



# Determining the long-term habitat preferences of the Duke of Burgundy butterfly, *Hamearis lucina*, on a chalk grassland reserve in the UK

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## Abstract

The Duke of Burgundy butterfly has undergone considerable range contractions across Europe and since the 1970s has lost around 84% of its former distribution in the UK. Despite its endangered status, the butterfly is understudied, with few papers directly investigating its habitat requirements. This limited research effort focusses on the larval life stage, with relatively little being known about the adults of the species. In this study, we investigated the habitat usage of both adults and larvae of the Duke of Burgundy. Fieldwork was carried out in association with the Bedfordshire, Cambridgeshire and Northamptonshire (BCN) Wildlife Trust on their Totternhoe Quarry Reserve in Bedfordshire. Using data collected over the course of a decade, we performed the first long term distribution analysis of the species and we identified habitat attributes associated with long-standing abundance hotspots of both adults and larvae on the reserve. We found both life stages to be conserved in their range, remaining in the same small areas of Totternhoe Quarry year on year, with adults often being more restricted in their distribution than larvae. Sheltered locations were important for both life stages, but small differences in habitat preference, such as slope and aspect, were also identified. These results emphasise the need to target management towards both life stages of the Duke of Burgundy, as supporting the larvae alone may not result in suitable environmental conditions for the adults.

**Keywords** Butterfly · Calcareous grassland · Distribution analysis · Duke of Burgundy · Habitat management · *Hamearis lucina* · Insect conservation

## Introduction

Butterflies are experiencing widespread global declines (Warren 1993; Cowley et al. 1999; Bourn and Thomas 2002; Beyer and Schultz 2010; Fox et al. 2011) and in the UK, 76% of native and regular migrant butterfly species have fallen in either abundance or occurrence over the last four decades (Fox et al. 2015). Much of this reduction is thought to be

due to agricultural intensification, relaxation of traditional management, and land abandonment, causing the loss and fragmentation of suitable habitats (Fartmann et al. 2013; Helbing et al. 2015). However, even on actively managed reserves declines are still taking place (Davies et al. 2007) and it is essential that optimal management plans are implemented to make best use of these isolated sites (Goodenough and Sharp 2016).

A complex life history results in many butterfly species requiring a wide range of resources, with adults, larvae and pupae often having a different set of specific requirements (Beyer and Schultz 2010). A reliance on so many habitat features means that even a small environmental change can have a large effect on butterfly populations. As a result butterflies are commonly used as biological indicators for habitat deterioration (Oostermeijer and Van Swaay 1998; Brown and Freitas 2000; Fleishman et al. 2005; Maes and Van Dyck 2005; Beyer and Schultz 2010). In order to stem butterfly declines, it is essential that research is carried out to investigate the specific habitat requirements of species

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throughout their lifecycle. Only then can effective management techniques be implemented to better conserve butterfly populations and associated communities (Kirtley 1995; Anthes et al. 2003; Turner et al. 2009; Henry and Schultz 2013).

The Duke of Burgundy butterfly (*Hamearis lucina* L. 1758) has undergone considerable range contractions across Europe (Fartmann 2006; Anthes et al. 2008) and since the 1970s has lost around 84% of its former UK distribution (Fox et al. 2015). It is listed as a species of principle importance under Section 41 of the Natural Environment and Rural Communities Act (NERC 2006) and is the only European representative of the ‘metalmark’ family, Riodinidae (Oates 2000; Hall 2008), making it of particular biogeographic and evolutionary significance (Leon-Cortes et al. 2003). This endemic European species has a Western Palearctic distribution (Bourn and Warren 1998), spreading east from Spain and the United Kingdom towards Sweden and the Balkan Peninsula (Oates 2000). Historically, populations in the UK reached as far north as Scotland (Kirtley 1995), but now only a few northern populations remain (Oates 2000; Ellis et al. 2011). Southern strongholds exist in Wiltshire, Hampshire and the Chilterns as well as on the limestone of the Cotswolds. However, evidence suggests that even here the distribution of *H. lucina* is becoming more restricted (Noake et al. 2008). From 2008 to 2012 *H. lucina* was only recorded from 160 sites across the UK. Furthermore, in most locations only very small colonies were found, with 65% having fewer than five adults observed during weekly transect counts (Jones et al. 2012). This, coupled with the fact that the *H. lucina* is thought to have a poor dispersal ability (Kirtley 1995; Fartmann 2006; Anthes et al. 2008), means that many colonies are under threat of permanent extinction (Kirtley 1997).

*Hamearis lucina* is found in two main habitat types across the UK: chalk or limestone grasslands, with extensive scrub or topographical shelter, and coppiced woodland sites, with plentiful clearings, rides or glades (Ellis et al. 2011). The species breeds on plants of the genus *Primula* (Oates 2000), with Cowslip *Primula veris*, Primrose *Primula vulgaris*, and their hybrid False Oxlip *Primula elatior* (Fartmann 2006), all being used on different sites. Historical accounts from the late nineteenth and early twentieth century indicate that *H. lucina* was almost exclusively a woodland species (Newman 1871; Frohawk 1934). However, the butterfly began spreading to calcareous grasslands after the First World War and then more rapidly from the 1950s onwards, as loss of rabbit populations, due to myxomatosis, and the relaxation of traditional grazing created more scrubby, sheltered grassland environments (Emmet and Heath 1989; Oates 2000). At the same time, a cessation of traditional woodland management and a shift from coppicing deciduous forests to harvesting timber from dense conifer plantations, lead

to open woodland areas becoming increasingly enclosed (Sparks et al. 1994; Oates 2000; Noake et al. 2008). As *Primula* foodplants were shaded out from woodland sites (Kirtley 1995), *H. lucina* is thought to have moved to the new scrubby grassland habitats (Butterflies Under Threat Team 1986; Fartmann 2006). Oates (2000) estimated that some 98% of woodland populations were lost from 1950 to 1990 and only 32 woodland sites are now thought to support *H. lucina* in Britain (Jones et al. 2012).

Despite its endangered status and unique nature, there are very few in depth studies focussing on the ecology and habitat requirements of *H. lucina*; either in the UK (Sparks et al. 1994; Oates 2000; Turner et al. 2009; Goodenough and Sharp 2016) or in continental Europe (Fartmann 2006; Anthes et al. 2008). Of this limited research, most has been focussed on larval habitat requirements and ovipositional cues, with females appearing to have specific requirements of host plant size, surrounding vegetation structure and associated microclimate when choosing where to lay their eggs (Sparks et al. 1994; Fartmann 2006; Anthes et al. 2008; Turner et al. 2009). As with most species of butterfly the habitat requirements of adult *H. lucina* have traditionally been considered broader and less important than those of the relatively immobile larvae (Bourn and Warren 1998; Thomas et al. 2011). However, Turner et al. (2009) found evidence that adults also utilise specific habitat features, of which shelter seems to be important for favouring sexual activity in poor weather conditions. In order to tailor conservation management for *H. lucina*, it is important that the habitat requirements for all of its life stages are understood, even if management for the larvae remains the key method of intervention (Turner et al. 2009; Thomas et al. 2011). It is also essential to understand whether these habitat requirements change over time depending on weather conditions, as this will help to inform conservation management under a shifting climate, which has the potential to alter the realised niche and habitable range of the species (Anthes et al. 2008).

Here, we perform the first long-term distribution analysis for *H. lucina* (but see Anthes et al. 2008) and examine the fine scale habitat use of larvae and adult butterflies from a single population at Totternhoe Quarry Reserve, Bedfordshire. With this information, we aim to determine: (1) whether the distribution of *H. lucina* is clustered on site; (2) if the distributions of the adult and larval life stages differ; (3) whether hotspots of high abundance remain in the same location year on year and, if so, (4) which habitat attributes are associated with them.

## Methods

### Study site

Totternhoe Quarry, Bedfordshire, is an unimproved chalk grassland reserve managed by the Bedfordshire, Cambridgeshire and Northamptonshire (BCN) Wildlife Trust (BCN Wildlife Trust, Totternhoe 2017). The original site used for this project spans 13.6 hectares (English Nature 1993), but additional areas have gradually been acquired from the surrounding agricultural land (BCN Wildlife Trust, About us 2017). Totternhoe Quarry supports several endangered plant and invertebrate species, including a good population of *H. lucina* (Proud 2000). Due to an extensive history of quarrying, the reserve has a very uneven topography with a diverse range of slopes of all aspects (Proud 2000). This variability allows easy comparisons of habitat preferences across a small area (Noake et al. 2008).

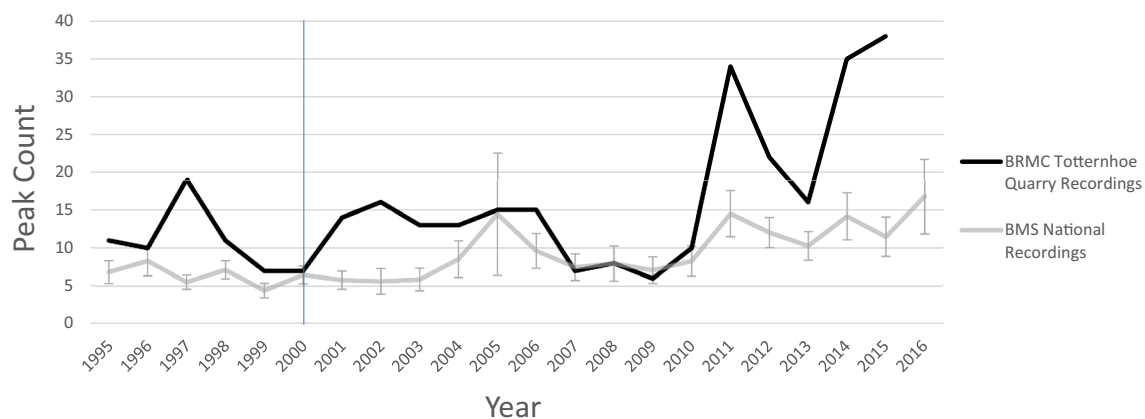
The population of *H. lucina* at Totternhoe Quarry sits at the eastern edge of the species range in the Chiltern Hills, with two larger populations existing nearby at Whipsnade Downs and Ivinghoe Beacon, creating a network of sites spanning just over 5 km. This important network is significant in having three substantial populations (Jones et al. 2012). However, dispersal over this distance is seen infrequently in *H. lucina* (Bourn and Warren 1998), and the extent to which these populations are linked is worthy of further study. One or two individuals are also occasionally spotted at Totternhoe Knolls and Sewel Cutting, two reserves which are within a kilometre of Totternhoe Quarry. However, individuals are not seen at these

sites every year and are thought to disperse here from the Quarry (Jones et al. 2012).

### Totternhoe Quarry *H. lucina* population

Peak counts give the highest number of individuals observed in 1 day at a reserve for a given year. These allow for a simple comparison of relative population sizes where complete sets of annual indices are not available. Peak counts of adult *H. lucina* at Totternhoe Quarry Reserve were acquired from the Bedfordshire and Luton Biodiversity Recording and Monitoring Centre (BRMC) from 1995 to 2015 (Bedfordshire and Luton BRMC, Data Requests 2017). Data collection by the BRMC involved walking formal transects across the reserve during the flight season of *H. lucina* and recording all individual butterflies encountered. The highest daily count each year was then used for analysis. National data on *H. lucina* peak counts were obtained from the UK Butterfly Monitoring Scheme for all monitored sites across the country from 1995 to 2016 (UKBMS, Obtaining Data 2017). These data were also gathered by walking set transect lines or, if sites lacked set transect routes, by performing a single timed count during peak flight season. Single day ‘reduced effort’ counts are used by the UK Butterfly Monitoring Scheme (UKBMS) to record relative densities of habitat specialist species, especially in more remote parts of the UK where frequent transect walks are not possible (UKBMS, Methods 2017). We calculated a mean peak count for each year, using all sites that *H. lucina* was observed on, to assess how the overall population trend in the UK has changed over time and to compare this to the population at Totternhoe Quarry.

Since the purchase of Totternhoe Quarry by the BCN Wildlife Trust in the year 2000 (Proud 2000) the *H. lucina*



**Fig. 1** Yearly peak counts of adult *H. lucina* for one day of observations at Totternhoe Quarry Reserve and averaged across all reserves in the UK with available data, from 1995 to 2016. The Totternhoe Quarry recordings display peak counts obtained from the Bedford-

shire and Luton Biodiversity Recording and Monitoring Centre (BRMC). The average national peak counts were calculated using data obtained from the UK Butterfly Monitoring Scheme (BMS) and are displayed  $\pm$  one standard error

population hosted on site has increased, with linear regression revealing a significant upward trend in population size from 2000 to 2015 ( $n = 16$ ,  $F_{1,14} = 8.933$ ,  $p = 0.010$ ) (Fig. 1). This population rise seems to have been mirrored on other sites throughout the UK, with peak counts averaged across the country also showing a significant increase over this time period ( $n = 16$ ,  $F_{1,14} = 10.59$ ,  $p = 0.006$ ) (Fig. 1). Together, these data sets support the findings of Fox et al. (2015) who found that the large declines of *H. lucina* across the UK since the 1970s have recently slowed or may even have begun reversing.

### Mapping the reserve

Over the course of November 2016 to January 2017 the entire 13.6 hectares of Totternhoe Quarry Reserve were mapped into areas of homogenous habitat. The smallest single area mapped covered 2.5 m<sup>2</sup>. A Trimble GeoExplorer 2008 Series Geographic Positioning System (GPS) Handheld Recorder, running Fastmap Mobile 7, and Geobeacon Receiver were used to record habitat boundaries. The perimeter of each habitat area was walked to record the GPS boundary locations and the key habitat features of each area were noted. Following Turner et al. (2009), vegetation type for each area was listed as either exposed ground or chalk, short grass (below 10 cm in height), tall grass (above 10 cm), encroaching scrub (25–75% area covered by scrub) or dense scrub (> 75% of the area was covered by scrub). The slope of each habitat polygon was judged by eye and assigned to one of the following categories: 10° or less, 11°–20°, 21°–30°, 31°–40°, or 41° or more. Aspect of the slope was then recorded. Finally, each area was given a value to describe its degree of shelter. From the centre of each habitat polygon, distance to a 1 m high barrier was paced out in the directions of each of the four points of the compass. Barriers commonly included scrubby borders or steep slope faces. The mean value of the four distances was then recorded and placed into a category: 5 m or less, 6–10 m, 11–15 m, 16–20 m or more than 20 m. Using ArcMap Geographic Information System (GIS) software (ArcMap 2017), the recorded shape files were then uploaded and stitched together to give a full GPS map of Totternhoe Quarry Reserve for 2016. Another map of Totternhoe Quarry from 2009 was obtained from the Wildlife Trust, providing a historical record of habitat types on the reserve. This used exactly the same habitat categories as the map produced in 2016 but lacked polygon shelter values.

### Butterfly GPS data collection

*Hamearis lucina* were recorded at Totternhoe Quarry Reserve from 2006 to 2017. For adult butterflies, 2 years of data, 2010 and 2011, are missing from this 12-year time

series. Surveying for this life stage involved systematically searching the entire reserve during the butterfly's flight period (May–June). The sex of adult butterflies was recorded whenever possible, but due to males being more active fliers (Bourn and Warren 1998), the majority of adults observed (78%) were male. Therefore, in this study we primarily analysed the habitat preferences of the male butterflies and their territory locations.

For *H. lucina* larvae, 5 years of distribution data are missing from the 12-year study period: 2010–2011, 2013–2014 and 2017. Larvae are nocturnal and hard to find, however, they create a distinctive peppering and panelling pattern as they feed (Oates 2000; Turner et al. 2009). Therefore, larval distribution data was gathered indirectly, by systematically surveying Totternhoe Quarry for the diagnostic foodplant damage at the end of the larval period (July–September) each year. For a larval location to be recorded, *Primula* damage had to be concentrated in the centre of leaves, with the majority of veins, midribs and leaf edges remaining intact. A progression of increasing hole sizes across the plant, produced as larvae grew and moved away from the leaf they were oviposited on, also had to be present. In 2006 additional recordings were made where every single *Primula* plant on the reserve was mapped, providing a record of the distribution of potential foodplants.

When an adult *H. lucina* or damaged foodplant was observed, its GPS location was recorded using a Garmin GPSMAP64s handheld navigator or noted down on a map of the reserve. Data were gathered with the help of Wildlife Trust volunteers, employees and several university students, who carried out projects on the butterfly with the Wildlife Trust (BCN Wildlife Trust Ecology Group Projects 2017). Excluding areas of dense scrub, the entire Totternhoe Quarry reserve was surveyed each year. However, over the course of this extended study period, the individuals recording data and the intensity with which the site was searched varied. Therefore, the distribution data reported here is not an account of the entire population on the reserve, but is instead representative of the relative density and distribution of *H. lucina*. Across the 12 years of study some areas of Totternhoe Quarry have consistently remained as dense scrub and have never been surveyed.

### Distribution analysis

ArcGIS 10.4.1 for Desktop (ArcMap 2017) was used for all mapping as well as clustering and hotspot analyses. R version 3.4.0, running the base package, was then used to compare habitat attribute values of hotspot locations with those of expected values.

Separate hotspot distribution analyses were run on male and female butterflies, using the Getis-Ord Gi\* statistic (Ord and Getis 1995), to assess whether there was a detectable



difference in distribution between the sexes and, therefore, whether these should be treated separately in later analyses. The distribution of female hotspots was found to overlap very closely with those of the males. Therefore, sexes were not differentiated between for subsequent distribution analyses.

Unsurveyed sections of dense scrub were excluded from all analyses, with the remaining area being used to analyse the clustering of observed GPS points. Separate GPS data layers of adult and larval distributions were created for each year of the study but to ensure sufficient survey effort only layers containing 30 or more GPS points were used for further analysis. Using Ripley's K function (Dixon 2002), observed distributions were compared to that of 100 iterations of an equal number of randomly generated points to assess whether butterfly distributions were more clustered than would be expected by chance. Clustering was analysed at 50 and 5 m scales, to assess whether habitat polygons (50 m scale) and finer scale habitat differences (5 m scale) have significant effects on *H. lucina* distributions. When fewer than 30 GPS points were present, an individual cluster analysis could not be carried out for that year. However, these data layers were incorporated into two overall analyses, with all 12 years of data points, to investigate cumulative adult and larval distributions. Finally, Ripley's K function was again used to perform cluster analyses at 5 and 50 m scales (Dixon 2002) on the distribution data set for all *Primula* plants on site in 2006 to assess how clumped foodplants were on the reserve.

The GPS map of the reserve was then used to assess whether clusters shifted location year on year or remained consistent in their distribution. Again, excluding areas of dense scrub, the reserve was divided into a 5 × 5 m grid, producing square polygons of a size just over the proposed limit of larval movement (Oates 2000). Optimised hotspot analyses, run using the Getis-Ord  $G_i^*$  statistic (Ord and Getis 1995), were undertaken for each data layer with sufficient survey effort (30 GPS points), to identify which squares in the grid and thereby which areas of the reserve were statistically significant hotspots for *H. lucina* distributions. Comparisons of *H. lucina* hotspot distribution maps were then carried out in pairs, analysing differences that occurred over time and between life stages.

Differences were assessed in a number of steps. Firstly, the number of grid squares that were significant hotspots to a 99% confidence level were counted. Out of the two distributions being compared, the record with the fewest hotspot grid squares was selected and the percentage of its hotspots overlapping with the other distribution was calculated. This helped account for the unequal survey effort between years as it showed whether smaller hotspots, produced from years with reduced survey effort, were contained within larger hotspot regions from years with more extensive surveys.

Overlap was again measured at two scales with the percentage of hotspots within 5 and 50 m of one another being counted. A distance of 50 m is larger than the mean length or width of all recorded habitat polygons, so beyond this distance hotspots are likely to be in different habitat types. All possible pairings of years for adult and larval hotspot distributions were first compared separately. Then, for years where both adult and larval location data had been recorded, the differences between the distributions of the two life stages were examined to assess whether the distribution of adults in the spring was associated with the distribution of larvae in the summer. The hotspots (Ord and Getis 1995) produced from the cumulative adult and larval distributions, created using data from all years of the study, were also compared. Finally, a separate hotspot analysis was undertaken using the distribution data set for all *Primula* plants on site in 2006 to highlight the locations at Totternhoe Quarry where foodplant abundance was especially high. By overlaying the 2006 larval distribution map on this, the percentage of larval-damaged foodplants within these hotspots was calculated, to assess whether more larvae were present in *Primula*-rich areas.

The observed percentage overlaps were compared to expected values derived from randomly positioning pairs of hotspot distributions across the GPS map of Totternhoe Quarry. Hotspots were generated for a *H. lucina* distribution with a clustering value 'K' as close as possible to the mean value observed for the yearly adult and larval distributions. 100 pairs of this hotspot distribution were then randomly generated in different positions across the gridded area of the reserve and their percentage overlaps within 5 and 50 m were calculated. The interquartile ranges from the percentage overlaps of the 100 iterations were calculated to give limits for high and low levels of overlap.

Overlaying the hotspot distributions on a GPS map of the reserve and using the recorded habitat polygon data then allowed the habitat attributes of the areas most commonly used by *H. lucina* to be determined. For distributions gathered from years 2006 to 2012, the map of Totternhoe Quarry produced in 2009 was used to determine habitat information. For distributions gathered from years 2013 to 2017, the 2016 map was used. The vegetation type, slope, aspect and shelter of all hotspot grid squares were recorded. These values were then compared with expected frequencies, derived from the proportional areas of each habitat type recorded on the GPS maps of Totternhoe Quarry. A series of one-dimensional Chi-squared tests were used to analyse habitat usage of the adults and larvae separately. In order to reduce the number of categories with expected values of <5, hotspot habitat attributes across all years of the study were analysed together. As shelter values were only recorded for the 2016 map of the reserve, hotspot shelter values were only tallied for 2013 onwards. Chi-squared tests of independence

were also used between each pair of habitat variables, using the data from all hotspot locations, to assess whether habitat variables were associated across the reserve.

## Results

### Reserve mapping

The 2016 GPS habitat map of Totternhoe Quarry (Fig. 2) shows the reserve to be largely dominated by dense scrub, with this habitat type making up 58% of the overall reserve area. The remainder of Totternhoe Quarry consists of: 11% encroaching scrub, 14% long grass, 14% short grass and 3% exposed ground or chalk. The percentage area containing dense and encroaching scrub has increased marginally since 2009 from 64% (Turner et al. 2009) to 69%.

### Distribution clusters

During the 12 year study 413 *H. lucina* adults and 609 larval damaged foodplants were recorded and both life stages were found to be unevenly distributed across Totternhoe Quarry. This is true for cumulative distributions summed across all years of the study (Fig. 3) and for each individual year (Fig. 4). For every year examined separately and the cumulative distributions, all observed K values were higher than that of any of the 100 permutations of random GPS points

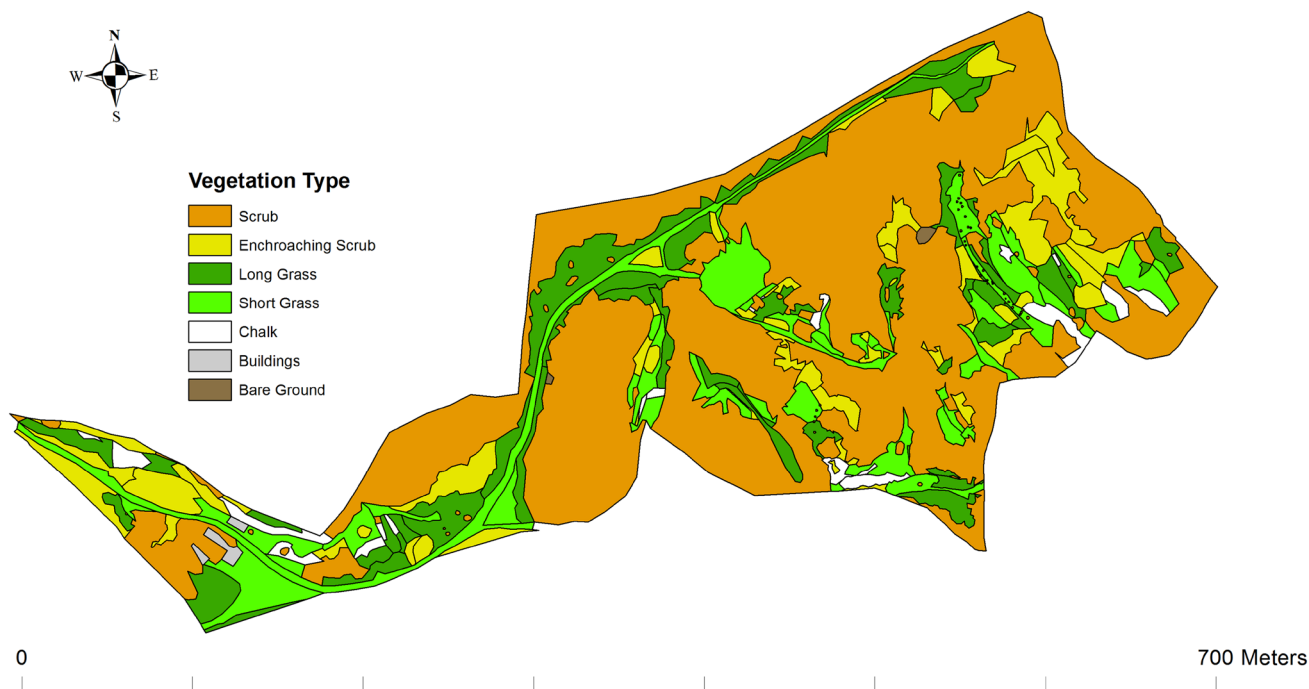
(Figs. 3, 4). This indicates that at both the 5 and 50 m scale, the distributions of adults and larvae are more clustered than would be expected by chance.

### Distribution shifts year on year

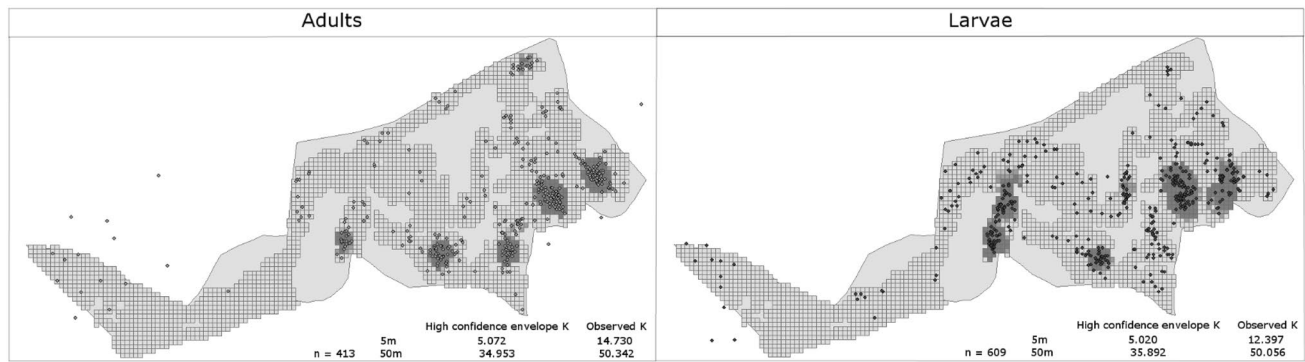
The 100 iterations of random hotspot pairs generated a distribution of expected overlaps with an upper quartile of 0 and 55% at scales of 5 and 50 m respectively. Therefore, the vast majority of observed distributions show large overlaps compared to that which would be expected from random chance (Table 1). Hotspot locations for both adults and larvae appear to be fairly consistent over time, whilst still shifting away from exactly the same location. Both life stages also occupy similar locations on the reserve to one another and comparison of the two cumulative distributions, for location data summed across all 12 years of the study, shows that this overlap in habitat use by the two life stages is consistent over time (Tables 1, 2).

### Potential factors influencing *H. lucina* microdistribution

As with the *H. lucina* butterflies themselves, their *Primula* foodplants were more clumped on site than would be expected with a random distribution. For the 8819 plants observed in 2006, K values of 11.438 and 50.450 were gained for clustering analyses performed at a scale of 5 and



**Fig. 2** Habitat polygon map of Totternhoe Quarry Reserve for winter 2016



**Fig. 3** Cumulative hotspot distribution maps for *H. lucina* adults (78% male) and larvae with 12 years of distribution data displayed together from 2006 to 2017. The gridded area covers the parts of the reserve that were surveyed for *H. lucina* during the course of the study with the rest being dense scrub. Dots represent the locations of

adult or larval *H. lucina* sightings with dark grid squares representing areas that are significant hotspots to a 99% confidence level. Clustering value 'K' is also given for each distribution and compared to that of the highest 'K' value derived from 100 permutations of an equal number of randomly generated points

50 m respectively. These were higher than that of any of the 100 permutations of an equal number of random GPS points, the highest of which was 4.867 for clustering at 5 m and 37.284 for clustering at 50. However, only 30 out of the 84 larval damaged *Primula* foodplants at Totternhoe Quarry in 2006 were located in the distribution hotspots created from the entire *Primula* population present on site that year (Fig. 5).

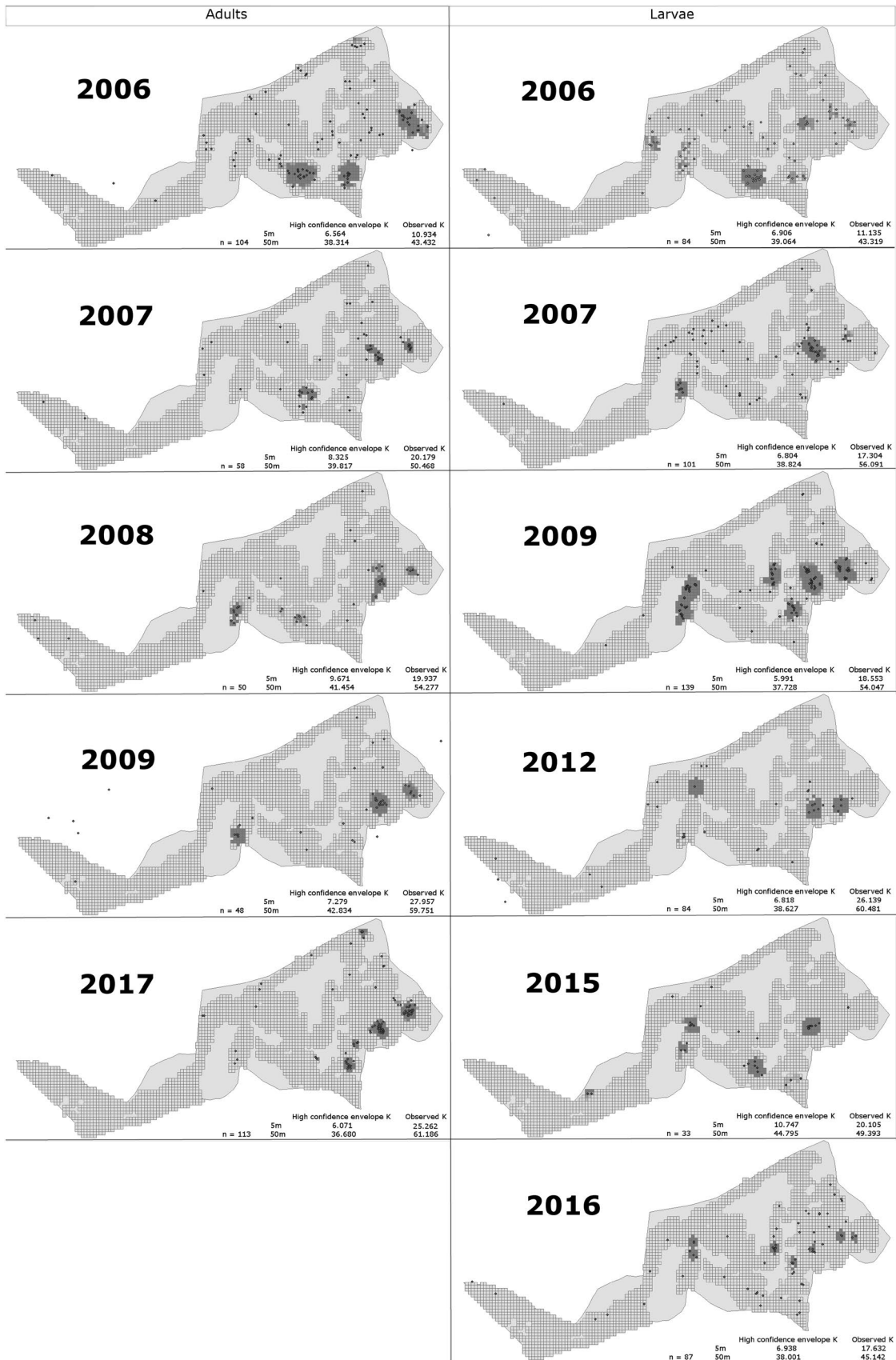
### Habitat attributes determining distribution

All four of the habitat attributes measured at Totternhoe Quarry differed significantly between hotspot and control areas (Fig. 6). Both adults and larvae used more sheltered locations on site, with adults being most commonly found in areas with the very highest shelter values (average distance to a barrier  $\leq 5$  m) and larvae being more common in both of the two highest shelter categories (average distance to a barrier  $\leq 10$  or  $\leq 5$  m) (Fig. 6). Similarly, both life stages avoided the very flattest areas on the reserve ( $< 10^\circ$ ) more than would be expected by chance (Fig. 6). Adults were found to have the strongest preference for south westerly aspects and were also found in quite large numbers on east and west facing slopes. Larvae were also common on east facing slopes, but were found less on south westerly aspects than would be expected by chance and were instead found in larger numbers on north easterly slopes (Fig. 6). The abundance of both life stages in short grass was higher than expected and they were less common in all other vegetation types (Fig. 6). None of the habitat attributes measured in this study were independent of one another (Table 3). For example, exposed chalk was far more likely to be found on steep slopes and areas with steep slopes were more likely to have higher shelter values.

### Discussion

This study shows that both larvae and adults of *H. lucina* appear to have exacting habitat requirements, which consistently restrict their distribution, so that populations occupy the same small areas of a reserve year on year. Slope, aspect, vegetation type and shelter all appear to play a role in determining fine scale habitat suitability for the butterfly. These findings support other studies from the UK and Central Europe (Sparks et al. 1994; Fartmann 2006; Anthes et al. 2008; Turner et al. 2009), which all find *H. lucina* to have a narrow ecological niche. The sensitivity of the species is traditionally thought to be due to the specific requirements of the larvae (Fartmann 2006). However, here we found that, despite their higher mobility, adult distributions on site (at least of the males which made up the majority of the recordings in this study) were equally, and in many cases more, clustered than those of the larvae. This demonstrates that the adult life stage also utilises specific habitat features and agrees with the findings of Turner et al. (2009), who have undertaken the only other study that directly assesses adult habitat requirements. It remains to be seen how much of an impact managing for adults as well as larvae could have on *H. lucina* populations but conserving features that are known to benefit multiple life stages, such as highly sheltered areas, may be important for the successful conservation of the species (Thomas et al. 2011).

The paired yearly comparisons of hotspots support the idea of fine scale habitat selection within a larger region and reveal, for the first time, the long-term effects that the narrow niche of this species can have on its distribution within a single reserve. For both larvae and adults, there is a high percentage overlap of hotspot locations between different years. However, overlap percentages are substantially larger within 50 m than they are within five. This indicates that





**Fig. 4** Hotspot distribution maps of *H. lucina* adults (78% male) and larvae at Totternhoe Quarry Reserve from 2006 to 2017, for years with sufficient survey effort. The gridded area covers the parts of the reserve that were surveyed for *H. lucina* during this study with the rest being dense scrub. Dots represent the locations of adult or larval *H. lucina* sightings with dark grid squares representing areas that are significant hotspots to a 99% confidence level. Clustering value 'K' is also given for each distribution and compared to that of the highest 'K' value derived from 100 permutations of an equal number of randomly generated points

although the population tends to remain in the same general area or habitat polygon, it does shift slightly within it.

One could argue that the repeated use of specific habitat patches is simply the result of the relatively low mobility of *H. lucina* and scrub on site restricting movement away from these locations. However, Turner et al. (2009) investigated patch occupancy and dispersal distances for the butterfly at Totternhoe Quarry. They found that adult dispersal across the site was reasonably high, with turnover and migration recorded between areas a few 100 m apart and separated by dense scrub. Therefore, distributions on site appear to be a product of habitat preferences, rather than poor mobility and isolation. This is further supported by the finding that *H. lucina* distributions at Totternhoe Quarry are not dictated by the abundance of their foodplants. *Primula* are highly clustered on site, but 64% of larvae were not found in the areas with highest *Primula* densities. Similarly, Turner et al. (2009) found that only a very low percentage, between 4.1 and 1.2% depending on year, of available foodplants were used for oviposition across Totternhoe Quarry reserve. Instead of simply tracking foodplant abundance, other factors or habitat attributes appear to dictate *H. lucina* distributions. Many butterfly species only select a small proportion of their available foodplants, exhibiting high levels of discrimination based upon a wide variety of characteristics (Elmes and Wardlaw 1982; Butterflies Under Threat Team 1986; Dennis and Shreeve 1991; Awmack and Leather 2002; Leon-Cortes et al. 2004; Dennis et al. 2005) and evidence suggests that this is also true for *H. lucina*. This highlights how vital a few key areas are for the entire population at Totternhoe Quarry and how little of the site is actively used by the species, even over the span of a decade. If this pattern is found across other sites containing populations of this threatened butterfly, it could further explain the vulnerability of the species.

Understanding the nature of the small hotspot locations identified in this study will be vital for providing information on how best to manage for *H. lucina* populations, both at Totternhoe Quarry and further afield. Larvae and adults were found to occupy very similar areas of Totternhoe Quarry over the 12-year study, but fine scale differences in habitat use were also uncovered. The cumulative distribution maps for both larvae and adults show that the long leg

to the west of the reserve is usually avoided in favour of the much more topographically varied east. This distribution can be explained by adult *H. lucina* showing a preference for more sheltered locations on steeper slopes, whilst also selecting such sites for oviposition. A preference for sheltered locations by adult *H. lucina* was also noted by Turner et al. (2009). As a spring flying butterfly, peak temperatures are relatively low during the flight season of *H. lucina* and sheltered locations may enable adult activity in sub optimum conditions by reducing the effects of wind cooling (Turner et al. 2009). Therefore, in the most sheltered locations adults can fly more often, for longer and potentially increase sexual activity levels, essential for supporting the continuation of a population. However, Turner et al. (2009) found *H. lucina* larvae to have a different relationship with shelter than that of the adults. Despite some degree of shelter appearing to be important and utilised foodplants often being associated with nearby scrub, the most sheltered areas on the reserve did not possess a higher number of foodplants with larval damage. This pattern of foodplant use may be explained by the limited mobility of the larvae. As larvae can only move a maximum of a few metres from their host plant, shelter within a short distance, perhaps helping to reduce the risk of host plant desiccation, may be more important than that at larger scales (Turner et al. 2009). Although this was not directly tested with the distribution maps in this study this theory is somewhat supported by our results. Although larvae were more commonly found within more sheltered habitat polygons, this relationship was reduced compared to that of adults, suggesting some drop in the importance of large-scale shelter for the larval stage.

The preference found for adults most commonly occurring on south westerly slopes also fits in well with the findings of Turner et al. (2009), where adults were consistently found more on southerly aspects. Slopes receiving more solar insolation will allow adults to warm up and become active sooner on any given day and may be the selective cause of these observed distributions (Turner et al. 2009). High abundances of adult butterflies on east and west facing slopes found in this study may similarly be linked to adults benefitting from both warming up earlier in the day or remaining active longer into the evening respectively. The reduced occurrence of larvae on south westerly slopes and an increase in occurrence on slopes with north easterly aspects compared to adults also supports the findings of other studies. In the Diemal Valley, Germany, Fartmann (2006) found selected foodplants were usually on west facing slopes, where increased humidity levels may reduce the chance of host plants drying out, ensuring that larvae have an adequate food source until pupation. Similarly, Turner et al. (2009) found larval damage to be more common on northerly slopes, where cooler and damper conditions are likely to increase long-term cowslip survival (Warren 1993).

**Table 1** Percentage of adult (78% male) and larval *H. lucina* hotspot distributions within 5 and 50 m of one another at Totternhoe Quarry Reserve for paired years from 2006 to 2017

|                  |         |      |                          |        | 1 year difference  |                          |         |      |      |      |
|------------------|---------|------|--------------------------|--------|--------------------|--------------------------|---------|------|------|------|
|                  |         |      |                          |        | 2 year difference  |                          |         |      |      |      |
|                  |         |      |                          |        | 3 year difference  |                          |         |      |      |      |
|                  |         |      |                          |        | >3 year difference |                          |         |      |      |      |
| Adults           |         |      |                          |        | Larvae             |                          |         |      |      |      |
| 5m               |         |      |                          |        | 5m                 |                          |         |      |      |      |
|                  | 2007    | 2008 | 2009                     | 2017   |                    | 2007                     | 2009    | 2012 | 2015 | 2016 |
| 2006             | 59%     | 20%  | 21%                      | 54%    | 2006               | 14%                      | 17%     | 2%   | 70%  | 7%   |
| 2007             | -       | 65%  | 57%                      | 48%    | 2007               | -                        | 97%     | 37%  | 53%  | 10%  |
| 2008             | -       | -    | 84%                      | 48%    | 2009               | -                        | -       | 56%  | 64%  | 82%  |
| 2009             | -       | -    | -                        | 64%    | 2012               | -                        | -       | -    | 38%  | 34%  |
|                  |         |      |                          |        | 2015               | -                        | -       | -    | -    | 39%  |
| 50m              |         |      |                          |        | 50m                |                          |         |      |      |      |
|                  | 2007    | 2008 | 2009                     | 2017   |                    | 2007                     | 2009    | 2012 | 2015 | 2016 |
| 2006             | 96%     | 46%  | 47%                      | 95%    | 2006               | 17%                      | 17%     | 14%  | 90%  | 56%  |
| 2007             | -       | 100% | 63%                      | 100%   | 2007               | -                        | 100%    | 70%  | 96%  | 62%  |
| 2008             | -       | -    | 93%                      | 69%    | 2009               | -                        | -       | 100% | 65%  | 100% |
| 2009             | -       | -    | -                        | 72%    | 2012               | -                        | -       | -    | 100% | 70%  |
|                  |         |      |                          |        | 2015               | -                        | -       | -    | -    | 74%  |
| Expected overlap | Minimum |      | 1 <sup>st</sup> Quartile | Median | Mean               | 3 <sup>rd</sup> Quartile | Maximum |      |      |      |
| 5m               | 0%      |      | 0%                       | 0%     | 4%                 | 0%                       | 85%     |      |      |      |
| 50m              | 0%      |      | 0%                       | 0%     | 22%                | 55%                      | 100%    |      |      |      |

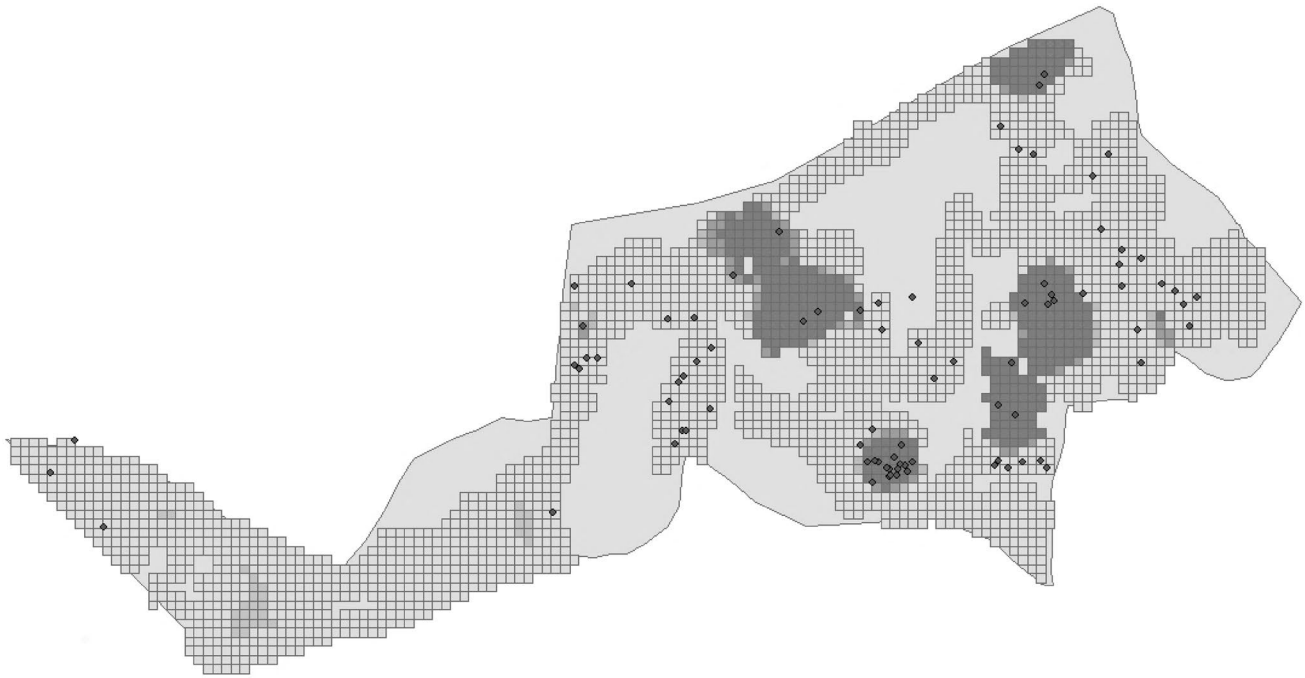
Lighter shading represents chronologically closer years. Summary data from expected percentage overlaps, generated from 100 iterations of randomly located pairs of hotspot distributions, is also displayed for comparison

**Table 2** Percentage of adult (78% male) *H. lucina* hotspots within 5 and 50 m of larval hotspots from the same year at Totternhoe Quarry Reserve

|           | 5 m  |      |      |           | 50 m      |      |      |           |
|-----------|------|------|------|-----------|-----------|------|------|-----------|
|           | 2006 | 2007 | 2009 | All years | 2006      | 2007 | 2009 | All years |
| 2006      | 67%  | -    | -    | -         | 2006      | 76%  | -    | -         |
| 2007      | -    | 39%  | -    | -         | 2007      | -    | 63%  | -         |
| 2009      | -    | -    | 74%  | -         | 2009      | -    | -    | 100%      |
| All Years | -    | -    | -    | 55%       | All Years | -    | -    | 87%       |

Finally, the fact that larval and adult *H. lucina* were most commonly found on short grass also fits quite well with previous findings, especially when considered alongside the preference for highly sheltered locations that was also detected in this project. Most research suggests that *H. lucina* relies on a short-lived transitional habitat, where their foodplants are thought to proliferate best in short vegetation but taller swards are also required nearby in order to prevent desiccation and protect adults from poor weather (Sparks et al. 1994; Fartmann 2006; Anthes et al. 2008; Turner et al. 2009). This type of habitat matches closely to one of highly sheltered areas of short grass. However, this highlights how the four habitat variables examined in this study (slope, aspect, shelter and vegetation) are not independent of one

another and all interact to influence distributions observed. This could cloud patterns of habitat choice relating to any single variable and does limit the inferences that can be made from this study. However, despite interaction between all habitat attributes, the clear trends revealed from this analysis in regards to slope, aspect and shelter provide important information for *H. lucina* habitat preferences and provide convincing explanations for the distributions observed in this study. In the future, a recording effort specifically targeting the more elusive adult females, the majority of which appear to have gone undetected in this study, could help to highlight differences in habitat preferences between the sexes. These data could provide important information on the habitat types traversed by female butterflies as they travel



**Fig. 5** *Primula* foodplants at Totternhoe Quarry Reserve with *H. lucina* larval damage from 2006 overlaid on the hotspot distribution map for all *Primula* plants on the reserve that year. The gridded area covers the parts of the reserve that were surveyed during the course

of the study with the rest of the site being dense scrub. Dots represent the locations of larval damaged foodplants whereas dark grid squares represent areas that are significant hotspots to a 99% confidence level for all of the *Primula* foodplants on site

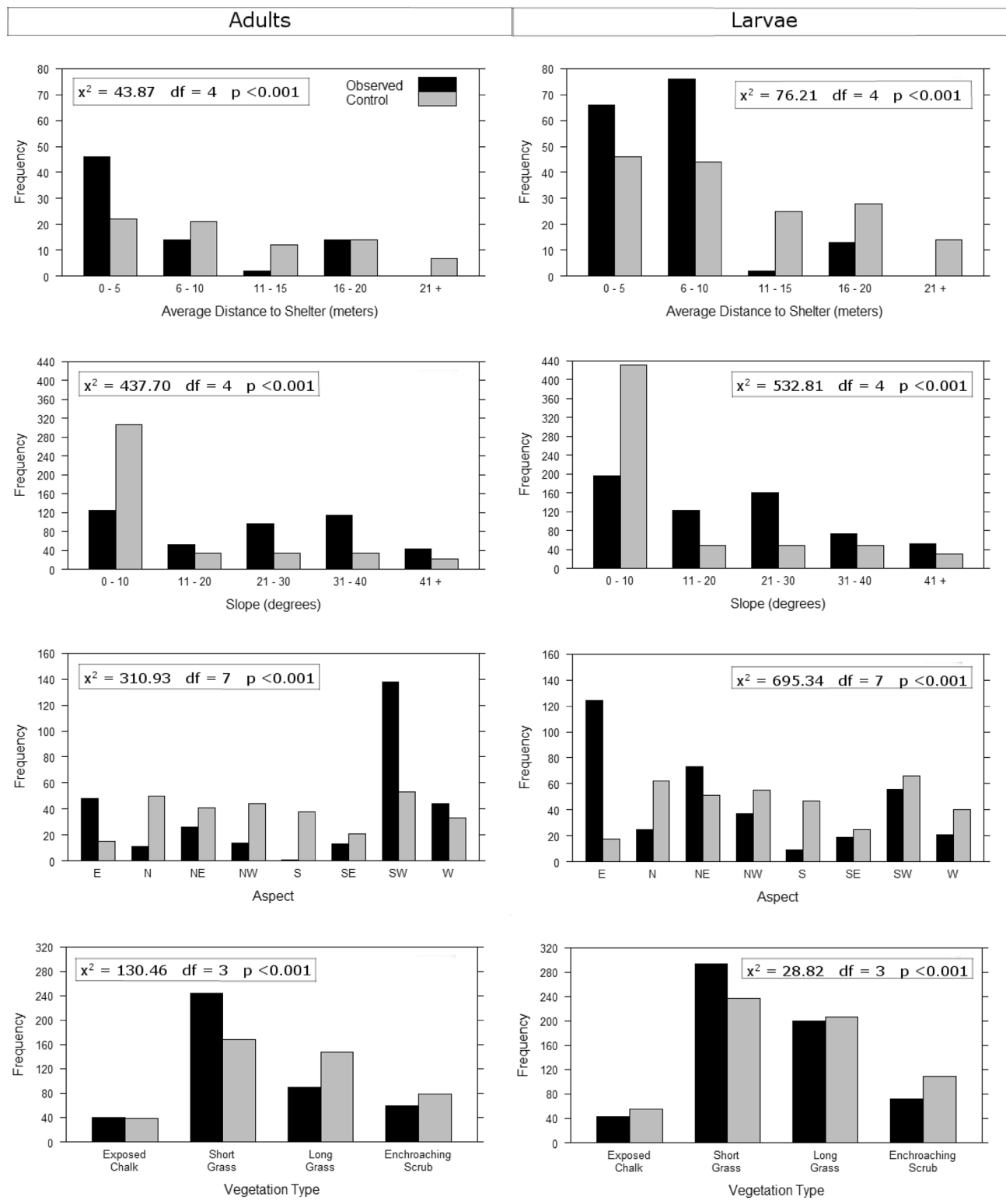
from male leks to oviposition locations, bridging the gap between the two life stages. This will be extremely important for enabling conservation management that can best support all individuals of the adult life stage.

### Implications for management

This study has revealed specific habitat features selected by male *H. lucina* for territorial locations and female *H. lucina* for ovipositional sites. This knowledge will allow areas containing favoured habitat attributes of each life stage to be targeted for management so that the species can be supported throughout its life cycle. Given the importance of shelter to both life stages, care must be taken to ensure that destructive management does not completely open up areas, whilst removing scrub to combat succession. Therefore, ideal locations for scrub clearance will include other shelter producing features such as steep slopes, which will benefit adults and larvae alike (Fartmann 2006; Turner et al. 2009). However, Totternhoe Quarry is only one small reserve and it remains to be seen whether or not the habitat preferences observed here hold true across multiple different sites or a wider area. Martin (2008), investigating *H. lucina* ovipositional requirements at Salisbury Plain Training Area in Wiltshire, a huge 14,000-hectare chalk grassland stronghold for *H. lucina*, found evidence suggesting that the butterfly's ovipositional

requirements were not as specific as those predicted by other studies. At this vast site, it could be that a difference in ovipositional niche reflects females having less restriction in their choice, resulting in different optimal oviposition locations across available habitats (Martin 2008). The next step will be to extend studies of this kind to more sites and larger areas, to achieve a more comprehensive understanding of habitat requirements for *H. lucina*. Surveying sites to find *H. lucina* hotspots will also be essential for targeting management on a site-by-site basis. Due to populations shifting within larger constrained regions, monitoring yearly population movements could help cyclical management to maintain suitable habitat for *H. lucina* whilst causing the least disturbance possible to the populations themselves.

As well as maintaining and expanding hotspot habitat qualities on isolated sites, the long term survival of *H. lucina* will rely on linking up populations within and between reserves (Bourn and Warren 1998). The fact that a large proportion of Totternhoe Quarry is consistently unused by the species provides a worrying insight into how difficult it will be to support large populations. Only a few small locations may be suitable for *H. lucina* on any given site, sustaining only a few individuals. Furthermore, with increasing scrub encroachment threatening Totternhoe Quarry and other wildlife reserves, the threat of these small hotspots and populations being isolated may increase. Effort must be



**Fig. 6** Habitat attributes of slope, aspect, shelter (cumulative distance to barriers in the directions of each of the four points of the compass) and vegetation for *H. lucina* adult (78% male) and larval hot-spots at Totternhoe Quarry from 2006 to 2017, compared to expected

values derived from the percentage area of each habitat type on the GPS map of the site. For aspect comparisons all observations on flat regions of the reserve were omitted from analyses. One-dimensional Chi-squared tests compare the observed and expected frequencies

**Table 3** Habitat attribute Chi-squared tests of independence for Totternhoe Quarry Reserve between 2006 and 2017

| Habitat feature | $\chi^2$ | df | p      | Observed relationship                                 |
|-----------------|----------|----|--------|---|
| Shelter         |          |    |        |   |
| Slope           | 64.412   | 16 | <0.001 | Higher shelter values on steeper slopes               |
| Aspect          | 106.58   | 28 | <0.001 | Higher shelter values have a wider variety of aspects |
| Vegetation      | 53.97    | 12 | <0.001 | Higher shelter values for taller vegetation           |
| Vegetation      |          |    |        |   |
| Slope           | 570.24   | 12 | <0.001 | Chalk or exposed ground most likely on steep slopes   |
| Aspect          | 378.75   | 21 | <0.001 | –   |
| Slope           |          |    |        |   |
| Aspect          | 529.44   | 28 | <0.001 | –   |

Data on slope, aspect and vegetation were available for all years but only 3 years of shelter values were available

made to maintain links between these hotspots, to maintain populations within a site in the same way as would be done for a metapopulation between multiple locations (Anthes et al. 2008).

## Conclusions

It is clear that both adults and larvae of *H. lucina* utilise specific habitat features, which are reflected by their limited and patchy distribution, even on a small reserve like Totternhoe Quarry. These preferences remain remarkably consistent year on year with the distributions of both life stages changing by very little over the course of a decade. Hotspots with high numbers of *H. lucina* at Totternhoe Quarry Reserve appear to be related to a number of abiotic factors, with steep slopes and high degrees of shelter being particularly important. Although adults and larvae show similar distributions on site, they have specific differences in habitat requirements and this emphasises the need to target conservation action to all stages of the butterfly's life cycle, not just its less mobile larvae (Turner et al. 2009). These results will be extremely useful for informing present and future conservation efforts for this species. Only by understanding the species' needs can we carry out the appropriate conservation action to ensure the long-term survival of *H. lucina* and protect populations from the effects of predicted climate change.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Research involving animals** No butterflies were harmed during the course of this project. All work was carried out with the full consent of the BCN Wildlife Trust on one of their reserves and they work closely with Natural England to ensure the best monitoring of species on their sites. Natural England also provided the BCN Wildlife Trust with written consent to undertake adult butterfly surveys of scarce species and Duke of Burgundy larval damage surveys specifically. Please see 'Consent of Natural England' form in Supplementary material.

**Informed consent** No data were collected from human participants during this project.

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