourn NAD, Riordan P, Macdonald DW (2009b) Effect of field margins on moths depends on species mobility: field-based evidence for landscape-scale conservation. Agric Ecosyst Environ 129:302–309

NE (2008) HLS Targeting: The new approach [and associated regional statements] www.naturalengland.org.uk. Source correct at 28th November 2008. Natural England

Nieminen M (1996) Migration of moth species in a network of small islands. Oecol 108:643–651

Öckinger E, Smith HG (2006) Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. Oecol 149:526–534

Parsons MS, Kirby P (1993) The sussex emerald moth (Thalera fimbrialis Scop.) Survey–1992. JNCC Report, Peterborough, UK

Parsons MS, Hoare D, Davis T, Green D (2005) The distribution of the UK Biodiversity Action Plan priority moth species 1999 to 2004. Atropos 25:5–20

Peach WJ, Lovett LJ, Wotton SR, Jeffs C (2001) Countryside stewardship delivers cirl buntings (*Emberiza cirlus*) in Devon, UK. Biol Cons 101:361–373

Peng RK, Sutton SL, Fletcher CR (1992) Spatial and temporal distribution patterns of flying Diptera. J Zool 228:329–340

Polasky S, Nelson E, Camm J, Csuti B, Fackler P, Lonsdorf E et al (2008) Where to put things? Spatial land management to sustain biodiversity and economic returns. Biol Cons 141:1505–1524

Pywell RF, Warman EA, Sparks TH, Greatorex-Davies JN, Walker KJ, Meek WR et al (2004) Assessing habitat quality for butterflies on intensively managed arable farmland. Biol Cons 118:313–325

Reid N, McDonald RA, Montgomery WI (2007) Mammals and agri-environment schemes: hare haven or pest paradise? J Appl Ecol 44:1200–1208

Richards SA (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecol 86:2805–2814

Ronkay L, Hacker H, Hreblay M (2002) Noctuidae Europaeae Vol. IV Hadeninae I. Entomological Press, Sorø

Rundlöf M, Smith HG (2006) The effect of organic farming on butterfly diversity depends on landscape context. J Appl Ecol 43:1121–1127

Rundlöf M, Bengtsson J, Smith HG (2008a) Local and landscape effects of organic farming on butterfly species richness and abundance. J Appl Ecol 45:813–820

Rundlöf M, Nilsson H, Smith HG (2008b) Interacting effects of farming practice and landscape context on bumblebees. Biol Cons 141:417–426

Schneider C (2003) The influence of spatial scale on quantifying insect dispersal: an analysis of butterfly data. Ecol Entomol 28:252–256

Skinner B (1998) Moths of the British Isles. Viking, Penguin Books Ltd, London

Stokes J, Hand K (2002) The hedge tree handbook. The Tree Council, London

Swift MJ, Izac AMN, van Noordwijk M (2004) Biodiversity and ecosystem services in agricultural landscapes: are we asking the right question? Agric Ecosyst Environ 104:113–134

Taylor LR, French RA (1974) Effects of light trap design and illumination on samples of moths in an English woodland. Bull Entomol Res 63:583–594

Thomas K, Davis T, Parsons M (2006) Update on UK Biodiversity Action Plan moths-a summary for the year 2005. In: Thomas K, Davis T, Parsons M (eds) Lepidoptera Conservation Bulletin Number 7. Butterfly Conservation, Wareham, UK, pp 8–15

Townsend MC, Merckx T (2007) Pale Shining Brown Polia bombycina (Hufn.) (Lep.: Noctuidae) re-discovered in Oxfordshire in 2005 and 2006–a nationally significant population of a UK Biodiversity Action Plan Priority Species. Entomol Rec J Var 119:72–74

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecol Lett 8:857–874

Tscharntke T, Tylianakis JM, Wade MR, Wratten SD, Bengtsson J, Kleijn D (2007) Insect conservation in agricultural landscapes. In: Stewart AJA, New TR, Lewis OT (eds) Insect conservation biology. CABI, Wallingford, UK, pp 383–404

Vanbergen AJ, Woodcock BA, Watt AD, Niemelä J (2005) Effect of land-use heterogeneity on carabid communities at the landscape scale. Ecography 28:3–16

Verhulst J, Kleijn D, Berendse F (2007) Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. J Appl Ecol 44:70–80

Vickery JA, Bradbury RB, Henderson IG, Eaton MA, Grice PV (2004) The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. Biol Cons 119:19–39

Waring P (2002) Records of the Pale Shining Brown *Polia bombycina* (Hufn.) (Lep.: Noctuidae) in Oxfordshire, Hampshire and Wiltshire in the 1970s and 1980s. Entomol Rec J Var 114:128–129

Waring P (2008) Moths–wildlife reports. Brit Wild 20:55–57

Waring P, Townsend MC (2009) Field guide to the moths of Great Britain and Ireland, 2nd ed. British Wildlife Publishing, UK

Warren MS (1992) Butterfly populations. In: Dennis RLH (ed) The ecology of butterflies in Britain. Oxford University Press, UK, pp 73–92

Wilson A, Vickery J, Pendlebury C (2007) Agri-environment schemes as a tool for reversing declining populations of grassland waders: mixed benefits from environmentally sensitive areas in England. Biol Cons 136:128–135

Woiwod IP, Stewart AJA (1990) Butterflies and moths–Migration in the agricultural environment. In: Bunce RGH, Howard DC (eds) Species dispersal in agricultural habitats. Belhaven Press, London, UK, pp 189–202

The action for threatened moths project (undated) Butterfly Conservation http://www.butterfly-conservation.org/downloads/915/saving_britains_moths.html