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ORIGINAL PAPER

Habitat preference and dispersal of the Duke of Burgundy butterfly (*Hamearis lucina*) on an abandoned chalk quarry in Bedfordshire, UK

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Abstract The Duke of Burgundy butterfly (*Hamearis lucina*) has declined severely since the 1970s and is a UK Biodiversity Action Plan Priority species. Its populations are mostly confined to scrubby calcareous grassland, where management for short-turf species can be detrimental to the butterfly. We briefly review the literature on the Duke of Burgundy and investigate their habitat preferences, survival and dispersal at a chalk grassland reserve in Bedfordshire, UK. We found that adults generally preferred more sheltered locations but that their habitat preferences were less restrictive than choice of food-plants. Females chose larger plants with longer leaves in denser patches on which to lay eggs. Adults showed reasonable dispersal ability with turnover recorded between areas isolated by scrub. Our results indicate that the species is able to use isolated areas of favourable habitat at a reserve scale and that conservation could therefore involve cyclic management to provide suitable habitat year-to-year.

Keywords Butterfly · Calcareous grassland · Duke of Burgundy · Habitat management · *Hamearis lucina* · Scrub encroachment

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Introduction

Many British butterflies are declining in numbers and becoming regionally and nationally rare or extinct (Asher et al. 2001; Fox et al. 2006). This can be due to a variety of factors, but is generally owing to changes in land-use and increased habitat fragmentation. Species with more specialised habitat preferences and restricted range of larval food-plants have declined more severely than habitat generalists (Brereton et al. 2006). This reduction in butterfly numbers is particularly worrying as they are the best known of the invertebrate fauna (Bourn and Thomas 2002; Brereton et al. 2006; Thomas 2005) and reflect changes in the rest of the insect community (Bourn and Thomas 2002; Thomas et al. 2004).

Butterfly declines may become more severe in future years. This is due not only to continuing unfavourable land management, but also to the preponderance of small and highly fragmented areas of habitat (Warren 1993a). Many existing populations of rare species may be unsustainable in the longer term and become extinct due to local fluctuations in their population that are not redressed by immigration (e.g., Bulman et al. 2007). This situation may also be worsened by climate change, which is predicted to increase the frequency of extreme weather events (King 2005) and force butterflies on small reserves out of their or their food-plant's preferred environmental conditions (Dennis and Shreeve 1991). Earlier emergence in the spring is being recorded in many butterflies (Roy and Sparks 2000) which may contribute to declines, as butterfly emergence and host-plant growth become mismatched (Roy et al. 2001). Moreover, over-arching government conservation policies may be failing to benefit rarer species due to inadequate protection (Warren 1993a) and different species-specific habitat requirements (Davies et al. 2007).

Understanding the natural history and specific habitat preferences of threatened butterflies is therefore crucial to their conservation. Only this will allow effective habitat management for both focal species and wider biodiversity.

The Duke of Burgundy butterfly (*Hamearis lucina* L. 1758) is one species that has suffered severe declines over the last 50 years (Asher et al. 2001). In the UK, its distribution has declined by 52% and its population by 28% since the late 1970s (58% between 1995 and 2004) (Fox et al. 2006), leading to it being designated a conservation Priority Species (UK Biodiversity Action Plan 2007). The Duke of Burgundy is also declining throughout Europe with serious losses reported in at least 10 countries (Asher et al. 2001; Bourn and Warren 1998). The butterfly is found in two main habitat types in the UK: open deciduous woodland and scrubby calcareous grassland, with the majority of sites being small and isolated (Oates 2000; Warren 1993a). Historically associated with the former habitat (e.g. Newman 1869), it was lost from most areas owing to reduced felling and coppicing in the early twentieth century and planting of ancient woodlands with conifers since 1945 (Bourn and Warren 1998; Greatorex-Davies et al. 1993; Warren 1993a). At the same time calcareous grassland sites became less managed as grazing became uneconomical. This led to widespread scrub encroachment, particularly following the outbreak of myxomatosis and crash in rabbit numbers in the 1950s. Large areas of grassland therefore became favourable for the Duke of Burgundy, as it provided a similar environment to sheltered woodland glades, and the species expanded its range into these areas (Bourn and Warren 1998; Oates 2000). However, escalating scrub encroachment is eliminating these novel habitats and leaving them too small and isolated. Conservation measures to cut scrub and graze calcareous grasslands, together with a resurgence in rabbit numbers, have also rendered some areas unsuitable (Bourn and Warren 1998; Brereton et al. 2006; Léon-Cortés et al. 2003). This is probably why the Duke of Burgundy appears to be faring better on Sites of Special Scientific Interest (SSSI) classed as being in ‘unfavourable’, rather than in ‘favourable’ condition (Davies et al. 2007).

The Duke of Burgundy has been ranked an equal 17th out of 56 butterfly species for vulnerability to climate change (based on a range of criteria) (Dennis and Shreeve 1991). In the UK the butterfly is on the northern edge of its range. It has expanded north across Europe in response to climate change (Parmesan et al. 1999) and is also emerging earlier in the spring (Fartmann 2006; Oates 2000). Global warming may therefore benefit the species in the UK by enabling it to spread to favourable habitats further north. However, atypical weather connected to climate change, especially in the spring, may lead to a heightened loss of the species from isolated reserves.

Understanding all aspects of the Duke of Burgundy’s habitat requirements is key to its conservation because of the interplay between a species’ ecology and management practices. In this paper we will explore the ecology of the Duke of Burgundy at a chalk grassland site. We also examine a wide range of its requirements and preferences at different stages of its life history, in the same population over 2 years. We will discuss our findings with reference to habitat management on small reserves.

Duke of Burgundy life history and habitat requirements

The Duke of Burgundy has a restricted food-plant range, laying predominantly on primrose (*Primula vulgaris*) in woodland areas and cowslips (*Primula veris*) in grassland (Thomas and Lewington 1991). Females generally lay batches of 1–4 eggs on the underside of food-plant leaves (Kirtley 1995, 1997; Oates 2000; Sparks et al. 1994). There is evidence that clutch sizes may be lower in calcareous grasslands, as plants here may die back earlier in the season and therefore only be able to support smaller numbers of larvae (Anthes et al. 2008). Snails are thought to be an important egg predator (Bourn and Warren 1998; Oates 2000) and up to 19% of clutches can be lost before hatching (Anthes et al. 2008).

As with many species of butterfly, the food-plants of the Duke of Burgundy are more widespread than the butterflies themselves, indicating that some particular characteristic of the food-plant is important for the larvae. A fairly low percentage of available food-plants appear to be used (7.1–27% recorded in some UK woodlands (Sparks et al. 1994)). In woodland sites in the UK, larvae prefer larger plants growing in early but not the earliest stages of succession (Sparks et al. 1994). Similarly in Southwestern Germany, closed canopy areas were rarely chosen for egg-laying, with more eggs being laid on plants with more leaves, in sunnier patches and in denser sward (Anthes et al. 2008). In chalk grassland sites, females generally favour larger plants that are sheltered by surrounding vegetation or dense turf, so the plant is unlikely to dry out during the summer (Fartmann 2006; Goldenberg 2004; Kirtley 1995, 1997; Léon-Cortés et al. 2003; Oates 2000). Fartmann (2006) also found that plants with eggs were fairly close to scrub, protecting them from drying. In contrast, in cooler or wetter areas, plants with eggs were up to 10 m away from scrub (Fartmann 2006). In calcareous grassland sites, where soils are drier, northerly or westerly slopes are preferred (Anthes et al. 2008; Fartmann 2006; Goldenberg 2004; Oates 2000; Warren 1993b), again presumably to avoid desiccation of the food-plant and starvation of the larvae. Goldenberg (2004) found that plants favoured by females on a chalk grassland site had lower stomatal conductance but higher CO_2 assimilation, indicating that chosen plants were less water-stressed and healthier. Denser patches of food-plants are also favoured (Anthes et al. 2008), probably because larvae can avoid starvation once one plant is exhausted or has yellowed by migrating to a new plant (Oates 2000). The caterpillars feed at night, producing a distinctive peppering of damage on the leaves (Oates 2000). When the larvae are fully grown in mid July, they pupate at the base of the plant or in nearby grass tussocks (Kirtley 1997; Oates 2000). It is thought that predation levels during pupation may be fairly high (Oates 2000).

The adults are active from late April to mid June and live on average about 5 days (but up to 22 days (Oates 2000)). Females are generally elusive and spend much of their life egg-laying and sun-bathing or nectaring as they move from plant to plant (Anthes et al. 2008; Kirtley 1995). Males are more often encountered, as they hold territories on perching points in sunny and sheltered locations, where they wait for passing females. In larger Duke of Burgundy sites, several males can hold territories next-door to each other and frequently spiral 7 or 8 m up into the air before returning to their perches (Oates 2000). In woodlands, adult butterflies favour open sunny rides with numbers declining dramatically with shade (Greatorex-Davies et al. 1993). Adults are also thought to prefer more sheltered locations in grassland sites, perhaps explaining why abandoned quarry sites with their steep valleys, are so favoured by the species. Adult male butterflies are thought to be fairly sedentary, rarely moving from one perching area to another (Kirtley 1995; Oates 2000). In contrast, females can disperse over 250 m (Oates 2000). On the whole, however, movement of adults and founding of new populations must be quite rare: Fartmann (2006) found that distributions of the butterfly in chalk grassland sites in central Germany were strongly related to the presence of ancient woodland in the surrounding area, which presumably provided the original source of the grassland populations. Similarly, Anthes et al. (2008) found that new habitat patches were not occupied by the butterfly if they were more than a few 100 m away from existing colonies. Modelling work on the species has found that higher rates of dispersal may lead to more rapid loss of isolated populations, as surrounding areas become sinks. Increased isolation of populations and environmental stochasticity were also found to increase the likelihood of the species disappearing (Léon-Cortés et al. 2003).

Study site

Fieldwork was carried out at Totternhoe Quarry Reserve (Grid ref: SP 986 225, survey area 8.9 ha) in Bedfordshire, UK. This abandoned chalk quarry is in the Northeast of the Chiltern Hills, in an area that has been mined since the middle ages. Most of the reserve is made up of excavated chalk, so the topography of the site is extremely variable. Soils are skeletal in places owing to steep cliffs or the activity of motorbikes, but in other places are calcareous with loamy textures (silty clay loam or silt loam). The vegetation over the site is also variable with conditions ranging from exposed chalk and short sward to mature stands of hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa*) and elder (*Sambucus nigra*). Aerial photographs of the site since the 1940s show that the area of grassland on the reserve has fallen from 85% in 1947 to only 13% in 2002, while dense scrub has risen from non-existent to 70% coverage in the same period. Three main calcareous grassland communities occur on Totternhoe, characterised by sheep's fescue (*Festuca ovina*), meadow oat grass (*Avenula pratensis*), and upright brome (*Bromus erectus*) and tor-grass (*Brachypodium pinnatum*) (two NVC sub-communities: CG4a and CG2a). Cowslip is widespread at Totternhoe Quarry and primroses also occur.

The site has been owned and managed by the Wildlife Trust for Bedfordshire, Cambridgeshire, Northamptonshire and Peterborough (BCNP Wildlife Trust) since 2003. Management cannot involve grazing as the site is commonly used by dog-walkers and motorbikes. Management has therefore included fencing to reduce motorcycle use, removal of waste, and winter scrub cutting. The site is a designated Site of SSSI and a County Wildlife Site, recognising its rich flora and fauna (Proud 2000). Lowland calcareous grassland is a national priority habitat (UK Biodiversity Action Plan 2007), with directives to maintain, restore and expand the habitat nationally. Approximately 303 ha of calcareous grassland currently exists in Bedfordshire and Luton, with 162 ha of this showing moderate to dense scrub encroachment. Totternhoe is listed as one of the best calcareous grasslands in the county (Bedslife and The Chilterns Conservation Board 2007). The reserve's varied topography and vegetation make it an ideal site on which to study habitat preferences, as a wide variety of conditions are found over a small area.

Methods

Fieldwork was carried out between May and August in 2006 and 2007. Data were collected with the help of a large number of volunteers and members of the BCNP Wildlife Trust's Ecology Group—a team of volunteers who carry out recording work on Wildlife Trust reserves to assess their state and the impact of management on wildlife.

Habitat survey

Totternhoe Quarry Reserve was mapped for slope, aspect, degree of shelter and vegetation type, in August–September 2006, with a *Geo-Trimble* back-pack GPS and the site divided into polygons of homogenous habitat. Each polygon (147 in total) was then given an individual code and the habitat characteristics recorded. For slope, polygons were classed as: very steep (>40°), steep (30–40°), average (20–30°), shallow (10–20°) or flat (<10°). Areas with a slope were recorded as North, East, South or West facing. The degree of shelter was also calculated by measuring the distance at 1 m from the ground from the centre of each polygon to a barrier in the directions North, East, South and West. Barriers could include vegetation or the side of a cliff. Readings for smaller distances were taken by pacing and for longer distances with a laser range-finder (Bushrell Corporation). Distances over 100 m were recorded as 100 m. An average of these distances was then taken to be an index of the degree of shelter for each polygon (longer average distance equals less shelter). For vegetation, polygons were classed by eye: dense scrub (closed canopy), encroaching scrub (small bushes with grass in between), long grass (generally over 10 cm height), short grass (generally under 10 cm height), exposed chalk (only scattered vegetation cover) or concrete (building foundations). Polygon areas were calculated using *MapInfo* (specialist mapping software).

Adult survey

Adult Duke of Burgundy were surveyed throughout their flight season in 2006 and 2007 (late April to mid June) on as many days as possible when the weather was good (generally sunny or over 17°C and not raining). Because adults may be difficult to see using traditional transect methods, recorders walked over the whole of the reserve area (excluding dense scrub) and recorded all individuals seen. To reduce bias for time of day, the direction in which the reserve was walked was varied. When an individual was observed, it was inspected using a close-focussing monocular and its activity recorded (flying, sunning or resting, perching, nectaring, egg-laying or interacting with another individual). If it was not already marked, the individual was then caught and its wing length (forewing base to tip) and sex recorded. The butterfly was then marked with an individual series of coloured dots (using *Staedtler Lumocolor* pens) and released. The number of recaptures necessary was reduced by using monoculars, as it was usually possible to see the marks without having to recapture the butterfly. After marking, the GPS position of the butterfly was recorded from a hand-held GPS (*Garmin* GPS 72) and the butterfly assigned to a particular polygon. Over the course of the two seasons we recorded where the butterflies were active across the reserve and their behaviour. By noting their individual GPS at each recapture we could also calculate how far they had travelled as a straight line.

Larval damage and food-plant survey

In July 2006 and 2007 the whole of the reserve was surveyed for cowslips or primroses showing Duke of Burgundy larval damage. When the larvae feed, they produce a very distinctive peppering of holes in the leaves, which indicates presence of the butterfly (Oates 2000). Where damaged plants were found, GPS position and polygon number were noted. In 2007 we also recorded their longest length and width (so that approximate plant area could be calculated) together with the distance to nearest scrub. In August and September 2006 all areas of the reserve (except dense scrub) were surveyed for cowslips and primroses and the location (again with a hand-held GPS) and the length and the width of all plants recorded.

Choice of egg-laying site and growth of the larvae

From May 17th until June 1st 2006 and May 4th until June 4th 2007, cowslips and primroses in areas of the reserve where adult Duke of Burgundy had been seen were searched for eggs. In total for 2006 and 2007, respectively, 1,371 and 1,878 cowslips and 261 and 176 primroses were searched. Where eggs were found, clutch size as well as the leaf length was recorded. Other characteristics of the food-plant were also recorded including: longest leaf length, plant length and width (to calculate an approximate area), number of other cowslips or primroses within 30 cm, distance to scrub and vegetation height immediately around the plant. Vegetation height was assessed by placing a light plastic tray of 30 cm by 22 cm on the vegetation and recording the level below which about 80% of the vegetation was estimated to be growing (based on the direct-measurement method (Stewart et al. 2001)). Where the leaves of neighbouring plants overlapped, these groups of plants were considered as single individuals and measurements were taken accordingly. We chose one control plant in the immediate area to compare with each food-plant. This was chosen by measuring a distance 1 m from the food-plant and choosing the nearest conspecific to this point. To avoid bias, the direction in which the metre out was measured was varied in turn from plant to plant in the directions North, South, East and West.

Plants and their controls were revisited every week from May until the beginning of August when the larvae were fully grown. Each week the number of eggs was recorded and the remaining plants searched for new eggs. In 2007 the presence of snails, snail faeces or snail damage was also recorded each week as well as temperature, relative humidity (using a *ThermoHygometer* 8708) and light (using a light-dependent resistor). An average of each of these microclimatic parameters was taken for analysis. When Duke of Burgundy larvae hatch they do not eat their entire eggshell, but leave a disk of it attached to the leaf, so it is also possible for us to record when the eggs had successfully hatched. From the 6th of July to the 26th of July 2006 and from the 4th of June to the 7th of August 2007, digital photos were taken of the food-plants each week. These images were then analysed using *ImageJ* computer software to find the area of the plant and damaged area, from which the area eaten from week to week was calculated. As the larvae are generally nocturnal, further visits were made to search the plants at night. Whenever larvae were found, their length was measured with calipers and a photo taken of the plant within a week.

Data analysis

Habitat preference of male and female Duke of Burgundy, larva-damaged food-plants and number and area of potential food-plants were analysed in relation to slope, aspect and vegetation type, by comparing observed numbers in each category to expected numbers (based on an even distribution over the reserve, excluding areas of dense scrub) using Chi-square goodness of fit tests. Where expected values were less than one, classes were removed or lumped with the most similar category. Density per m^2 of butterflies, damaged plants and food-plants were calculated for each polygon and compared to degree of shelter using Spearman's rank correlations. Differences in preference of egg-laying sites between cowslips and primroses and plants with and without flowers were compared using chi-square tests of difference. Differences in the recorded characteristics of plants with eggs and controls were compared using paired *t*-tests or Wilcoxon's tests (a non-parametric equivalent). Larval damage in relation to length of the larvae observed in that week was compared using a linear regression (damage area ln-transformed prior to analysis). The total larval damage and the amount of damage per day was investigated in relation to potentially influential factors using stepwise regressions (with a *P*-to-enter ratio set at 0.05 and a *P*-to-remove ratio set at 0.10). Factors included were number of eggs laid, plant density surrounding study plants, longest leaf length of plant, plant area and vegetation height and, for 2007 only, distance to scrub, snail incidence and average plant temperature, relative humidity and light. Distance travelled by individual butterflies was calculated from the first GPS position recorded to the last. Factors that could affect distance travelled (year, day of capture, sex, wing length, region caught and days between capture) were investigated using a General Linear Model (GLM), with distance travelled $\log_{10}$ transformed. For 2006 this only included Totternhoe Quarry Reserve, but for 2007 also included a small area of the SSSI adjacent to the reserve. Turn-over was also calculated between three areas of the reserve, isolated by dense scrub (Fig. 1). This was done by recording the number and percentage of individuals that were originally captured in one area, but re-caught in another.

Results

Reserve habitats

Detailed mapping showed that over 60% of the reserve was under dense scrub, with a further 4% under encroaching scrub, 14% under long grass, 18% under short grass and 3% under exposed chalk (Fig. 1). Vegetation and slope were significantly associated with each other ($\chi^2 = 24.09$, $df = 9$, $P = 0.004$) with areas of exposed chalk being more frequent on steep slopes.

Duke of Burgundy habitat preferences

Male Duke of Burgundy in 2006 (Spearman's correlation, $r = -0.393$, $n = 138$, $P < 0.001$) and females in 2007 (Spearman's correlation, $r = -0.196, n = 138, P = 0.022$) showed a preference for more sheltered areas on the reserve (Fig. 2). Males in 2007 also showed a similar, but not significant trend (Spearman's correlation, $r = -0.164$, $n = 138, P = 0.055$). There was no significant relationship with the level of shelter for female Duke of Burgundy in 2006 (Spearman's correlation, $r = -0.070$, $n = 138$, $P = 0.417$) nor damaged plants in either year (Spearman's correlation for 2006, $r = -0.111$, $n = 138$, $P = 0.198$; for 2007, $R = -0.123$, $n = 138$, $P = 0.154$).

Adult Duke of Burgundy and damaged plants were also associated with slope, aspect and vegetation type across the site (Table 1; Fig. 3). Males and damaged plants were found more commonly on steeper slopes than expected. Higher numbers of damaged plants in 2007 were also associated with easterly slopes. This contrasted with the distribution of adults, which tended to occur more commonly on southern slopes, although no significant trend was found. Vegetation type did not appear to affect the distribution of adults or damaged plants.

Cowslip and primrose habitat preferences

Both the number (Spearman's correlation, $r = -0.204$, $n = 138, P = 0.017$) and area (Spearman's correlation, $r = -0.235$, $n = 138$, $P = 0.006$) of cowslips and primroses

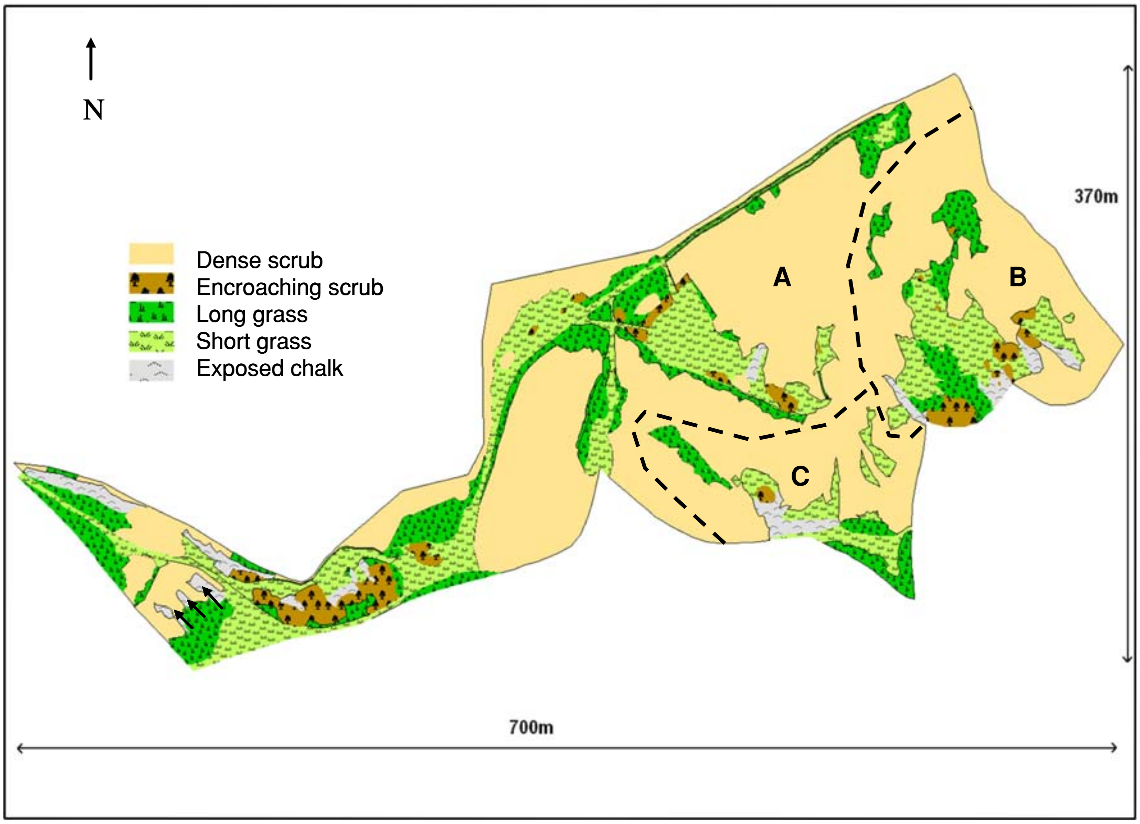

Fig. 1 Map of different vegetation types at Totternhoe Quarry Reserve, Bedfordshire, showing a large area of dense scrub. *Arrows mark* the three areas of building foundations. *Stippled lines* divide three areas of the reserve (marked A–C) isolated by dense scrub

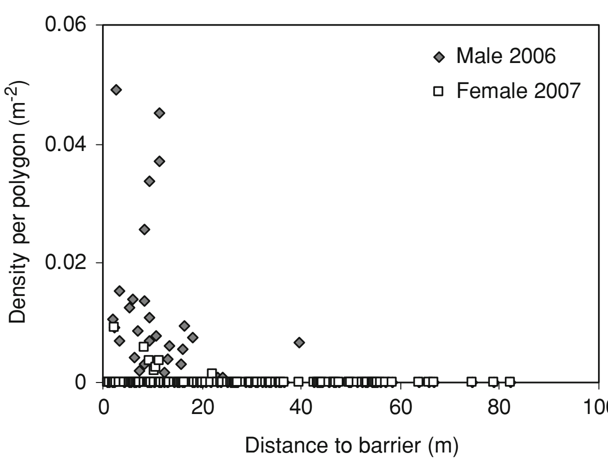

Fig. 2 Average distance to a barrier from the centre of each habitat polygon (an index of degree of shelter) versus male Duke of Burgundy density m^{-2} over the course of the flight season in 2006 and female Duke of Burgundy density in 2007. Both showed a significant negative correlation

was correlated with the degree of shelter. Cowslips and primroses were also found more commonly on steeper, northerly and easterly slopes and in areas of shorter grass (Table 1; Fig. 3).

Choice of food-plant and egg survival

A very low proportion of potential food-plants were laid on: only 4.1% of cowslips (56/1,371) and 1.9% (5/261) of primroses in 2006 and 1.2% of cowslips (23/1,878) and 1.7% of primroses (3/176) in 2007. There was no difference in preference for cowslips or primroses for either year (2006–$\chi^2 = 2.70$, $df = 1$, $P = 0.100$, 2007–$\chi^2 = 0.288$, $df = 1$, $P = 0.592$), although cowslips were much more widely used, being more abundant. The total proportion of plants used in 2007 was significantly lower than that in 2006 ($\chi^2 = 22.94$, $df = 1$, $P < 0.001$). Moreover, on average more eggs were laid on each plant in 2006 (4.5 eggs per plant), than in 2007 (2.73 eggs per plant) (Mann–Whitney, $W = 2{,}992$, $P = 0.004$). Of plants with eggs present at first survey, 16.4% in 2006 (10/61) and 15.4% in 2007 (4/26) had more eggs laid on them later in the season.

Egg survival to hatching appeared to be fairly high in both 2006 and 2007, with 59.9% (162/275 eggs) definitely hatching (egg disk found) in 2006 and 62.0% in 2007 (44/71). Of plants with eggs only 4.9% in 2006 (3/61) and 11.5% (3/26) in 2007 had no evidence of hatching (no eggs recorded as hatching and no larvae or larval damage found). There was no year-to-year difference in egg

Table 1 Habitat preferences of adult Duke of Burgundy males and females in 2006 and 2007, larvae-damaged plants in 2006 and 2007, and number and area of cowslips and primroses in 2006 in relation to slope, aspect and vegetation type at Totternhoe Quarry Reserve, Bedfordshire

Habitat feature	Population	χ^2	*df*	*P*	Preference
Slope	Male 2006	23.69	4	<0.001	>20°
	Female 2006	2.59	4	0.628	–
	Male 2007	15.18	4	0.004	20°–40°
	Female 2007	3.24	2	0.198	–
	Damage 2006	19.54	4	<0.001	30°–40°
	Damage 2007	82.12	4	<0.001	10°–40°
	Cowslip number	798.64	4	<0.001	20°–40°
	Cowslip area	1.88	4	0.76	–
Aspect	Male 2006	7.00	3	0.072	–
	Female 2006	2.56	3	0.464	–
	Male 2007	2.58	3	0.461	–
	Female 2007	1.96	2	0.374	–
	Damage 2006	3.85	3	0.278	–
	Damage 2007	110.41	3	<0.001	E
	Cowslip number	61.97	3	<0.001	N/E
	Cowslip area	3.13	3	0.372	–
Vegetation	Male 2006	2.39	3	0.495	–
	Female 2006	1.71	3	0.635	–
	Male 2007	7.37	3	0.061	–
	Female 2007	2.81	1	0.094	–
	Damage 2006	5.25	3	0.154	–
	Damage 2007	8.83	4	0.066	–
	Cowslip number	855.20	4	<0.001	Short grass
	Cowslip area	162.69	4	<0.001	Short grass

See Fig. 3. Differences in preference are calculated using chi-square goodness of fit tests between observed and expected values. Preferences refer to apparent differences between observed and expected values for significant comparisons

hatching success between 2006 and 2007 ($\chi^2 = 0.06$, $df = 1$, $P = 0.814$) or in plants showing evidence of hatching ($\chi^2 = 1.06$, $df = 1$, $P = 0.304$). Over the course of the survey, grazing animals (probably rabbits) only ate one of the plants and therefore destroyed the eggs.

Of the microclimatic variables measured, only light was found to differ between plants with eggs and control plants, and was significantly lower on plants with eggs (Table 2; Fig. 4). Several other characteristics also differed between plants with eggs and controls. Plants with eggs had a higher snail incidence (total number of times that snails, snail faeces or snail damage were recorded over the season), longer leaves, were surrounded by higher densities of potential food-plants, and were larger (average plant area 2006: plant with eggs = 137 cm^2, control plant = 76 cm^2; average plant area 2007: plant with eggs = 138 cm^2, control plant = 60 cm^2). The presence of flowers, the distance to scrub, and vegetation height around the plants did not differ between plants with eggs and controls (although distance to scrub was marginally lower for plants with eggs) (Table 2; Fig. 5). For all damaged plants recorded over the site in 2007, distance to scrub was an average of 1.5 m (range 0–5.2 m) and the average size of the plant was 188 cm^2 (range 16–1,250 cm^2).

Larval growth

Area damaged on plants significantly predicted the length of the larvae over the season (for both years combined: $F_{1,60} = 76.67$, $r^2 = 55.4$, $P < 0.001$; larval length (mm) = 0.97 + 1.79 length(absolute damage (mm^2)). There was considerable variability in the amount of damage per plant (Fig. 6). Only the number of eggs originally laid predicted the amount of damage both in total ($t = 2.59$, $r^2 = 13.68$, $n = 37$, $P = 0.014$) and per day ($t = 2.84$, $r^2 = 16.44$, $n = 37$, $P = 0.007$), shown by a stepwise regression over both years including number of eggs, plant density, longest leaf length, plant area and vegetation height. For 2007 data only, neither distance from scrub, snail incidence, temperature, relative humidity nor light predicted either total damage or amount of damage per day.

Adult migration and turnover of individuals between areas

In 2006, 40% of adults (36/89) were recaught at least once and in 2007, 30% (18/60). Time between the first capture and last recapture varied considerably but was a mean of 10.0 days in 2006 (range 1–27) and 8.2 days in 2007 (range 1–26). Dispersal of adults over this time period was a mean of 76.6 m (range 3–192 m, $n = 32$) in 2006 and 63.9 m (range 2–207 m, $n = 18$) in 2007. A GLM (explanatory variables: year, day of capture, sex, wing length, region caught and days between capture) showed that only number of days was significant in predicting dispersal distance ($F_{1,39} = 5.83$, $P = 0.021$). This level of dispersal allowed easy migration of individuals between different regions of the quarry divided by dense scrub, with 37.5% of recaptures in both years made in different areas of the quarry than where individuals were originally caught. Although sex was not a significant factor in predicting turnover, it should be noted that only a limited number of females were recaught (5 in both years). In 2006 all five moved between areas of the reserve; in 2007 only one did.

Adult behaviour

Females were most commonly observed to be resting or sunning (61% of first observations) or flying (33%). Males were most commonly observed perching (45%), resting or

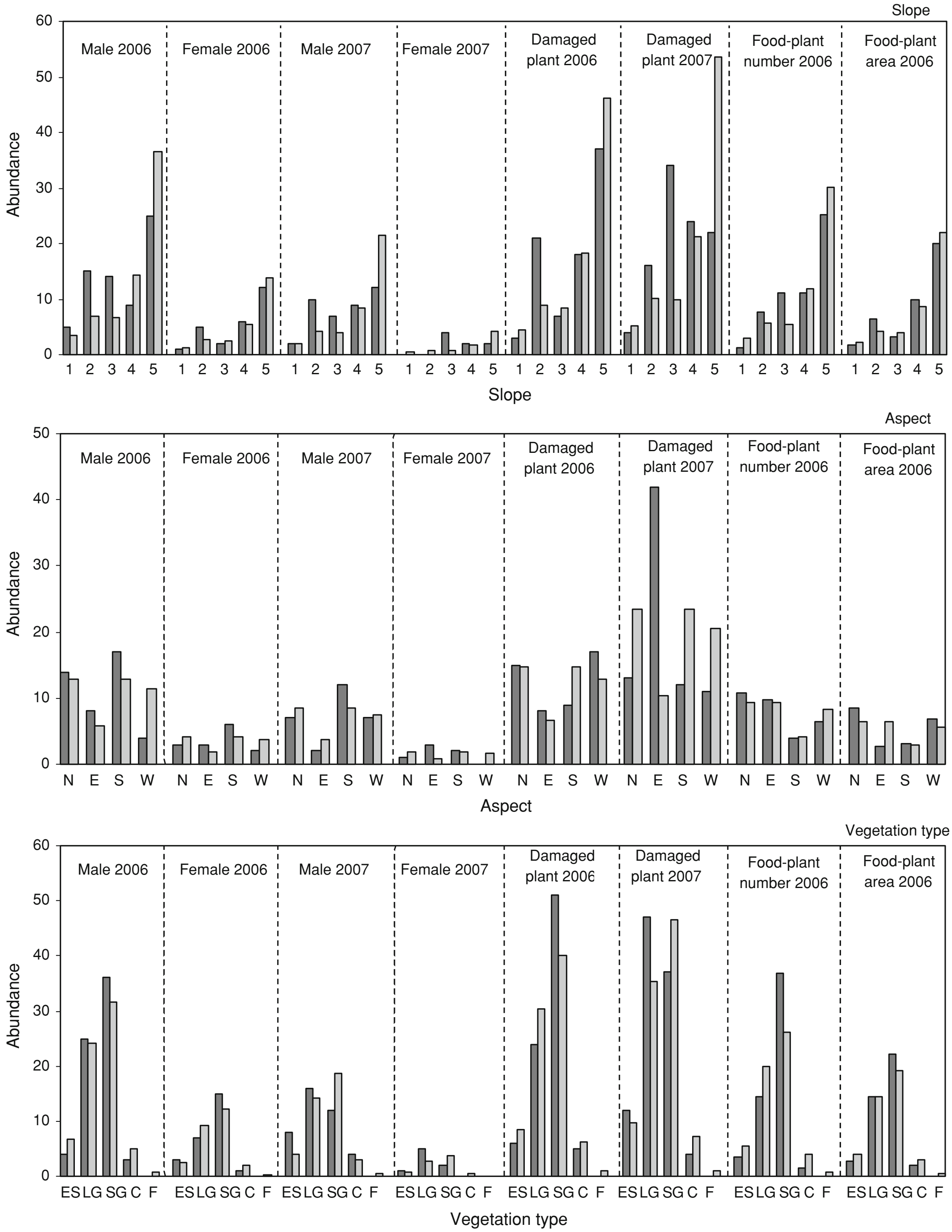

Fig. 3 Habitat preference of adult male and female Duke of Burgundy in 2006 and 2007, damaged plants in 2006 and 2007 and number and area of food-plants in 2006 in relation to slope, aspect and vegetation type at Totternhoe Quarry Reserve, Bedfordshire. *Dark bars* show total number of observations in each habitat and *light bars* the expected number of observations given an even distribution over the site (dense scrub excluded). For slope: 1 = over 40°, 2 = 30°–40°, 3 = 20°–30°, 4 = 10°–20° and 5 = less than 10°. For Aspect: N = North, E = East, S = South and W = West. For vegetation type: ES = encroaching scrub, LG = long grass, SG = short grass, C = exposed chalk and F = foundations of buildings. Owing to the very high density of cowslips on the site, cowslip and primrose numbers are given in 100s

Table 2 Tests of difference in measured characteristics between food-plants with eggs and their control plants each year

Characteristic	2006			2007		
	Test statistic	*N*	*P*	Test statistic	*N*	*P*
Presence of flower	$\chi^2 = 0.04$	61	0.840	$\chi^2 = 1.49$	26	0.222
Temperature	–			$t = -0.9$	26	0.372
Relative humidity	–			$w = 179.5$	26	0.929
Light	–			$w < 0.01$	26	<0.001
Vegetation height	$w = 839.0$	61	0.173	$w = 173.0$	26	0.294
Longest leaf length	$w = 1{,}272.0$	61	0.019	$w = 314.5$	26	<0.001
Plant density	$w = 827.0$	60	0.005	$w = 213.0$	26	0.005
Plant area	$w = 1{,}507.5$	61	<0.001	$w = 293.0$	26	0.003
Distance to scrub	–			$w = 90.0$	26	0.053
Snail incidence	–			$w = 245.5$	26	0.001

Chi-square tests of difference were used to compare the frequency that food-plants and control plants had flowers present. Paired *t*-tests and Wilcoxon's tests were used to compare the other characteristics between food-plants and control plants in the same area. *N* refers to the number of food-plant/control plant pairs included in each test

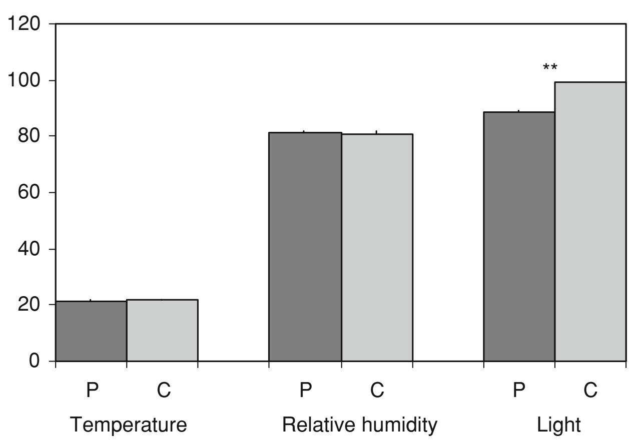

Fig. 4 Temperature (°C), Relative Humidity (%) and light (relative difference between plant and full light) averaged from observations over the season compared between plants with eggs (*P*) and controls (*C*) for 2007. **P* < 0.05, ***P* < 0.01. *Standard error bars* are shown. See Table 2 for statistics

sunning (36%), flying (12%) or interacting with another male or butterfly (7%). Neither sex was often seen nectaring, although butterflies were observed to take nectar from cypress spurge (*Euphorbia cyparissias*), cow parsley (*Anthriscus sylvestris*) and hawthorn (*Crataegus monogyna*) over the course of the study. One individual was also observed to drink from damp chalk.

Discussion

Our study demonstrates that Duke of Burgundy have specific habitat requirements on chalk grassland sites as both adults and larvae, as do both their food-plants. The degree of shelter is particularly important in determining the distribution of adults, as might be expected for a spring-flying species, when peak daytime temperatures may be relatively low. Sheltered locations enable adult activity in sub-optimum conditions. The highest densities of males were found in the most sheltered locations on the reserve, such as at the bottom of deep gullies. The adults, larvae and food-plants also preferred steeper areas of the reserve. This may be partially related to shelter, as areas with varied topography would also receive protection from the wind. The higher numbers of food-plants in these areas indicates that this might also be owing to more favourable growing conditions for cowslips and thus for larvae. Cowslip germination relies on disturbance (Brys et al. 2004) and it is likely that steeper areas of the reserve provide this, with occasional landslides on unstable ground.

For areas with slopes, aspect will considerably influence the microclimatic conditions. As a result, preferences vary significantly between different stages of the butterfly's life cycle. The adults were consistently found more commonly on southern slopes: areas that would be warmer and therefore allow the butterflies to become active sooner. Correspondingly in woodlands, higher levels of activity are seen in open, sunny rides (Greatorex-Davies et al. 1993). In contrast, cowslips and larval-damaged food-plants were found more commonly on northern and eastern slopes. Such areas would be cooler and remain damper than southern slopes, perhaps increasing cowslip survival in periods of dry weather. Larvae in these areas would have a higher density of plants to feed on, and each of these plants would be in damper soil and therefore continue to provide the caterpillars with green foliage over the summer. Over large areas of the reserve, vegetation did not appear to have any consistent effect on adult or larval distribution. However, both the number and area of food-plants were higher on areas of short grass, again reflecting this species' need for grazing or disturbance to allow germination of the seeds and to prevent out-competition by other plants.

Despite the very high number of food-plants recorded at Totternhoe Quarry (over 8,700), only a low percentage were used for oviposition by female Duke of Burgundy, with a fairly high frequency of these being laid on again later in the season. Choice of these plants therefore appears to be extremely restrictive. As in earlier studies (Fartmann 2006; Goldenberg 2004; Kirtley 1995, 1997; Léon-Cortés et al. 2003; Oates 2000), larger plants (average plant area 137.5 cm^2 compared to 71.3 cm^2 for the control plant) in

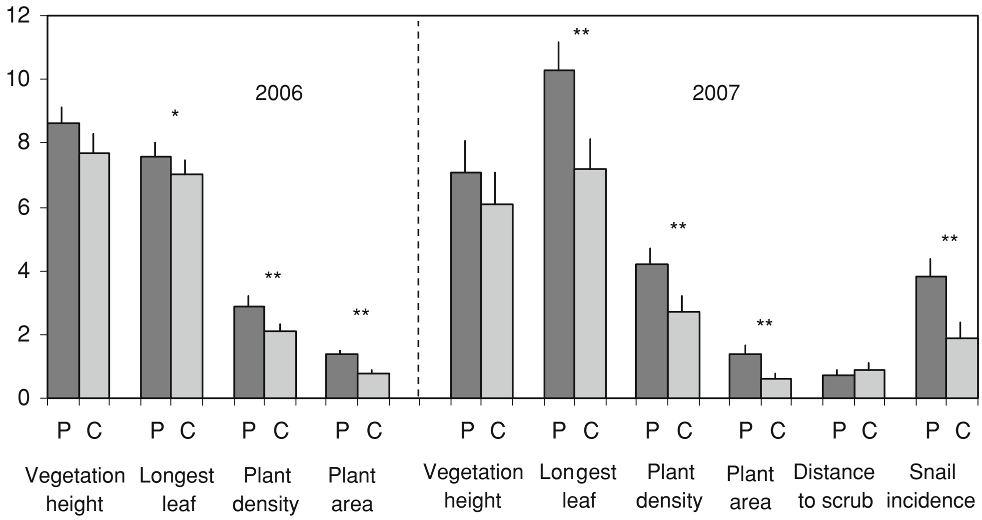

Fig. 5 Physical characteristics compared between plants with eggs (*P*) and controls (*C*) for 2006 and 2007. $^*P < 0.05$, $^{**}P < 0.01$. *Standard error bars* are shown. See Table 2 for statistics

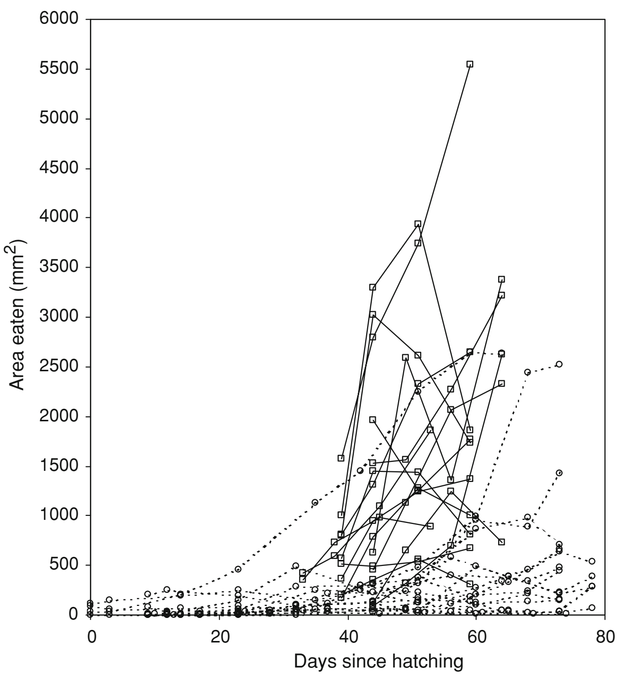

Fig. 6 Amount of damage in mm^2 for each measured plant that showed larval damage in 2006 and 2007 against days since eggs hatched (to nearest week). *Intact lines*—2006, *stippled lines*—2007

denser patches were consistently preferred, reflecting the larval requirement for sufficient food to reach pupation size. Larvae are readily able to move between food-plants (Oates 2000), so this volume of plant material can either be provided by large plants or by plants growing in dense patches. Although not significant at the scale measured, there was also a consistent trend for plants with eggs to be surrounded by higher vegetation, supporting the idea that the water status of plants is important to Duke of Burgundy larvae. Taller grass sward may reduce water loss from the soil and allow plants to remain green and palatable throughout the summer. Plants with eggs were in a significantly darker location and had a higher incidence of snail presence, again indicating that plants in damper locations are preferred. The fact that these differences were all found within a relatively small area and distance between the food-plants and control plants, reflects the heterogeneity that is present on the site at these small scales and again underlines the specificity of female oviposition site choice. The association of food-plants with scrub contrasts to some extent with the results of habitat preference for the whole reserve, where more sheltered areas did not have higher number of plants with larval damage, but did have higher numbers of adults. This is likely to be a matter of scale. As the adults are relatively mobile, a larger sheltered area is required, which is therefore detectable at the reserve scale. In contrast, the larvae are restricted to ground level and will probably only move a few metres during the course of the season. As a result shelter at the reserve scale may not appear to impact on them, but rather the level of cover within a few metres of where they are present.

Area of larval damage significantly predicted the length of larvae found on plants during the season. This relationship can thus be used as a tool to calculate the success of different areas in raising larvae. This could be achieved by calculating the area of damage on plants in different sections of a habitat at the end of their season, and using this to calculate the final size of the larvae. This provides a quantitative scale from which to judge the success of larval areas. There was considerable variation in the amount of damage recorded between plants, with number of eggs being a significant factor in predicting the amount of damage seen both per day as well as total damage at the end of the season, indicating a reasonable level of egg and larval survival. Indeed, loss of eggs only occurred infrequently with disappearance and failure to hatch being the commonest causes of failure and grazing animals in one case destroying the food-plant. Therefore neither snails nor rabbits, which have previously been suggested as significant causes of egg-loss (Bourn and Warren 1998; Oates 2000), appeared to be important factors in determining egg survival in this study.

Adult dispersal over the reserve was fairly high with regular turnover between areas isolated by dense scrub. However, it should be noted that our study concentrated on a small reserve, so dispersal distances are only indicative of movement within a limited habitat area. Duke of Burgundy could therefore readily use a network of small habitat patches, separated by up to 100–200 m on a reserve. Management for the species could therefore focus on creating favourable habitat patches, as the species is able to move over unfavourable habitat. As in previous observations (e.g., Anthes et al. 2008; Kirtley 1995; Oates 2000), behaviour differed between the sexes, with males spending most of their time perching. Adults were observed to nectar only occasionally and their choices of nectar plants seem to be fairly wide-ranging, so availability of this resource is unlikely to be limiting.

Overall management for the Duke of Burgundy on chalk grassland reserves should focus on creating several specific habitat features. The first of these is a network of sunny, sheltered areas, where adults (particularly perching males) can remain active in poor weather. Such a requirement highlights the potential importance of old quarry sites for the species (as has been noted before for other animals and plants (Davies 1979)), providing shelter and varied topography. Successful habitats must also contain areas with high densities of large cowslips or primroses in locations where the plants will not dry out during the course of the summer. These damper locations might be provided by shady slopes or by the presence of taller vegetation or nearby scrub edge. Suitable areas for the Duke of Burgundy need not be the same from year to year, nor need they be connected, as long as the distance between patches is sufficient to allow adults to spread. Such conditions could be created on chalk grassland sites by clearing areas of dense scrub within existing large scrub blocks. Such areas can still have high densities of cowslips present, as plants are able to survive several decades under progressively closing canopies. Cowslips also produce a seed bank and adults have been found to show increased growth and rapid flowering as soon as the canopy is opened up (Endels et al. 2005). In addition, recruitment of cowslips depends strongly on seed-production the previous year (Brys et al. 2004), so flowering in the first year after clearing is likely to generate a rapid increase in cowslip density in future years. As cowslips require exposed soil to germinate successfully, clearance of scrub could also include scarifying of the soil surface and removal of any leaf litter. Clearance of dense scrub patches could therefore provide fairly high densities of food-plants. A network of such clearings would also be fairly sheltered as they would be surrounded by dense scrub and be fairly damp due to scrub shading the edges. Management of reserves for the Duke of Burgundy in this way may also have the advantage of reducing the competition for space between scrub edge-specialists such as the Duke of Burgundy and other chalk grassland species, which frequently prefer a shorter sward. Indeed, species such as the Duke of Burgundy and small blue (*Cupido minimus*), which require a varied habitat structure, have fared particularly badly on sites where heavy grazing and scrub cutting have take place to benefit species, such as the silver-spotted skipper (*Hesperia comma*) and the Adonis blue (*Polyommatus bellargus*), which require a short-turf (Davies et al. 2007).

Conclusion

Our study highlights the specific habitat requirements of the Duke of Burgundy and how these differ at different stages of its life cycle. It also clearly demonstrates that these requirements are different from many other chalk grassland plants, invertebrates and butterflies, which prefer short, grazed turf. Understanding these specific differences for a single species such as the Duke of Burgundy is crucial for its management on reserves and ultimately for its survival in the UK. It also provides an insight into the risks of a too general management regime on chalk grassland reserves. Severe scrub-cutting regimes or heavy sheep grazing on reserves may result in other species with similar requirements to the Duke of Burgundy also disappearing, impoverishing this diverse habitat.

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