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What type of hedgerows do Brown hairstreak (*Thecla betulae* L.) butterflies prefer? Implications for European agricultural landscape conservation

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Abstract. 1. Agricultural intensification is the main driver of global biodiversity loss. Agri-environment schemes (AES) are policy tools to counter this, but they need to be made more effective.

2. Here, we focus on the resource quality of hedgerows and woodland edges, which are widespread elements of most agricultural landscapes in Europe. We analyse a set of structural factors and assess their relative importance for the Brown hairstreak butterfly. This species suffered severe declines because of agricultural intensification that may be indicative of changes for other widespread insect species that use hedgerows as resources.

3. Egg-deposition preferences were assessed by comparing egg densities among hostplant sections in two study landscapes. All sections were systematically searched during four consecutive years, resulting in 745 observed eggs.

4. We demonstrate that the ground plan outline and aspect of landscape elements, the relative position within landscape elements, and the amount of young hostplant growth are particularly relevant in explaining observed egg densities, and we link their importance with the butterfly's behavioural biology.

5. Our study provides evidence that management focused on providing ample young growth, and transforming the landscape element ground plan outline from linear to a scalloped pattern, would benefit ectothermic species by providing more sheltered micro-climates when they use these structural resources for breeding, feeding and moving through typically exposed agricultural landscapes. We believe that integrating such management options within general AES would translate into effective, large-scale conservation measures for Brown hairstreaks and other species alike.

Key words. Agri-environment schemes, landscape ecology, landscape-scale conservation, micro-climate, *Prunus spinosa,* shelter.

Introduction

Agricultural land use intensification is the main driver of the severe loss of global biodiversity (Matson *et al*., 1997; Tilman *et al*., 2001; Tscharntke *et al*., 2005). Habitat loss, fragmentation, eutrophication and landscape homogenisation are the often inter-related processes associated with intensified farming practices (Wilson *et al*., 1999; Öckinger *et al*., 2006). Not only do these processes negatively affect populations of rare, and typically localised species, but even widespread habitat generalists are affected, resulting in often severe declines in abundance and distribution of once common species in a variety of taxonomic groups (Aebischer, 1991; Sotherton, 1998; Chamberlain *et al*., 2000; Donald *et al*., 2001; Benton *et al*., 2002; Conrad *et al*., 2006; Van Dyck *et al*., 2009). As a result, agriculture and biodiversity conservation have been traditionally viewed as incompatible, and ecologists and conservationists often focus on more or

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less pristine, *natural* sites (Tscharntke *et al*., 2005). However, recognition is increasing that such a conservation focus is of limited value (Bengtsson *et al*., 2003; Henle *et al*., 2008), basically for two reasons: (i) the agricultural land use footprint covers a large fraction of land area [2007 data: 73% UK; 45% EU; 38% world (FAOSTAT, 2009)] – this dominant footprint may well increase over time with a growing human population, and a higher per capita demand for food, meat, fibre and fuel (FAO, 1997; Eickhout *et al*., 2006; ESA, 2009); and (ii) at least in Europe, many species became adapted to widespread mosaics of extensively managed and dynamic landscapes of semi-natural habitats, resulting in many complex and highly diverse ecosystems (Bignal & McCracken, 2000; EEA, 2004; Firbank, 2005; Billeter *et al*., 2008).

These observations indicate that large-scale conservation measures in agricultural landscapes are bound to provide a critical contribution to the successful global conservation of biodiversity, and that there exists ample scope for reversing widespread biodiversity declines by addressing farmland conservation. As part of the EU Rural Development Policy (RDP), agri-environment schemes (AES) provide financial rewards to landowners for the delivery of biodiversity as a public good. By countering negative impacts of intensive agricultural systems through relatively simple measures, AES are considered to be the most realistic policy instruments to tackle the decline of biodiversity in agricultural landscapes (EEA, 2004). A significant budget of the EU Common Agricultural Policy (CAP) is dedicated to their implementation. There are, however, issues with their current cost-efficiency (Kleijn & Sutherland, 2003; Kleijn *et al*., 2004, 2006), as national governments do not fully use the environmental opportunities provided by the RDP (Boccaccio *et al*., 2009). Nevertheless, there is scope to significantly increase scheme delivery by (i) landscape-scale targeting in line with landscape contexts (Rundlöf *et al*., 2008; Kleijn *et al*., 2009), (ii) optimising uptake levels through better advice to farmers (Merckx *et al*., 2009a), and (iii) evidence-based implementation of effective scheme options, where payment levels are fine-tuned to the burden of commitments and to the expected biodiversity outcome (Boccaccio *et al*., 2009; Merckx *et al*., 2009a).

The key to successful conservation is that AES should provide sufficient levels of habitat heterogeneity and general resource quality, in line with habitat resource requirements of regional species sets (Pywell *et al*., 2006). General schemes can be adjusted to benefit species of specific conservation interest (e.g. Peach *et al*., 2001; Pinto *et al*., 2005), and it is indeed desirable to complement general AES with species-specific conservation measures (Kleijn *et al*., 2006; Reid *et al*., 2007; Tscharntke *et al*., 2007). However, the precise ecological requirements and risk status are not known for a majority of species, which makes it a challenge to design general AES that deliver improvements for this low-profile part of biodiversity as well (Merckx *et al*., 2010). To meet this challenge, a possible way out may well be to align AES options with the resource requirements of a sensitive multi-species set of *umbrella* species from the variety of trophic functional groups (e.g. microsymbionts, herbivores, decomposers, predators, pollinators, parasitoids; see also Roberge & Angelstam, 2004; Maes & Van Dyck, 2005; Woodcock *et al*., 2007; Liira *et al*., 2008; Smith *et al*., 2008).

Here, we focus on the resource requirements of a butterfly species – the Brown hairstreak *Thecla betulae* L. – that may function as indicators for many Lepidoptera and other flying insect species that use farmland hedgerows and woodland edges as breeding sites. The species is considered an indicator of well-managed hedgerow landscapes as it responds positively to sensitive hedgerow management (Bourn & Warren, 1998). The highly diverse and often abundant group of Lepidoptera plays an important role in farmland ecosystems as parasite hosts, prey, herbivores and pollinators (Fox *et al*., 2006). As a result, Lepidoptera are generally considered good indicators for terrestrial biodiversity (Luff & Woiwod, 1995; New, 2004; Thomas, 2005; van Swaay & van Strien, 2008). The group as a whole has undergone severe declines as a result of agricultural intensification and the accompanying erosion in resource quantity and quality (van Swaay & Warren, 1999; Conrad *et al*., 2006). The extent of the Europe-wide network of hedgerows has undergone a massive decline (Baudry *et al*., 2000). Furthermore, the resource quality of the remaining hedgerows has dropped dramatically with the switch from rotational management on a several-year cycle to abandonment or mechanised yearly trimming. As a result of trimming, mortality levels of the Brown hairstreak are so high (Thomas, 1974) that we believe that many hedgerows now function as population sinks or possibly even ecological traps. As a result of these losses in hedgerow quantity and quality, many local Brown hairstreak populations have become extinct, and the species has declined substantially throughout its range (Bourn & Warren, 1998; van Swaay & Warren, 1999). In the UK, for example, where the species' trends in distribution are best known, it was once fairly widespread across England and Wales, but it has undergone a severe decline in range (a loss of 43% of 10 km^2) between the periods 1970–1982 and 1995–2004 (Fox *et al*., 2007), in line with a net hedgerow loss estimated at 24% (i.e. 147.000 km) between 1984 and 2007 (Carey *et al*., 2008). Furthermore, the extent of the range contraction is likely to be an underestimate as (i) not many people were actively searching for it during the seventies, and (ii) the decline probably started directly after 1945 with the advent of agricultural intensification, in line with the 20% loss of managed hedgerows in Great-Britain between 1945 and 1970 (Pollard *et al*., 1974). Moreover, distribution declines in general considerably underestimate population losses (Thomas & Abery, 1995). As a result of this severe population loss, the species is now a priority species of the UK Biodiversity Action Plan (UK BAP, 2009).

Our aim is to determine hedgerow preferences of the Brown hairstreak. As such, we follow the resource-based habitat approach (Dennis *et al*., 2003, 2006; Vanreusel & Van Dyck, 2007; Vanreusel *et al*., 2007; Turlure *et al*., 2009; Turlure & Van Dyck, 2009), as the quality and isolation of habitat patches are key to determine where butterflies persist in fragmented landscapes (Thomas *et al*., 2001; see also Fleishman *et al*., 2002; WallisDeVries, 2004). Knowing the extent of the species' biotope, or even the precise amount of hedgerow within the agricultural biotope, is indeed not of direct practical relevance, as hedgerows are bound to differ considerably in terms of habitat quality. Rather, we try to look to the habitat *through the eyes* of individual Brown hairstreak butterflies. More specifically, we focus on the precise sites selected for egg-deposition, and we assess preferences by comparing densities of deposited eggs. The rationale behind the inclusion of the immature stages is that these often have more stringent habitat requirements (Van Dyck *et al*., 2000; Maes *et al*., 2004; Árnyas *et al*., 2006; Batáry *et al*., 2008; Eichel & Fartmann, 2008; Turlure *et al*., 2009). Furthermore, the immature stages are more susceptible to negative management than the adult stage, because of their lower mobility (Thomas, 1991; Bourn & Thomas, 2002; García-Barros & Fartmann, 2009). Also, immature stages are sometimes easier to detect than the adult stages, especially for lycaenids such as the Brown hairstreak, and surveys are not weather dependent. Nevertheless, the direct observation of both the movement pattern of female adults and their egg-laying preference might have given further insights (e.g. Kőrösi *et al*., 2008).

Our study into resource quality and preference of hedgerows and woodland edges as breeding sites for the Brown hairstreak is innovative in two ways: it is the first study on Brown hairstreak to be carried out on a landscape-scale, and by using the information-theoretic approach our study is able to assess the relative importance of a multitude of habitat variables. As such, we provide a model approach for other insects that use hedgerows as habitats, although different structural resources and other utility resources and conditions will be required to be studied in addition to those in this work. The study was carried out in two lowland agricultural landscapes, characteristic of many intensively managed landscapes in Europe. The applied landscape-scale and multi-year approach enables us to test the existing literature on oviposition preferences and to come up with practical conservation prescriptions for improved hedgerow management. Our findings can be translated into simple hedgerow management options for inclusion into widespread and general AES.

Methods

Study species

The Brown hairstreak (*Thecla betulae* L.) is a lycaenid butterfly that uses Prunus species, mostly Blackthorn (*Prunus spinosa* L.), as host plants. It is widely distributed across the Palaearctic between latitudes 40°N and 60°N (Thomas, 1974; Thomas & Emmet, 1989; Karsholt & Razowski, 1996) and is characteristic of landscapes containing extensive networks of hedgerows, woods and copses, generally on heavy soils where Blackthorn is abundant (Bourn & Warren, 1998). This univoltine species mainly flies in late July to September. It is an elusive butterfly that spends most of its life either canopy dwelling or hidden amongst hedgerows, and it occurs at relatively low densities – hence often described as a rare species – but it does so over wide areas of countryside (Thomas, 1974; Bourn & Warren, 1998). Nevertheless, intensive egg surveys reveal that egg density varies from year to year (M. Williams, pers. comm.) and that the egg distribution is quite variable and patchy. Relatively high egg densities do occur [e.g. 9 eggs per 10 m hedgerow (Fartmann & Timmermann, 2006); up to 6.7 eggs per 10 m hedgerow, occasionally coming across very dense patches of usually small *sucker* bushes with 6–14 eggs (D. Redhead, pers. comm.)]. Brown hairstreak butterflies rely mainly on aphid honeydew as a food source. Nectar-rich flowers are also visited, but mainly by females and when honeydew is less abundant (Thomas, 1974; Bourn & Warren, 1998). Both sexes congregate early in the flight season on large, bushy *master* trees to mate, after which females start to disperse over several kilometres as they deposit their matured eggs at suitable sites. As with all ectothermic insects, temperature and thermoregulation are key factors (Van Dyck & Wiklund, 2002), with female Brown hairstreaks basking extensively when sunlight is weak, and mainly flying on warm days (>20 °C) (Thomas, 1974), although there is evidence that they can fly at much lower temperatures (Middleton & Goodyear, 2008). Females feed in bouts, punctuated by long periods of egg-laying (5–15 eggs), when flying along woodland edges and hedgerows, periodically landing on a projecting leaf and examining a twig – which may take several minutes – until a single egg, occasionally up to six (D. Redhead, pers. comm.), is laid on bark, usually on young growth, typically at the base of a spine (Thomas & Lewington, 1991; Bourn & Warren, 1998; Fartmann & Timmermann, 2006). These white, bun-head sized eggs are the stage of the life cycle that is easiest to monitor, as they are relatively easy to find, contrasting conspicuously with the dark twigs through winter (Bourn & Warren, 1998; Fartmann & Timmermann, 2006). Female fecundity correlates with individual longevity, with a maximum observed value of 39 days and 147 eggs (Thomas, 1974). Larvae hatch in late April when leaf buds unfurl, feeding at dusk on tender leaf-tips. They pupate close to the ground, and are sometimes tended by ants (Stefanescu, 2000). Natural mortality during the egg, larval and pupal stages is very high (50–70%) and predators include invertebrates, birds and small mammals (Thomas, 1974; Bourn & Warren, 1998; D. Redhead, pers. comm.).

Study method and landscapes

All hedgerows and woodland edges (inside and outside woodland) containing Blackthorn in two study landscapes – Rillaar (Rr, 730 m in 15 km^2) and Walenbos (Ws, 1530 m in 18 km^2) in central Flanders (N-Belgium) were intensively searched during four consecutive winters (2001–2002 until 2004–2005), resulting in a total of 745 observations of Brown hairstreak eggs. The two landscapes are typical intensively managed lowland agricultural landscapes, with Blackthorn as an abundant species within the hedgerows and wood edges. Although both landscapes have a similar percentage of agricultural land (arable + pastures) (Rr 57%; Ws 55%), Ws has a much higher amount of wooded area (Rr 15%; Ws 33%) (Fig. 1). The studied linear landscape elements ($N_{\mathrm{total}} = 63$) varied in length between 1 and 250 m. They were each split up into sections of 10 m. However, sections were shorter for those cases where the total length of the landscape element was shorter than 10 m, or for most sections at the physical end of a landscape element. For the relatively small number of these shorter sections, the total number of eggs was first corrected for sections of 10 m length. For each section, we

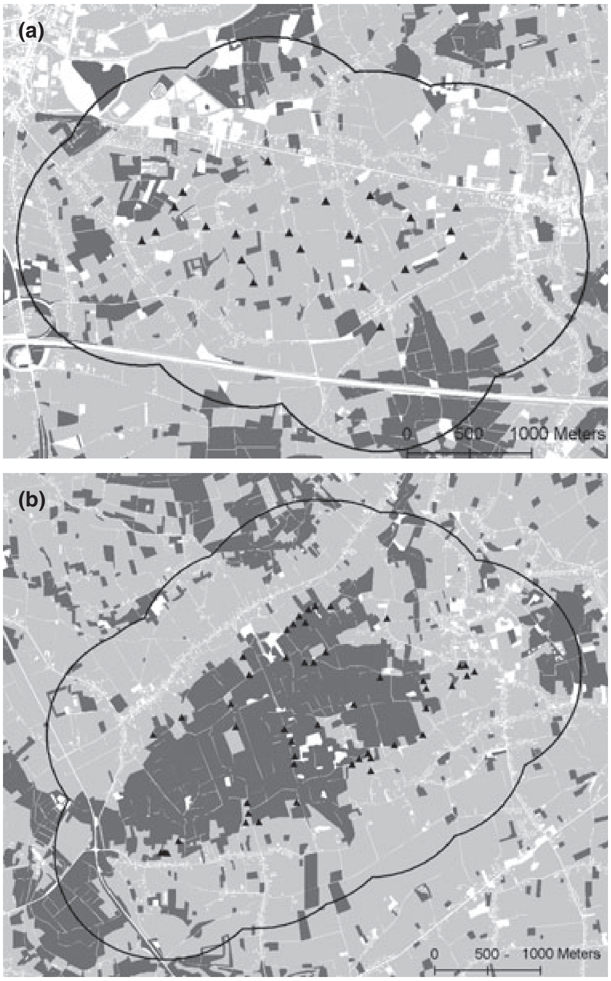

Fig. 1. Locations of surveyed landscape elements (▲) containing Blackthorn (*Prunus spinosa*) in two agricultural landscapes [(a) Rillaar, (b) Walenbos] differing in the amount of wooded biotopes (i.e. woodland and orchard; dark grey). Arable fields and pastures are shown in light grey; all other land use categories are shown in white. Land use percentages (see 'Methods') are calculated within a 1-km-buffer (solid black line) around the landscape elements.

assessed 12 variables (Table 1). Within each section, we intensively searched and systematically checked for eggs on all Blackthorn present, and for each located egg, we recorded the height above ground (in cm), the position (3 classes: fork; bud; bare bark), and whether it was laid singly or otherwise.

Statistical analyses

For each of these sections, and for each of the four consecutive years, the total number of sampled eggs was $\log_{10}$-transformed ($\log N + 1$) prior to using them as a dependent variable in the statistical analyses. The Information Theoretic (IT) approach (Burnham & Anderson, 2002; Richards, 2005) is well suited for analysing the types of data of this observational study that incorporates a multitude of causal factors (Whittingham *et al*., 2006). We used this approach to compare a large set of biologically plausible models that capture key elements of the system under study. The IT approach aspires to find the best of a suite of models, with the fewest parameters absolutely necessary (Johnson & Omland, 2004; Boyce *et al*., 2007). The additive models were generalised linear models (GLM) that contrast the effects of several variables (see before), i.e. fixed effects, on egg abundance. We followed a three-step approach. First, models were compared for a dataset ($N_{\text{sections}} = 673$) including all linear landscape elements (hedgerows + woodland edges). We excluded the variable *tree* as this variable was only assessed for hedgerows and not for woodland edges. All possible combinations of the retained fixed effects gave a total of 1023 different models. Secondly, we focused only on woodland edge sites ($N_{\text{sections}} = 335$), excluding both the variables *tree* (see before) and *distance to forest* (always 0), and 511 possible models were compared. Thirdly, we focused only on the hedgerows (away from woodland; $N_{\text{sections}} = 338$) and included both the variable *tree* and *distance to forest*. The least important variable (i.e. direct environment), judged from the first two steps, was now excluded so as to keep a reasonable total number of possible combinations ($n = 1023$). In every model, we included *year* (4 classes: 2001–2004) as a categorical blocking variable. The parameter *section* (25 classes) nested within *(h)edge(row)* (63 classes) 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; SAS 9.1), the models were sorted from lowest to highest AICc.

For each of the three steps, we defined a *confidence set* of models which have similar levels of substantial support from the data, and which have more support than all other models tested (Table 2). All models where the Akaike's difference with the top-ranked model was smaller than 2.0 were retained in this confidence set (see Burnham & Anderson, 2002, 2004; Richards, 2008), and these were the models – often *nested* within each other – considered to assess, and order, the variables in their ability to explain the abundance of Brown hairstreak eggs. Inference is then principally based upon the simplest models in the confidence set, whereas factors present in the more complex models (but absent from the simpler models) in the confidence set only receive marginal support. To specifically assess the direction and strength of effects, we always ran the best-ranked GLM to assess the variables they contained (Proc Mixed, SAS 9.1). Other, less-ranked models were run only to assess additional variables when these first appear within models going down the ranking within the confidence set. Degrees of freedom were calculated using the Satterthwaite option (Littell *et al*., 1996). Model residuals were normally distributed (Shapiro–Wilk). Differences of least squares means (DLSM) were calculated. To assess the effects of all additional variables, we also ran the highest ranked models including each specific variable.

Table 1. Overview of the total set of 12 tested explanatory variables, and their abbreviations, with regard to hedgerow sections. Classes are given for each of the 11 class variables.

Variable	Abbreviation	Classes
Area	Area	2: Rillaar (Rr); Walenbos (Ws)
Aspect	Asp	4: North; east; south; west
Direct environment	Envir	4: Arable; pasture; scrub; road
Distance (m) to nearest woodland (> 1 ha)	Dist	0 (continuous variable)
Ground plan outline	Dors	4: Scalloped; oval; boxed; with gaps
Frontal profile	Front	3: Pyramidal; straight; mushroom
Hedgerow tree	Tree	2: Absent; present
Height	Height	3: 0–1.5 m; 1.5–3 m; > 3 m
Relative position	Pos	3: End of hedge; within hedge; within hedgerow but end of Blackthorn patch
Sucker abundance	Suck	3: Absent-very little; present in small amounts; moderate to abundant
Width	Width	4: 0–1 m; 1–2 m; 2–3 m; > 3 m
Year	Year	4: 2001; 2002; 2003; 2004

Results

The overwhelming majority of the 745 observed eggs are laid singly (87.8%), rather than as part of a duplet (9.4%; 35 duplets) or triplet (2.8%; 7 triplets). Most eggs are positioned in a fork (82.0%), although some were observed at the base of a flower bud (8.5%) or on bare bark (9.5%). The mean height above ground was 1.26 ± 0.021 (SE) m, with the majority of eggs deposited between 0.5 and 2 m (0–0.5 m: 2.2%; 0.5–1 m: 31.7%; 1–1.5 m: 41.4%; 1.5–2 m: 15.8%; 2–2.5 m: 6.1%; 2.5–5.5 m: 2.8%). These observations are in line with those of Fartmann and Timmermann (2006) and Williams (2007).

Hedgerows and woodland edges

Egg abundance varied from year to year ($F_{3,\ 497} = 5.81$, $P = 0.0007$). Compared with the winter of 2001, abundance was 56% higher in 2002, and 69% higher in 2003 ($t_{481} = -3.45$, $P = 0.0006$; $t_{514} = -3.25$, $P = 0.0012$, respectively), whereas overall abundance in 2004 was similar to 2001 ($t_{503} = -0.99$, $P = 0.32$). A total of nine models were retained in the confidence set of models. Four variables – ground plan outline, relative position, aspect, and distance to nearest woodland – were invariably part of all these models. The most parsimonious model, containing these four variables only, was the second best-ranked model overall (Table 2a). Hence, out of the total set of factors, these four variables are most powerful in explaining the distribution of deposited Brown hairstreak eggs on Blackthorn sections.

Sections with scalloped borders had significantly more eggs than those with straight borders (i.e. 2.7, 4.2, and 4.6 times more than *gappy*, boxed, and oval ground plan outlines, respectively) ($F_{3,\ 274} = 27.45$, $P < 0.0001$). The three ground plan outlines with straight borders did not differ significantly in egg abundance ($0.09 < P < 0.82$). Relative position of a section within the (h)edge(row) had a significant overall effect ($F_{2,\ 234} = 6.89$, $P = 0.0012$). Significantly more eggs were deposited at the physical ends of the landscape elements than at the inner sections (+69%; $t_{215} = 3.70$, $P = 0.0003$). Numbers were higher, but not significantly so, at inner sections where whole stretches of Blackthorn terminated in stretches of other tree species ($P = 0.43$). North-facing sections had significantly fewer eggs than sections facing other directions ($F_{3,\ 233} = 5.24$, $P = 0.0016$; 47%, 51% and 54% less than south, east, and west facing sections, respectively). South, east and west facing sections did not differ in egg abundance ($0.18 < P < 0.60$). Egg numbers increased slightly, but highly significantly, with increasing distance from woodland (estimate: 0.060 ± 0.014; $t_{265} = 4.34$, $P < 0.0001$; $F_{1,\ 265} = 18.84$, $P < 0.0001$).

There were only slight trends for an overall effect of the amount of suckers, of the frontal profile, and of hedgerow width, on egg abundance ($F_{2,\ 433} = 2.46$, $P = 0.086$; $F_{2,\ 333} = 2.31$, $P = 0.10$; $F_{3,\ 262} = 2.02$, $P = 0.11$, respectively). Nevertheless, sections with moderate to abundant young growth had significantly more eggs (+39%) than sections with smaller amounts of suckers ($t_{365} = -1.98$, $P = 0.048$). Although no difference could be detected between the pyramidal and straight frontal profile ($t_{278} = -0.90$, $P = 0.37$), the latter profile was associated with more than twice the amount of eggs than the mushroom profile ($t_{402} = -2.04$, $P = 0.042$). Also, the widest hedgerows had between 39% and 63% more eggs than the three other hedgerow width classes ($0.017 < P < 0.18$), which hardly differed in egg abundance ($0.50 < P < 0.79$). There was no overall effect of hedgerow height ($F_{2,\ 260} = 1.73$, $P = 0.18$), although there is a trend for hedgerows between 1.5 and 3 m tall, and hedgerows higher than 3 m, to have more eggs than lower hedgerows (ca. 2.5 times as much; $t_{290} = -1.82$, $P = 0.070$; $t_{301} = -1.81$, $P = 0.072$, respectively). The study area and direct environment had no effect on egg abundance on the blackthorns present ($F_{1,\ 273} = 0.18$, $P = 0.67$; $F_{3,\ 216} = 0.32$, $P = 0.81$, respectively).

Table 2. Ranking of the best 10 statistical models, following the Information-Theoretic approach, for (a) both hedgerow and woodland edge sections, (b) only woodland edge sections, and (c) only hedgerow sections.

Ranking	Variables	AICc	Δ	Cumulative weight
(a) All				
1	Dors pos asp dist suck front	203.2	0.00	0.10
2	**Dors pos asp dist**	**203.6**	**0.39**	**0.18**
3	Dors pos asp dist suck	203.8	0.53	0.26
4	Dors pos asp dist front	204.1	0.90	0.33
5	Dors pos asp dist front width	204.2	0.95	0.39
6	Dors pos asp dist front width height	204.7	1.49	0.44
7	Dors pos asp dist front suck width	204.9	1.62	0.48
8	Dors pos asp dist front suck width height	205.1	1.84	0.52
9	Dors pos asp dist front suck area	205.2	1.97	0.56
10	*Dors pos asp dist front suck height*	*205.4*	*2.12*	*0.59*
(b) Woodland edges				
1	**Dors area suck**	**−22.4**	**0.00**	**0.32**
2	*Dors area suck front*	*−19.8*	*2.59*	*0.40*
3	*Dors area suck asp*	*−19.8*	*2.63*	*0.49*
4	*Dors area suck height*	*−18.9*	*3.53*	*0.54*
5	*Dors area suck pos*	*−18.5*	*3.94*	*0.59*
6	*Dors area*	*−18.5*	*3.95*	*0.63*
7	*Dors area suck front height*	*−17.1*	*5.33*	*0.65*
8	*Dors area suck front asp*	*−17.0*	*5.38*	*0.68*
9	*Dors area asp*	*−17.0*	*5.39*	*0.70*
10	*Dors area suck width*	*−16.8*	*5.64*	*0.72*
(c) Hedgerows				
1	Pos asp height dors width	175.4	0.00	0.08
2	**Pos asp height dors**	**175.6**	**0.19**	**0.15**
3	Pos asp height dors front	176.1	0.69	0.20
4	Pos asp height width	176.7	1.26	0.25
5	Pos asp height dors width area	176.9	1.47	0.28
6	Pos asp height dors tree	177.4	1.94	0.31
7	*Pos asp height dors width dist*	*177.4*	*2.04*	*0.34*
8	*Pos asp height dors width tree*	*177.6*	*2.22*	*0.37*
9	*Pos asp height dors dist*	*177.7*	*2.29*	*0.39*
10	*Pos asp height dors area*	*177.7*	*2.30*	*0.42*

Explanatory variables and AICc values are given for each model, as well as the Akaike's difference (Δ) with the top-ranked model, and the cumulative weight of these models starting with the top-ranked model. All models, where Δ was smaller than 2.0, were retained in the confidence set of models. Models that fell outside this confidence set are given in italic. The most parsimonious models are given in bold. Abbreviations refer to variables listed in Table 1.

Woodland edges

Egg abundance again varied from year to year ($F_{3,\,258} = 2.56$, $P = 0.055$). Only one model was retained in the confidence set, and three variables only – ground plan outline, sucker abundance, and area – were part of this best-ranked model (Table 2b). Hence, out of the total set of factors, these three variables are most powerful in explaining the distribution of deposited Brown hairstreak eggs on woodland edges. Again, sections with scalloped borders had significantly more eggs than those with the three ground plan outlines characterised by straight borders ($F_{3,\,180} = 27.11$, $P < 0.0001$), which amongst them did not differ significantly in egg abundance ($0.34 < P < 0.58$). There was also a similar, but now significant overall effect of the amount of suckers on egg abundance ($F_{2,\,223} = 4.02$, $P = 0.019$). Egg abundance was higher in Rr than in Ws ($F_{1,\,87} = 11.40$, $P = 0.0011$). Frontal profile, aspect, height, relative position, width, and direct environment had no significant effect on egg abundance ($F_{2,\,205} = 0.84$, $P = 0.43$; $F_{3,\,133} = 1.22$, $P = 0.30$; $F_{2,\,149} = 0.39$, $P = 0.68$; $F_{2,\,131} = 0.18$, $P = 0.83$; $F_{3,\,168} = 0.29$, $P = 0.83$; $F_{3,\,157} = 0.08$, $P = 0.97$, respectively), although numbers were again lowest at the mushroom profile, and at north-facing sections.

Hedgerows

Egg abundance similarly varied from year to year ($F_{3,\,321} = 6.76$, $P = 0.0002$), with higher numbers in 2002 (+26%), and especially in 2003 (+53%), which was almost significantly higher than the second best year ($t_{321} = -1.94$, $P = 0.053$). A total of six models were retained in the confidence set. Four variables – relative position, aspect, height, and ground plan outline – were part of all six models, except the latter variable, which was absent from only one of these models. Again, the most parsimonious model, containing these four variables only, was the second best-ranked model overall (Table 2c). Hence, out of the total set of factors, these four variables are most powerful in explaining the distribution of deposited Brown hairstreak eggs on hedgerows.

The relative position of a section had a significant overall effect ($F_{2,\,321} = 5.60$, $P = 0.0041$), with an increasing gradient in egg abundance from inner, full sections, over sections not fully covered by Blackthorn, to sections where the linear landscape elements come to a physical end. North-facing sections had significantly fewer eggs than sections facing other directions ($F_{3,\,321} = 7.57$, $P < 0.0001$; 14%, 27% and 40% less than south, east, and west facing sections, respectively). West-facing sections had higher egg loads than sections facing other directions ($0.0001 < P < 0.019$). Significantly more eggs were laid on hedgerows lower than 1.5 m than on taller hedgerows ($F_{2,\,321} = 4.44$, $P = 0.013$). There is a strong overall trend for an effect of ground plan outline ($F_{3,\,321} = 2.53$, $P = 0.057$), with sections characterised by scalloped borders having approximately twice the amount of eggs than those with straight borders (*t*-tests: $0.0072 < P < 0.011$). Again, the three ground plan outlines with straight borders did not differ significantly in egg abundance ($0.70 < P < 0.97$).

There was only a slight trend for an overall effect of width on egg abundance ($F_{3,\,321} = 2.19$, $P = 0.089$), with egg abundance decreasing with increasing section width. The frontal profile of sections, area, presence of hedgerow trees, distance to nearest woodland, and amount of suckers had no significant effect on egg abundance ($F_{2,\ 140} = 1.87$, $P = 0.16$; $F_{1,\ 169} = 0.74$, $P = 0.39$; $F_{1,\ 91.6} = 0.48$, $P = 0.49$; $F_{1,\ 111} = 0.20$, $P = 0.66$; $F_{2,\ 228} = 0.45$, $P = 0.64$, respectively), although numbers were again lowest at the mushroom profile, and in Ws, and highest at sections where young growth was most abundant.

Discussion

Habitat preference

By using the IT approach in analysing this landscape-scale, and multi-year study on habitat preferences of the Brown hairstreak butterfly, we managed to assess the relative importance of a set of factors relevant for Brown hairstreak populations. Overall, we demonstrate that four factors are particularly relevant in explaining observed egg densities on the butterfly's host plant: ground plan outline and aspect of landscape elements, relative position within landscape elements, and amount of young Blackthorn growth. These four factors can be linked with aspects of the butterfly's behavioural biology.

Hedgerows and woodland edges were characterised by consistently lower densities of Brown hairstreak eggs at their north-faced sides. This observation can either result from an egg-deposition strategy not to lay eggs at sites where the micro-climate might negatively affect larval growth, or adult butterflies may simply avoid flying in colder conditions. As an ectothermic insect, adult activity is limited by air temperature (Van Dyck & Wiklund, 2002; Merckx *et al*., 2006, 2008), with female Brown hairstreaks mainly flying on warm days (>20 °C), and basking extensively when sunlight is weak (Thomas, 1974; but see Middleton & Goodyear, 2008). As the Brown hairstreak's flight season in 2003 was considerably warmer than the three other flight seasons [mean ± SE of maximal day temperatures for July–September – 2003: 23.8 ± 0.5 vs. 2001: 21.3 ± 0.5; 2002: 21.1 ± 0.4; 2004: 22.0 ± 0.4; Royal Meteorological Institute of Belgium (KMI)], we attribute the higher overall abundance in the winter of 2003–2004 to better thermal flight conditions for the species. A result that can be interpreted along similar lines is that egg densities were higher at hedgerows and woodland edges when they had scalloped, rather than straight ground plan outlines. We believe that scalloped edges indeed result in more favourable micro-climatic conditions compared with straight-edged linear landscape elements (see also Warren & Fuller, 1990).

Sections with ample young growth were characterised by consistently higher egg densities than sections where young growth was restricted. This observation confirms the common knowledge among people carrying out Brown hairstreak distribution surveys that eggs are more likely to be found on young than on older growth (e.g. Williams, 2007). It also corroborates the study of Fartmann and Timmermann (2006) that showed a strong preference for young growth, which has been interpreted in terms of larval growth. However, it requires further evaluation whether this is either because of avoidance of inter-specific competition, or because of better host plant quality (i.e. nutrient quantity; Fartmann & Timmermann, 2006).

Relatively more eggs were laid at the physical ends of hedgerows. This pattern was repeated to a lesser extent at inner hedgerow sections, where such sections contained higher egg densities when Blackthorn was juxtaposed to sections of other tree species, compared with sections only containing Blackthorn. We interpret this pattern as being part of a bet-hedging strategy. Under natural conditions, and still to a certain extent in intensive agro-ecosystems, the host plant resources are distributed under fairly dynamic patterns of vegetation succession, as Blackthorn is associated with the early phases of grassland succession. It hence makes evolutionary sense for Brown hairstreaks to be relatively mobile, and to spread out eggs as wide as possible (i.e. several square kilometres). Nevertheless, finding new patches of suitable host plants within such a dynamic system is not guaranteed, or may take a long, costly and risky time, as host plants may be considerably spread out. It consequently makes sense to drop off a few extra eggs before leaving a suitable Blackthorn patch in search for the next patch. The egg-laying pattern may also result from individuals entering the Blackthorn patch, and having more eggs than usual to deposit after a long flight. The Brown hairstreak is indeed considered to be a fairly mobile butterfly species (Thomas, 1974). We similarly interpret the lack of an effect on egg numbers whether the direct environment was arable land, pasture, scrubland, or even a road, as typical for more mobile species. Indeed, one expects a predominant influence of local processes only on sedentary species, whereas more regional processes are expected to have an increasing influence with increasing mobility (Merckx *et al*., 2009b; Öckinger *et al*., 2009).

There was no effect of distance to forest on numbers of eggs laid on hedgerows. Hence, the overall slight increase with distance to forest may have been an artefact, simply because of lower numbers of eggs on woodland edges compared with hedgerows. Another artefact, we believe, was an observed effect of study area, with numbers of eggs higher at woodland edges in one study area than in the other. However, the number of woodland edge sections in one study area was only 3.6% of the total amount of woodland edge sections (12 in Rr; 323 in Ws), which could easily bias results. In the overall analysis, as well as the analysis restricted to hedgerows, egg numbers did not differ between the more wooded and the less wooded study areas (see 'Methods'). Hence, the absence of both an effect of distance to forest and of study area indicates that this rather mobile species seems to have adapted well to find its resources within agricultural landscapes.

The results with regard to an effect of the height of the linear landscape elements are not clear-cut. Although there was no significant overall effect of height on egg numbers, we observed a trend for higher numbers with increasing height of the host plant structures. However, the height of host plants near a woodland edge had no effect on observed egg numbers, and hedgerows lower than 1.5 m had significantly more eggs than taller hedgerows. We have no explanation for why lower hedgerows would be better than taller, other than chance. We interpret these opaque and counterintuitive results as an indication that other factors than height are more important in explaining observed egg numbers (see before). Other less important factors are the presence of hedgerow trees within the host plant structure, the width, and the frontal profile of this structure. Although the presence of hedgerow trees is known to be beneficial for species dependent on shelter in exposed agricultural landscapes (Merckx *et al.*, 2009a), and as master trees for the Brown hairstreak (Bourn & Warren, 1998), there was no impact on the number of Brown hairstreak eggs. Neither the width nor frontal profile of the host plant structure seemed to be important variables with regard to the observed number of eggs, although numbers were consistently lower on mushroom-shaped host plant structures.

Conservation implications

Our study demonstrates that effective conservation measures to increase population densities of the Brown hairstreak would need to focus on two factors. First, establishing a scalloped pattern may transform hedgerows and woodland edges into better habitat resource structures for this butterfly species, and most probably for many other insect species similarly constrained by micro-climatic conditions. Secondly, allowing young Blackthorn growth, either by grazing exclusion or by rotational coppice management, can have a major positive impact on egg density, with counts generally peaking 2- to 3 years after coppice management (Williams, 2007, D. Redhead and M. Oates, pers. comm.). In addition, the fairly high mobility of the species demands that these two measures be implemented at a landscape-scale, as each individual butterfly uses resources over a wide area. Moreover, as active flight is temperature-restricted for ectothermic insects, it would be beneficial to transform typically open, exposed countryside into landscapes where more and warmer habitat resources can be found. In general, such landscapes could be achieved by increasing the degree of habitat heterogeneity, which would increase the density of shelter-providing structures, while decreasing distances in between them. Such more hospitable landscapes are likely to increase individual fitness, as the most obvious factor limiting the amount of eggs laid is the amount of time suitable for active flight.

Another important factor that needs to go hand-in-hand with improving the landscape infrastructure is an improved management of host plant resources. On top of the high natural mortality of 50–70%, annual mechanic cutting of hedgerows considerably increases mortality, removing up to 80% of the eggs laid (Thomas, 1974), or even more (95–99%; D. Redhead; M. Williams, pers. comm.), as eggs are almost invariably laid on recent growth, and hence the very outer surface of hedgerows and woodland edges, rather than deep within these structures (own observation). Modelling the impact of differing hedgerow-cutting regimes confirmed that a scenario of annual cutting of all hedgerows and woodland edges would cause a population to go extinct in only 3 years (J.A. Thomas, unpubl. in Bourn & Warren, 1998). The longest surviving populations in these models were those on hedgerows that were cut on longer rotations such as a most practical 3-year rotation with a third of hedgerows cut each winter (Bourn & Warren, 1998). Brown hairstreaks also seem to respond well to rotational scrub coppicing (Fartmann & Timmermann, 2006; M. Oates; D. Redhead, pers. comm.). Such a practice drastically rejuvenates Blackthorn scrub, and provides young, vigorous growth, but should not be carried out overzealously so as to keep a sufficient amount of shelter (Bourn & Warren, 1998). Changes in woodland management moving away from coppicing are also likely to have had a negative impact because of a lower frequency of sunny open areas within woodland where blackthorn might flourish and provide ideal laying conditions (Williams, 2007).

We have anecdotal evidence from a closely monitored population in Oxfordshire that the recent, high uptake of AES options (including rotational hedgerow management) may have resulted in the recent slight range expansion of the Brown hairstreak (D. Redhead, unpubl. data). We believe that optimised hedgerow management, ideally within optimised general AES (see also Williams, 2008) targeted at the landscape-scale, has the potential to make a significant contribution to reversing general declines in farmland biodiversity, not only for the Brown hairstreak, but for many species associated with this prominent and abundant landscape feature within agricultural landscapes (Dover, 1996; Dover *et al.*, 1997; Dover & Sparks, 2000).

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