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Accounting for habitat when considering climate: has the niche of the Adonis blue butterfly changed in the UK?

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Abstract

The dramatic recovery of three species of grassland specialist butterfly threatened with extinction at their high latitude range limits in the 1980s has been attributed to two factors: increased grazing on calcareous grassland sites and warmer air temperatures. Both result in the warming of soil surface temperatures, favourable to the larvae of these species. We address the influence of both of these factors on the habitat usage of the butterfly *Polyommatus bellargus*, undergoing recovery at its northern range edge. We test the hypothesis that the larval niche of *P. bellargus* has become less constrained in the past three decades, whilst controlling for changes in habitat structure. Once habitat change has been accounted for we find no evidence for a broadening of the larval niche of *P. bellargus*. Further, we show that coincident with the recovery of *P. bellargus* there have been drastic reductions in average turf height across UK chalk grasslands, but changes in air temperature have been highly variable. We conclude that changes to soil surface temperatures caused by reducing turf heights will have been a more consistent influence than air temperature increases, and so habitat improvements through increased grazing will have been the major driver of recovery in *P. bellargus*. We consider the need to account for changes in habitat when exploring the impacts of recent climate change on local habitats in thermophilous species, and emphasise the continued importance of habitat management to support such species under variable local climates.

Keywords: Larval niche, Climate warming, Habitat management, Habitat quality, Thermophilous.

Introduction

Insects, like many small poikilotherms, respond strongly to changes in temperature, especially at higher latitudes within species' ranges, where populations are often restricted to small patches of habitat that possess microclimates warm enough for larval development (Dennis 1991; Thomas 1993). During recent decades in West Europe, two factors have influenced the ambient temperature of the received microclimates for many grassland species whose larval stages live at or near the soil surface. Firstly, climate warming has elevated spring–autumn air temperatures (Roy and Sparks 2000; Trenberth et al. 2007). Secondly, agricultural changes have directly or indirectly altered the structure of most semi-natural grasslands, transforming the shading and insulation properties of swards (Thomas 1983, 1991). The combined impact of both factors can be synergistic (Thomas et al. 2009) or opposing (Warren et al. 2001) but their relative contributions to changes in habitat use by a thermophilous species have not been quantified. The relative degree of influence that each factor has had on the quality of habitats will inform how conservation management strategies are adapted, or not, in the future.

Many ground-breeding butterflies and other insects are restricted to warm, early successional stages within ecosystems near the (cooler) climatic edges of their ranges (Thomas 1993; Thomas et al. 1999). The numerous population extinctions of UK butterfly species in semi-natural grasslands were largely attributable to a cooling of their habitat following the near universal abandonment of semi-natural swards by farmers during the first 80 years of the twentieth century, exacerbated by the loss of rabbits through myxomatosis in the 1950s (Thomas 1991). The resulting taller swards lead to cooler microclimates at ground level. For example increasing the mean sward height of a grassland from just 1 to 5 cm can reduce daytime soil surface temperatures in March–October by up to 5 °C (Thomas 1983, 1993). Since the 1980s, many semi-natural grasslands in lowland England have gradually returned to close-cropped states following targeted conservation management, agri-environment schemes and the recovery of rabbit populations. For example, the re-introduction and recovery of the butterfly *Maculinea arion* (large blue) was driven by carefully controlled (heavier) grazing regimes in selected protected areas, which support higher densities of *M. arion*'s main larval resource, the ant *Myrmica sabuleti* (Thomas et al. 2009). The grazing intensity needed to generate the

threshold density of the ant host to support the butterfly had eased under the respective air temperatures of the 1970s and 2000s (Thomas et al. 2009, 2011), but the relative influence of habitat management and changes in air temperature in improving habitat quality has not been addressed.

Global warming is an equally well-documented driver of change in insects, affecting phenology, voltinism, niche breadth, population stability and density, and geographic ranges (Altermatt 2010; Davies et al. 2006; Hill et al. 2002; Oliver et al. 2012; Parmesan 2006; Parmesan et al. 1999; Roy et al. 2001; Roy and Sparks 2000; Thomas et al. 2001). Thermal constraints at higher latitudes can be relaxed, broadening the amount of habitat available to a species by enabling its larvae to occupy cooler aspects and slopes, and to exploit food plants in later successional stages; this in turn may facilitate range expansion and recovery in species that have undergone declines (Oliver et al. 2012; Thomas et al. 2001). The role of climate change in the range expansion of the butterfly *Hesperia comma* in the UK has been extensively studied (Davies et al. 2005; Thomas et al. 2001; Wilson et al. 2009, 2010). Davies et al. (2006) show that a key factor enabling this expansion was a widening of *H. comma*'s realized larval niche under warmer air temperatures. However, since the 1980s the habitat of many *H. comma* sites has been managed to optimise larval habitat (as defined by Thomas et al. 1986), and so warmer temperatures and habitat management will have been acting on *H. comma* populations concurrently.

Polyommatus bellargus in the UK

P. bellargus is bivoltine in the UK and its sole larval host plant is *Hippocrepis comosa*, with the offspring of the second adult generation overwintering as larvae. Between 1950 and the 1980s, 70 % of *P. bellargus* colonies in the UK had gone extinct and its range had retracted by 42 % (Thomas 1983; Warren et al. 1997). Since receiving Priority Species status in the UK Biodiversity Action Plan in the 1990s, the number of UK colonies of *P. bellargus* has increased fourfold compared to its nadir in the 1980s, including a 30 % range increase in the past decade; consequently in 2006 its national status was downgraded to a UK Biodiversity Action Plan Species of Conservation Concern (Asher et al. 2001 ; Bourn and Thomas 2002; Fox et al. 2006).

The recovery of *P. bellargus* coincided with the restoration of grazing to many former sites, but it has also been suggested that a warmer climate has broadened its realized niche (Asher et al. 2001; Fox et al. 2006; Roy and Thomas 2003). A seasonal switch exists between the niches occupied by successive generations of larvae, with the summer-feeding cohort exploiting *H. comosa* plants growing in 2 to 7-cm-tall swards (in 2000), and the autumn/spring-feeding larvae constrained to those growing in short turf (<3 cm) within sheltered depressions. These microhabitat constraints ensure a warm microclimate but also impose an annual population bottleneck on overwintering generations (Roy and Thomas 2003). A broadening of the realized niche of this second, temperature-constrained generation might therefore have contributed to the UK recovery of *P. bellargus*. Here we explore the hypothesis that the larval niche of the second, more constrained generation of *P. bellargus* has become broader in its habitat preferences than in previous decades, whilst accounting for changes in habitat structure that have occurred. Further we consider how both air temperatures and habitat structure have changed within the study region, and how this might explain their respective influence on the habitat usage in *P. bellargus* in recent decades.

Materials and methods

Study sites

In 2009 three nature reserves in Dorset, UK, were selected to record the oviposition preferences of second-generation *P. bellargus* females [Ballard Down, Swanage (SZ0281); Fontmell Down, Shaftesbury (ST8817); Five Marys, East Chaldon (SY7884)]. These are managed nature reserves of calcareous grassland on south-facing slopes known to sustain stable populations of *P. bellargus*. These sites were selected because historical data on the oviposition preferences of *P. bellargus* exist for Ballard Down in 1981 (J. A. Thomas, unpublished data) and for Five Marys Down in 2000 (Roy and Thomas 2003). All analysis was carried out in the statistical computing package R, version 2.15.2 (R Core Development Team 2012).

Oviposition preferences of *P. bellargus*: 1981 and 2009

Stratified random sampling was used for both data sets; to make sure that the different habitat structures within each site were sampled proportionally. Prior to sampling each site was surveyed and divided into broad areas based on the habitat structure, classed as 'short turf', 'long turf' or 'scrub'. Sampling of host plants was then conducted at random within each stratum, with the search time being proportional to its area within the site.

In late August and early September 1981 data were collected on Ballard Down using stratified, random egg searches across the site. For each *H. comosa* plant sampled the turf height (see Stewart et al. 2001) and degree of shelter were recorded. Shelter was defined as one of three categories: open downland with even, unsheltered terrain; limited shelter from tracks, scrapes and depressions; and complete shelter in tracks, scrapes, hoofprints and similar depressions (after Thomas 1983). The number of eggs found on each plant was also recorded. Data for 1981 were analysed using a generalised linear model with quasiPoisson errors, to correct for overdispersion.

Data for 2009 were collected in early August to mid September, the flight period of the second generation of *P. bellargus*. For each site, host plants were first sampled from the entire population using stratified random sampling, to describe the available population of host plants. Plants that had been oviposited on were at first sampled by following ovipositing females and recording plants on which they selected to lay eggs (after Roy and Thomas 2003). However, this technique proved time consuming, and so to ensure adequate data were collected stratified egg searches were used. A quadrat was thrown to a random point within each stratum and *H. comosa* plants found within it were searched for eggs, and the search was terminated when an egg was found or all plants had been searched. These searches were repeated in all strata for 15–30 min at a time depending on the size of the strata, and this was repeated as necessary until around 50 plants with eggs on had been located. For each plant the variables of turf height (cm) and shelter category were recorded, along with the percentage cover of bare ground and host plant using a 25 × 25-cm quadrat. Due to differences in topography between sites, as a matter of caution the shelter categories 2 and 3 were amalgamated, to avoid any false distinctions between sites. The two shelter categories were recorded as (1) open downland with even, unsheltered terrain; (2) shelter from tracks, scrapes and depressions (adapted from the shelter categories of Thomas 1983). Bare ground was recorded as it increases the temperature of the surrounding soil, and is

specifically recommended as favourable to *P. bellargus* in the Biodiversity Action Plan (Bourn and Warren 1998). A total of 146 *P. bellargus* eggs were observed across the three field sites (ca. 50 per site), with 37 of these located by observing the oviposition events and 109 by stratified eggs searches. Data were also collected for 174 random plants, split approximately equally between sites, again using stratified randomly thrown quadrats to select each plant sampled and collecting data for only one plant per quadrat. A presence-only logistic regression model was used to estimate the effect of turf height and shelter category on oviposition preferences. This utilised the expectation maximisation method of Ward et al. (2009), which accounts for the fact that although the presence of eggs recorded in this data set are true presences, the random plants represent pseudo-absences, in that eggs were present on some of these plants. The degree of contamination with eggs in the random host plant population was estimated to be four in 100 plants by checking each host plant sampled for eggs. The expectation–maximisation procedure utilises this estimate to adjust a logistic regression model to provide more reliable parameter and probability estimates (Ward et al. 2009). Checks for co-linearity between explanatory variables, using variance inflation factors (VIFs) revealed that no variables were correlated enough to cause concern, as all VIF values were <2.

To examine how modelling the number of eggs on a plant for the 1981 dataset, as opposed to a presence–absence modelling approach, might have affected the conclusions, a presence–absence analysis was also run using the 1981 data. Plants with any number of *P. bellargus* eggs on were grouped as presence plants and those with no eggs remained as absence. A generalised linear model with binomial errors was used.

The effect of year on oviposition preferences

Two analyses were carried out to assess if the oviposition preferences of *P. bellargus* had altered with regard to the turf height and shelter category; one comparing preferences on Ballard Down in 1981 with those in 2009 and another comparing preferences on Five Marys in 2000 with those in 2009.

Oviposition data for Five Marys in 2000 were collected from observations of ovipositing females. Turf heights and shelter categories were recorded for these plants. Stratified

sampling of random plants for turf height and shelter category was also carried out, for a total of 700 plants from the available host plant population.

Two problems had to be overcome in analysing these dataset pairings.

- The 1981 data set being a true presence–absence dataset: these data were made comparable to the 2009 sampling regime by generating a random population of host plants through sampling from the entire 1981 dataset 200 times, with replacement. As the 1981 dataset represents a random sample of the original host plant population, this provided an equivalent of the random host plant data sets collected in 2009.

- Changes in habitat usage being confounded with changes in habitat structure: comparing single-year models of oviposition preferences or running a logistic regression with year as a categorical variable would not distinguish whether this was due to changes in habitat structure or climate. To overcome this a methodology was used that would distinguish between change that resulted from habitat change and that caused by year. The proportion of plants falling into turf height–shelter category combinations was calculated to create a response variable that was standardised across years. Plants were allocated to a class based on their turf height value (1–15) and their shelter category (1 or 2). For the 1981 and 2001 shelter categories 2 and 3 were amalgamated into one category to make them comparable with the 2009 data set. For each site, within each year, the proportion of all egg bearing plants falling into each class was then derived (PE). The same process was also carried out for the random plants sampled, to give the proportion of plants for the population of a whole site that fell into the categories represented for egg-bearing plants (PR).

These data were then analysed using the linear model defined below, with PE representing the proportion of egg-carrying plants falling into each category, PR representing the proportion of random plants falling into each category and Yr representing year.

$$\text{Arcsine } \sqrt{\text{PE}} = \text{PR} + \text{Yr}$$

An arcsine square root transformation was applied to PE to normalise the distribution of the residuals. The null hypothesis is that the variance in PE is explained by PR, that is the variation in plants selected for laying is explained purely by the availability of plants within the larger population. The addition of Yr to the model would show whether year explains

any residual variation in oviposition preferences, so indicating if a shift in oviposition preferences has occurred over the intervening decades.

The effect of turf height and shelter on the temperature of the soil underneath host plants

In October 2011, while the second instar larvae were still feeding between resting at the base of the plant or in soil crevices below it, the soil temperature was measured underneath 102 *H. comosa* plants. Measurements were made on Ballard Down over 2 days (40 plants on 1 October 2011 and 62 plants on 2 October 2011), along with the ambient air temperature and the surrounding turf height and shelter category. All measurements were made under clear sky and low wind conditions, between 1300 and 1500 hours the first day and 1330 and 1530 hours on the second day. Soil temperature was measured at a depth of 5 mm under the soil surface and the probe (EcoScan Temp 5, ± 0.5 accuracy; Eutech Instrumental) was left there until the temperature reading became stable. Ambient air temperature was measured by placing an air temperature probe (Precision Thermometer, ± 0.5 accuracy; ETI) approximately 10 cm above the soil surface, left to stabilise for the duration of taking ten to 15 soil readings. The soil-ambient temperature difference was calculated (soil temperature–ambient temperature). Initial model fitting with a quadratic term for turf height suggested that the relationship was non-linear and so a generalised additive model was employed to fit a non-linear trend in the final model, using the mgcv package in R (Wood 2011).

Changes in turf height structure on *P. bellargus* sites

Surveys of the sward structure of 48 calcareous grassland sites in Dorset were made in 1979 and again in 1998–1999. For each site, turf height was measured at 30 random points, with stratified sampling where necessary and the mean turf height was calculated. A pairwise *t*-test was used to examine whether turf heights for 1979 were significantly greater than in 1998–1999. Both data sets were square root transformed to achieve normality prior to analysis. The turf heights of Ballard down in 1981 and 2011, derived from all plants searched for eggs in 1981 and recordings of turf structure across the site in 2011, were

tested with a Mann–Whitney *U*-test to examine if turf height in 2011 was significantly shorter than in 1981.

Changes in temperature in the Dorset region

Soil surface temperatures reflect those experienced by caterpillars at the host plant level and are known to be dependent on air temperatures, with higher air temperatures resulting in a warmer surface temperature (Morecroft et al. 1998). Mean temperature data for August and September, the months in which *P. bellargus* fly and oviposit, for the Dorset region were taken from the UK MET office (The National Weather Service) data from the Hurn weather station from 1970 onwards, which is approximately 30 miles away from each of the sites. A linear model was used to assess if mean temperatures in August and September, when adults select the plants for their autumn/spring-feeding larvae, had increased significantly over the past 40 years in the local region. This would in turn imply that soil surface temperatures would also have increased on average.

Results

Oviposition preferences in *P. bellargus*

Sward structure explained around 46 % of the variation in the number of *P. bellargus* eggs on *H. comosa* plants in the 1981 dataset. Turf height accounted for around 68 % of the explained deviance [$F_{(1,314)} = 148.6, P < 0.001$], with the number of eggs on a plant decreasing with increased turf height ($\beta = -0.549 \pm 0.069$). Increased shelter independently increased the number of eggs found on a plant [$F_{(2,312)} = 35.4, P < 0.001$], with shelter category 2 having, on average, significantly larger numbers of eggs than shelter category 1 ($\beta = 1.470 \pm 0.336$), as did shelter category 3 ($\beta = 2.043 \pm 0.318$) (Fig. 1). When the data were converted to presence-absence, the results of the logistic regression were similar with around 34 % of the deviance explained and both turf height and shelter category maintaining their relationships and explanatory power.

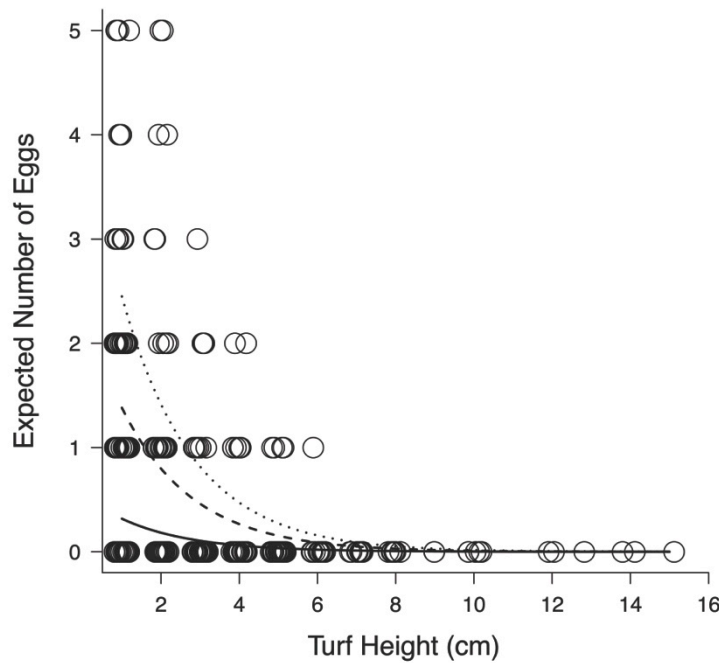


Fig. 1 Predicted relationship between the number of eggs on a plant and the height of turf in which a plant was located on Ballard Down in 1981. The solid line represents predictions for shelter category 1, the dashed line for shelter category 2, and the dotted line for shelter category 3. Shelter categories are as follows: (1) open downland with even, unsheltered terrain; (2) limited shelter from tracks, scrapes and depressions; and (3) complete shelter in tracks, scrapes, hoofprints and similar depressions. The points show the actual data for the number of eggs found in each turf height, though two data points for an egg number of eight and one data point for an egg number of ten are not shown on the y axis, to keep the model predictions clear. Data points are staggered to provide a clearer picture of their distribution

For 2009, the additional variables of bare ground and *H. comosa* cover were removed from the model in a stepwise fashion as they were not significant predictors of egg presence. This permitted 105 extra random plants with records only for turf height and shelter category to be added to the data set to improve the statistical power of the model, and the model re-run with just these variables. This model explained 23 % of the variation in oviposition preference [$\text{pseudo-}R^2 = 0.23$, $\chi^2_{(6,400)} = 127.0$, $P < 0.0001$], with turf height again having a negative effect on the probability of a plant bearing an egg [$\beta = -1.026 \pm 0.136$, $z_{(405)} = -7.5$, $P < 0.001$] and accounting for the majority of the deviance explained [$\chi^2_{(1,405)} = 57.4$, $P < 0.001$] (Fig. 2). Shelter category was not a significant predictor of oviposition preferences for Ballard Down [$\beta = -0.4671 \pm 0.4784$, $z_{(402)} = -0.9$, $P = 0.329$] (Fig. 2a), but the interaction term between shelter category and site showed that shelter category 2 increased the probability of oviposition on Fontmell [$\beta = 1.590 \pm 0.695$, $z_{(401)} =$

2.2, $P < 0.022$], and Five Marys Downs [$\beta = 1.480 \pm 0.650$, $z_{(400)} = 2.3$, $P = 0.023$] (Fig. 2b, c). Though significant, the overall explanatory power of shelter was much lower than that of turf height [$\chi^2_{(2,400)} = 6.9$, $P = 0.0305$].

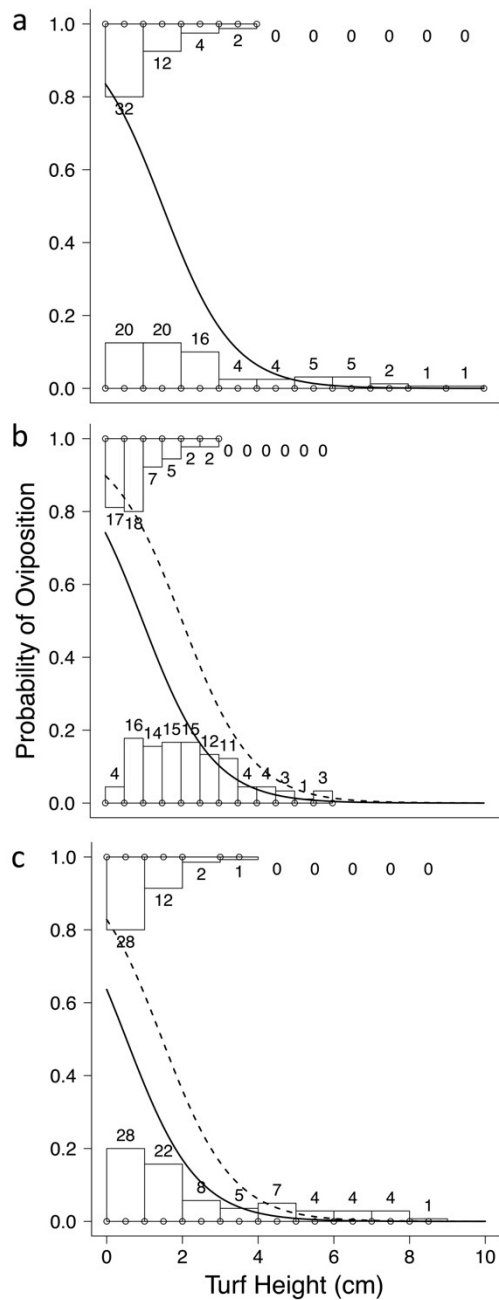


Fig. 2 Logistic regression curves for the probability of a plant having *Polyommatus bellargus* eggs upon it in relation to height of the turf surrounding it, in 2009, for **a** Ballard Down, **b** Fontmell Down and **c** Five Marys. *Top histograms* represent the turf height distribution of plants with eggs on, *bottom histograms* represent turf height distribution of random plants within the host plant population. The *solid line* represents predictions for shelter category 1 and the *dashed line* for shelter category 2

Niche expansion in *P. bellargus*

The minimum adequate model for the years 1981 and 2009 (Ballard Down) contained only PR (the proportion of plants within the overall population in each turf-shelter category selected for egg laying), as year was not a significant predictor of PE [$\beta = 0.001 \pm 0.003$, $t_{(15)} = 0.6$, $P = 0.583$]. Increased representation of plants in a given turf height-shelter category in the host plant population increased the proportion of plants with eggs found in that category [$\beta = 1.999 \pm 0.589$, $t_{(16)} = 3.4$, $P = 0.004$], explaining around 38 % of the variation in PE [adjusted (adj.) $R^2 = 0.38$, $F_{(1,16)} = 11.5$] (Fig. 3a). The model for data from the years 2000 and 2009 provides a similar picture, with year removed from the model as it was not a significant predictor of PE [$\beta = -0.008 \pm 0.005$, $t_{(39)} = 0.4$, $P = 0.725$]. The final model explained 30 % of the variation in PE [adj. $R^2 = 0.30$, $F_{(1,10)} = 5.7$, $P = 0.038$] with PR being a significant, positive predictor of PE [$\beta = 2.195 \pm 0.362$, $t_{(39)} = 7.9$, $P < 0.0001$] (Fig. 3b). For both of these analyses, year was also fitted as a categorical variable, as differences between years may not follow a linear trend, but this did not alter the significance of the term in either the model.

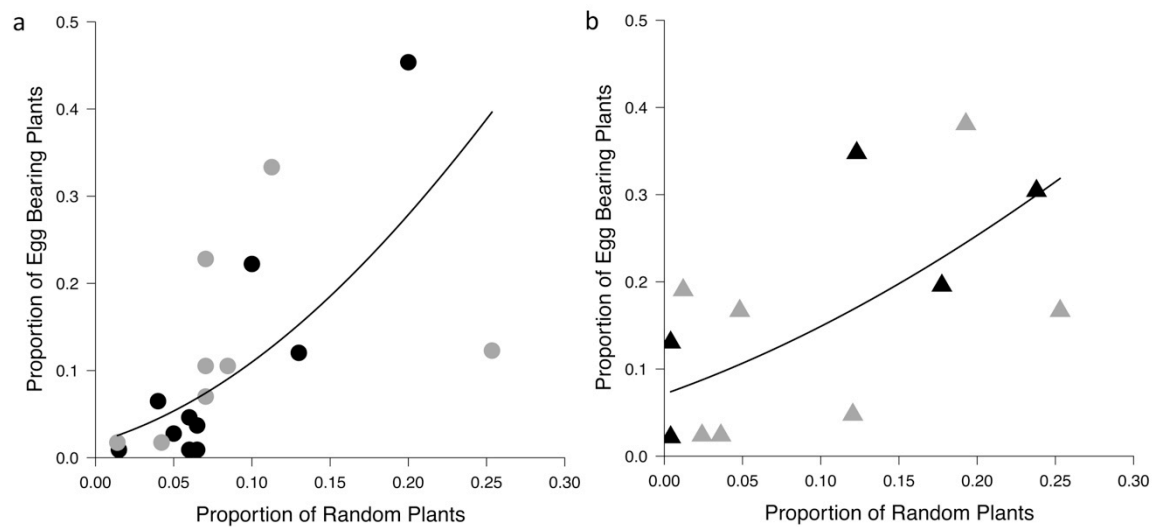


Fig. 3 The relationship between the proportion of egg bearing plants falling into turf height-shelter category and the estimated proportion of plants in the host plant population falling into this category for a) Ballard Down from 1981 – 2009 and with black circles representing 1981 and grey circles representing 2009, with black triangles representing 2001 and grey triangle representing 2009. The predicted values have been square root-arcsine back transformed.

The effect of turf height and shelter on the temperature of the soil underneath *H. comosa* plants

The final model included terms for turf height, shelter category and day, explaining around 45 % of variation in air–soil temperature difference (adj. $R^2 = 0.45$). Turf height was a significant, negative predictor of air–soil $P < 0.05$], with an increase in shelter increasing the difference between the soil and air temperature ($\beta = 1.078 \pm 0.424$) (Fig. 4). Recording day was also significant [$F_{(1,97)} = 6.3$, $P < 0.05$], with temperature difference increasing between days ($\beta = 1.044 \pm 0.417$). This difference between days is likely due to the fact that on the second day (2 October) the temperature records were begun 30 min later in the day, meaning that the ground will have been more heated.

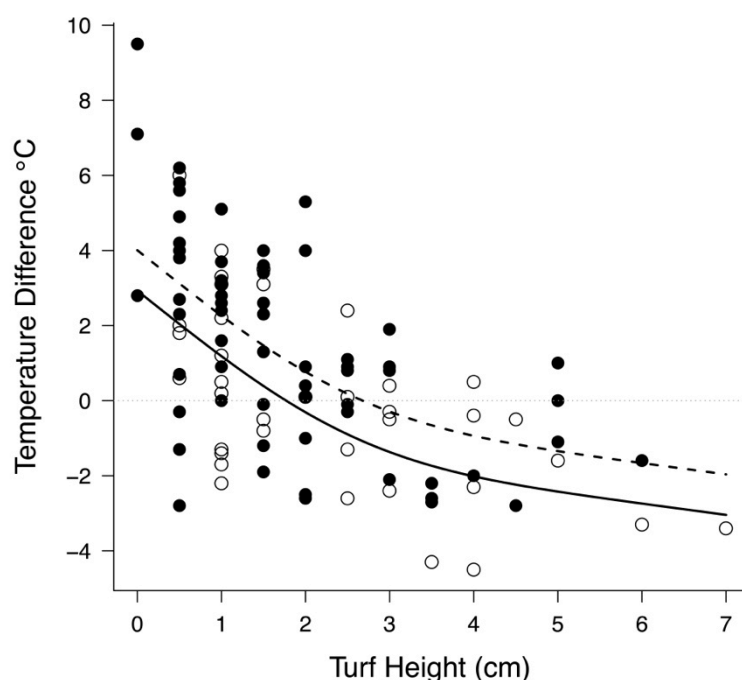


Fig. 4 The predicted effect of turf height on soil temperature relative to air temperature under *H. comosa* plants on 1st and 2nd of October 2011 on Ballard Down, from a Generalized Additive model. Soil temperature was measured with the probe tip 5mm below the soil surface and air temperature was measured at 10cm above the soil surface. The solid line represents shelter category 1 (open downland with even, unsheltered terrain) (n=38) and the dashed line shelter category 2 (shelter from tracks, scrapes and depressions) (n=64) and points representing the original data. The points are the original data, with clear circles representing shelter category 1 and black circles representing shelter category 2. The coefficient for day kept at the average temperature between days (0.521°C) to represent the intermediate scenario.

Changes in sward height of calcareous grassland sites in Dorset

The average sward height of sites in 1979 was significantly taller than in 1998-99 (1979 $\bar{x} = 20.75 \pm 1.76\text{cm}$, 1998-99 $\bar{x} = 4.92 \pm 0.33\text{cm}$, $t_{(47)} = 11.4$, $p = <0.001$). The turf height on Ballard down in 1981 was also significantly taller than in 2009 (1981 $\bar{x} = 3.42 \pm 0.14\text{cm}$, 2009 $\bar{x} = 2.197 \pm 0.11\text{cm}$, $W = 28684.5$, $p < 0.001$).

Changes in air temperature in the Dorset region over four decades

Year did not explain a significant amount of variation in mean August temperature over the past four decades ($F_{(1,39)} = 2.3$, $\text{adj}R^2 = 0.031$, $p = 0.137$). For September, year explained around 14% of the variation in mean temperature ($\text{adj}R^2 = 0.142$, $F_{(1,39)} = 7.7$, $p = 0.008$), with average temperature increasing with year ($\beta = 0.035 \pm 0.012$) (Fig. 5).

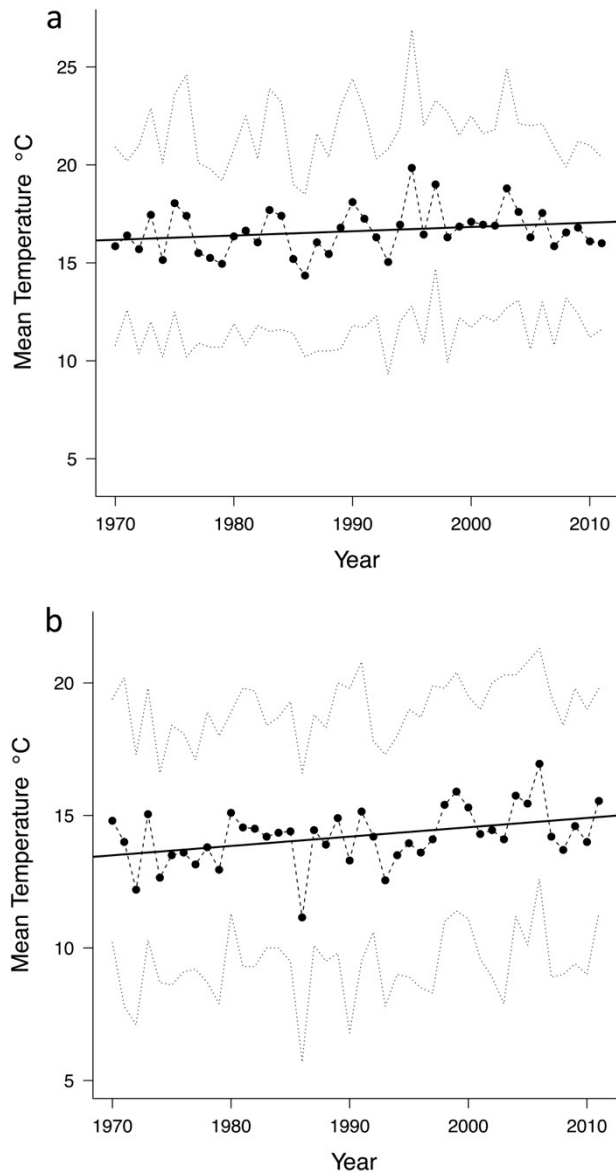


Fig. 5 Mean temperatures in Hurn, Dorset, from 1970 to 2010 for **a** August and **b** September, showing the line of best fit as predicted by a linear model and the maximum and minimum temperatures as *dotted lines* above and below the mean values. The model for August temperatures was not significant [$F_{(1,39)} = 2.3$, adjusted (adj.) $R^2 = 0.031$, $P = 0.137$] and the model for September temperature showed a significant increase in temperatures [adj. $R^2 = 0.142$, $F_{(1,39)} = 7.7$, $P = 0.008$]

Discussion

The larval niche of *P. bellargus*

It has been speculated that a warmer climate has broadened the larval niche of *P. bellargus* in the UK, and that habitat management practices for this species may need to change as a result (Asher et al. 2001; Fox et al. 2006; Roy and Thomas 2003). However, once changes

in the availability of host plants in optimal microhabitats over the past three decades have been accounted for there is no evidence to suggest an expansion in the realized niche of *P. bellargus* in the UK.

Historical turf height data for 48 calcareous grassland sites in the UK clearly show large changes in habitat structure, between 1979 and 1998–1999, with turf height across sites being reduced by 15 cm on average. These reductions will have resulted in warmer microclimates at the host plant level; we found that a decrease in turf height from 3 to 1 cm could increase the temperature of the soil (and larval niche) below a plant by around 2.0 °C, but turf heights above 3 cm will result in soil surface temperatures cooler than that of the air. Parallel air temperature increases in the region over the past 40 years (significant for September but not August) show high levels of inter-annual variation, meaning a warming effect has not been constant across the years. For instance, the mean September temperatures for 1981, 2000 and 2009 were 14.6 °C, 15.3 and 14.6 °C, respectively. A lack of change in the realized niche of *P. bellargus* is consistent with the variability in the magnitude of temperature differences between years. In some years warmer temperatures certainly may have relaxed the microhabitat constraints on *P. bellargus*, but the inter-annual variability will make a consistent effect upon habitat availability, and so populations, unlikely. The changes in microclimate caused by increased grazing pressure on sites will therefore have been larger and, where management has been sustained, a more consistent influence on microclimate than those caused by rises in air temperature.

It must be acknowledged that the reduction in turf height over the decades makes the prospect of observing a shift in the niche of *P. bellargus* more remote. The number of host plants found in tall turf will have been reduced, which in turn reduces the opportunities available for females to oviposit in longer turf. *P. bellargus* may also have responded to climate change in other ways that would benefit its populations, such as earlier emergence and longer flight periods (Altermatt 2010; Roy and Sparks 2000). Our results also show that the influence of shelter category on oviposition was less than that of turf height, especially in 2009, and for Ballard Down in 2009 it was not a significant predictor of egg presence. The influence of shelter may be related to local wind speeds and topographies, and further data on soil temperatures at different sites are required to explore this further.

Overall our results suggest that periods of heavy grazing of calcareous grassland, to maintain areas of short turf, should remain a priority in the management of habitats for *P. bellargus*. This will serve to ensure the availability of suitably warm microhabitats in the face of variable temperatures, and will be particularly important in maintaining populations in cooler regions of the species range (Lawson et al. 2012) and cooler than average years. These findings also show that when considering the impacts of climatic warming on species we must be careful to consider the actual magnitude of local temperature changes. Global temperatures have undoubtedly risen in recent decades, altering the ecology of many systems (Parmesan 2006), but the degree of warming has been variable between regions and across time and this should be accounted for. Further, changes to a species environment that have occurred concurrently with climate change, such as those influenced by management, should be controlled for. If we had compared the single models of the 1981 and 2009 oviposition preferences we may have concluded that the larval niche of *P. bellargus* had become less constrained, as the importance of turf height and shelter explained 34-46 % of variation in oviposition preferences in 1981, but only 23 % in 2009. By controlling for alteration in the structure of microhabitats over the decades, we show that the influence of turf height on habitat preferences has been reduced not because longer turf is more suitable, but because turf heights are, on average, much shorter. This is particularly important if habitat management protocols for a species are modified, as has been suggested for *P. bellargus*, because taking the wrong course of action could be detrimental.

Broader implications

Mair et al. (2012) found that in the past two decades there have been significant increases in the range expansion rates of specialist butterfly species, without significant changes in air temperatures. This corroborates our findings and suggests that habitat management is not only helping populations locally, but facilitating larger scale processes such as colonisation. Others have suggested that the importance of local habitat quality in generating connectivity in landscapes has been under-emphasised recently, both as a tool for conservation and with regard to facilitating range expansion in itself (Hodgson et al. 2009; Lawson et al. 2012). Indeed, metapopulation models of the expansion of *Hesperia comma* suggest that an increase in the quality of habitat patches (i.e. nature reserves) has facilitated its population increase and range expansion (Wilson et al. 2009). From this

perspective, more work considering the role that habitat change within nature reserves has played in species undergoing range expansion would be valuable.

We have demonstrated that changes to the sward structure of grassland sites has made habitats more favourable to *P. bellargus*, but the relationship between management activities and population change has yet to be quantified in the way that it has for *Maculinea arion* (Thomas et al. 2009). Future work to examine how populations of *P. bellargus* have responded to the management regimes on nature reserves across its range would be useful, and this could be extended to the impacts of management for thermophilous species on the populations of other butterfly species. *P. bellargus* is in a minority with regard to its recovery; 72 % of UK butterfly species show a continued decline in numbers on monitored sites over the past decade and 54 % show reductions in the extent of their UK distribution (Fox et al. 2011; Thomas et al. 2004). The intensive grazing that encourages species such as *P. bellargus* and *H. comma* can decrease the suitability of habitat for butterflies and other insect species (Davies et al. 2007; Kruess and Tscharrntke 2002; Turner et al. 2008). Research into the impacts of recent targeted habitat management on the populations of other species would help in creating management objectives for habitats that accommodate the requirements of different species.

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