Kent Academic Repository

Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming

ZOE G. DAVIES, ROBERT J. WILSON*, SOPHIE COLES and
CHRIS D. THOMAS†

Centre for Biodiversity and Conservation, School of Biology, University of Leeds, Leeds LS2 9JT, UK

Summary

1. The impact of climate change on the distribution, abundance, phenology and ecophysiology of species is already well documented, whereas the influence of climate change on habitat choice and utilization has received little attention. Here we report the changing habitat associations of a thermally constrained grassland butterfly, *Hesperia comma*, over 20 years.

2. Between 1982 and 2001–2, the optimum percentage of bare ground within habitat used for egg-laying shifted from 41% to 21%.

3. Egg-laying rates are temperature-dependent and females actively adjust microhabitat usage in response to temperature variations; relatively warmer host plants are chosen or oviposition at low ambient temperatures, and cooler host plants at high ambient temperatures.

4. Climate warming has increased the availability of thermally suitable habitat for *H. comma* at the cool, northern edge of the species' distribution, therefore increasing: (a) egg-laying rate and potentially the realized rate of population increase; (b) effective area of habitat patches as more microhabitats within a given vegetation fragment are now suitable for egg-laying; (c) buffering of populations against environmental variation as eggs are laid within a wider range of microhabitats; and (d) the number of habitat patches in the landscape that are currently available for colonization (including the use of more northerly facing aspects; Thomas *et al.*, *Nature*, 2001, **411**, 577–581).

5. Conservationists often assume the habitat requirements of a species to be constant, and manage habitats to maintain these conditions. For many species, these requirements are likely to change in response to climate warming, and care must be taken not to manage habitats based on outdated prescriptions.

Key-words: climate change, conservation, fecundity, microhabitat, niche.

Introduction

Ectothermic animals on the edge of their geographical range are frequently constrained by temperature and,

Correspondence: Z.G. Davies, Centre For Evidence-Based Conservation, School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK. Tel.: +44 (0)121 4144090; Fax: +44 (0)121 4145925; E-mail: z.g.davies@bham.ac.uk
*Present address: Área de Biodiversidad y Conservación, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Tulipán s/n, Móstoles, E-28933 Madrid, Spain.
†Present address: Department of Biology (Area 18), University of York, PO Box 373, York YO10 5YW, UK.

as such, may be restricted to specific habitats that are rare within the landscape. In the temperate zone of the northern hemisphere, species are often limited at their northern range boundaries to warm locations, such as sheltered south-facing hillsides of early successional grassland (Thomas *et al.* 1986; Thomas *et al.* 1999; Asher *et al.* 2001; Bourn & Thomas 2002; Roy & Thomas 2003). These limitations are frequently recognized in descriptions of the ecological requirements of such species, and conservation actions aim to ensure that locations where these conditions are found are protected and maintained, if necessary through site-based habitat management. Thus, conservation biologists often

implicitly assume the habitat requirements of a species to be constant. However, temperature or moisture-based habitat requirements would be predicted to change in response to climate change, just as they can in response to interannual fluctuations in weather conditions (Kindvall 1996). In these circumstances, the 'best' habitats for certain species may cease to occur within the originally protected locations, and habitat management designed to create formerly 'ideal' conditions for a given target species may no longer be appropriate.

With increasing evidence that climate warming is driving changes in the distribution, phenology, abundance and diversity of species (e.g. Crick & Sparks 1999; Parmesan *et al*. 1999; Roy & Sparks 2000; Blaustein *et al*. 2002; Parmesan & Yohe 2003), empirical work is also beginning to report that species near their northern range margins are utilizing a wider range of habitat types (Thomas *et al*. 2001; Roy & Thomas 2003). An appreciation of the mechanisms behind such niche shifts is important when predicting how species' requirements and populations may respond to continued climate change. It has been demonstrated that the overwintering mortality of insects' immature stages decreases with climate warming at cool range margins and, consequently, expands the range of locations where populations can persist (Virtanen, Neuvonen & Nikula 1998; Crozier 2004a). However, climate warming can also affect the fecundity of females by increasing the time available for egg-laying (Crozier 2004b), the rate of egg-laying, or by altering the range of thermally suitable locations for egg-laying (Roy & Thomas 2003).

In this paper, we document the changing habitat associations of a butterfly species currently undergoing rapid metapopulation expansion on the north-western edge of its geographical range. This case study investigates how these changes may have been mediated by the effects of climate on fecundity and microhabitat choice, and the implications for future conservation.

Methods

STUDY SYSTEM

During the twentieth century, the silver-spotted skipper butterfly *Hesperia comma* L., became increasingly rare in Britain (Asher *et al*. 2001) and, by 1982, was reduced to fewer than 70 populations (Thomas *et al*. 1986). In the UK, the species is on the north-western

edge of its range and is thermally constrained to suitable habitat located in southern England. The refuge colonies that survived in 1982 conformed to a remnant metapopulation structure and were located in eight habitat networks (Thomas & Jones 1993).

The declining status of this butterfly was a result of the widespread reduction of sparse, short-turfed calcareous grassland containing the species' sole larval host plant, sheep's fescue grass *Festuca ovina* L. (Thomas *et al*. 1986). Subsequently, the availability of suitable habitat within the species' former distribution has increased due to grazing management (Warren & Bourn 1997), the recovery of wild rabbit *Oryctolagus cuniculus* L. populations after myxomatosis (Wells *et al*. 1976; Trout, Tapper & Harradine 1986; Trout *et al*. 1992) and increases in the range of aspects that the butterfly can utilize (Thomas *et al*. 2001; Table 1). The result of these changes has been rapid metapopulation recovery and re-expansion (Davies *et al*. 2005).

Hesperia comma is a univoltine species and the flight period typically lasts from late July into early September. The females have specific ecological requirements for oviposition. Traditionally, eggs have been individually laid on the leaf blades of small tufts (1–5 cm tall) of *F. ovina*, generally situated in a warm hollow and growing adjacent to bare ground (Thomas *et al*. 1986; Warren, Thomas & Wilson 1999). It is common to find large numbers of eggs on favourable host plants.

The study sites utilized in this investigation were in Surrey, located in the chalk hills of the North Downs, south of London. Distributional surveys of the species in 1982 (Thomas *et al*. 1986), 1991 (Thomas & Jones 1993), 2000 (Thomas *et al*. 2001; Davies *et al*. 2005) and 2001 (R.J. Wilson, unpublished data) recorded population density, using the standard transect method developed by Pollard (1977), and the overall turf composition of every area of suitable habitat within the Surrey patch network. A habitat patch was defined as any area of suitable habitat, bounded either by a continuous barrier of woodland or scrub, or by at least 25 m of unsuitable grassland. The turf composition of a site consisted of an estimate of the percentage bare ground and the percentage *F. ovina* (< 10 cm tall) available to the butterfly. In 1982, 45 habitat patches were occupied by *H. comma*. In the subsequent 18-year period, the species expanded and, by 2000, a further 29 patches were colonized within the habitat network (Davies *et al*. 2005).

Table 1. The proportion of occupied habitat patches at each aspect in 1982, and colonized between 1983 and 2000

| Year | Proportion of occupied patches at each aspect | | | | | | | |
	N	NE	E	SE	S	SW	W	NW
1982 (*n* = 64 habitat patches)	0·00	0·00	0·01	0·09	0·41	0·39	0·05	0·05
2000† (*n* = 179 habitat patches)	0·14	0·09	0·12	0·23	0·06	0·10	0·14	0·12

†(not including sites already populated in 1982).

CHANGES IN OPTIMUM SWARD COMPOSITION FOR EGG LOCATION

During 1982, quadrat data were collected from stratified transects at Old Plantation Banks, a well established refuge population site in Surrey, in order to determine the sward composition that maximized the probability of finding an egg (Thomas *et al*. 1986). The methodology was repeated in 2001 and 2002, along transects that followed the same route as those in 1982. Successive 25×25 cm quadrats were systematically searched for eggs, and the percentage bare ground and *F. ovina* cover within each quadrat were recorded. Logistic regression was used to generate a 2001 and 2002 model, directly comparable with that produced by Thomas *et al*. (1986), describing the probability of egg presence within a 25×25 cm area of sward as a function of the percentage bare ground and *F. ovina*; all models included terms to represent the positive effects of bare ground and host plant cover, and the negative effects of (bare ground)^2 and (*F. ovina* cover)^2, such that an optimum percentage cover of each variable could be calculated. Quadratic terms were incorporated into the model as excessive levels of one variable would be at the expense of the other (Thomas *et al*. 1986).

To test the predictions of the 1982 and 2001 models for optimal sward composition, additional quadrat data were collected from six independent sites in Surrey during 2001. The percentage bare ground and *F. ovina* cover, and presence/absence of eggs, were recorded within 25×25 cm quadrats placed at 1-m intervals along stratified transects at each site. Logistic regression was used to determine the extent to which the presence/absence of an egg within these quadrats could be described as a function of the probability of finding an egg, derived by either the 1982 or 2001 model. The predictive power of each model was then evaluated using the area under the curve (AUC) for Receiver Operating Characteristic (ROC) curves of observed vs. predicted probability of egg presence (Fielding & Bell 1997).

The 1982 and 2001 models were used to estimate the relative suitability of all occupied habitat patches in the Surrey network, based on turf composition data collected in 1982, 1991, 2000 and 2001. The association between observed adult population density and predicted habitat suitability was evaluated for each year using Spearman's Rank Correlations.

EGG-LAYING RATES IN NORTH AND SOUTH-FACING MESOHABITAT

Six 1×1 m fixed quadrats (mesohabitats) were used to compare egg-laying rates on a north and south-facing slope, over a 10-day period in 2002. The two hillsides are a distance of 8·3 km apart and both support long-established *H. comma* populations, within the same metapopulation. Three fixed quadrats were placed on each site, the locations of which were chosen to ensure that each quadrat contained a range of bare ground and *F. ovina* cover, from areas with substantial bare ground through to areas with complete grass cover (i.e. each area of mesohabitat contained a choice of host plants growing within a similar variety of microhabitats). Females were contained within cages over, and slightly larger than (in order to avoid possible edge-related effects on egg-laying), the fixed quadrats. The cages were constructed using white bridal veil netting and tent pegs to an approximate height of 15 cm. The construction and material of the cages was designed to minimize the shading of the sward within the fixed quadrat. Temperatures inside the cages were equivalent to outside ambient temperatures and the female butterflies behaved naturally during oviposition when placed within the cages (females naturally fly very close to the ground when searching for egg-laying sites, so the height of the cage was not a constraint). Prior to starting the investigation, each fixed quadrat was thoroughly searched for eggs, and those found were removed.

Three *H. comma* females were placed within each cage between 11.00 and 16.00 British Summer Time (10.00–15.00 GMT) each day. The females were caught earlier the same morning and selected if they had a swollen abdomen and little evidence of wing wear. Such females were expected to have relatively large numbers of eggs available for oviposition. An artificial nectar source was provided within each cage, consisting of coloured cotton wool saturated in 10% sugar solution with a pinch of salt per litre, positioned in a corner outside the 1×1 m area of the fixed quadrat. The butterflies were observed feeding regularly throughout the day and showed neither preference for, nor avoidance of, egg-laying in the vicinity of the nectar source. At 16.00 h, the females were removed and the turf was systematically searched for eggs; a 10×10 cm quadrat was placed centrally over every egg found, and the percentage bare ground and percentage *F. ovina* surrounding the egg were recorded as measures of microhabitat. The eggs were then removed from the cage.

Ambient temperature readings were collected every 15 min during the investigation period. On both sites, three TinyTalk data loggers (Orion Components Ltd, Chichester, UK) were situated adjacent to the fixed quadrat cages, at ground level, but out of direct sunlight.

The investigation could not be replicated at site-level due to a number of constraints, such as the short time period when high female densities were available, and a lack of appropriate locations (e.g. in terms of aspect, distance to a nearby comparator or sustaining suitably large populations). Although site-level replication would have been desirable, any observed behavioural trends are likely to be robust as the female butterflies are responding individually to the ambient temperatures they are experiencing in the six experimental cages, rather than to the aspect of the site.

EGG-LAYING RATES IN MICROHABITATS

Egg-laying rates were also measured in smaller experimental plots for 7 days during 2002. Eight white fine

mesh netting food covers, with an apex height of 20 cm and enclosed ground area of 30×30 cm, were positioned on the south-facing slope. Care was taken to make sure that the percentage cover and quality of *F. ovina* available to the females was equivalent in all cages. A single female, meeting the condition criteria previously described, was placed within each cage between 11.00 and 16.00 BST. At the end of each investigation period, the microhabitat was searched for eggs and the number present was recorded. The eggs were then removed before repeating the investigation the following day.

AMBIENT TEMPERATURE VS. OVIPOSITION SITE TEMPERATURE

The effects of ambient temperature on female egg-laying were investigated at two high-density *H. comma* populations within the Surrey network, during a 2-week period in August 2001. Individual free-flying females, displaying oviposition flight behaviour, were followed until an egg was laid; the time of egg-laying was noted and temperature at the oviposition site was recorded using a hand-held probe thermometer (Checktemp HI-98509, Hanna Instruments Ltd, Bedfordshire, UK; ± 0.5 °C outdoor accuracy).

The ambient temperature at the time each egg was laid was later calculated by linear interpolation between readings taken at 30-min intervals, throughout the day, at each site; these were recorded using a thermometer, permanently positioned out of direct sunlight, 20 cm above ground level. The UK Meteorological Office standardized air temperature measurements are taken 1·25 m above the ground, the thermometers being shielded from external radiation within louvered wooden white screen boxes (Met Office 2001). The UK Meteorological Office air temperature measurements are therefore likely to be considerably lower than the boundary-layer ambient temperatures recorded in this investigation (whether by data loggers or thermometers) and experienced by these butterflies, which are subject to greater heat radiation from the soil and vegetation surface.

Results

CHANGES IN OPTIMUM SWARD COMPOSITION FOR EGG LOCATION

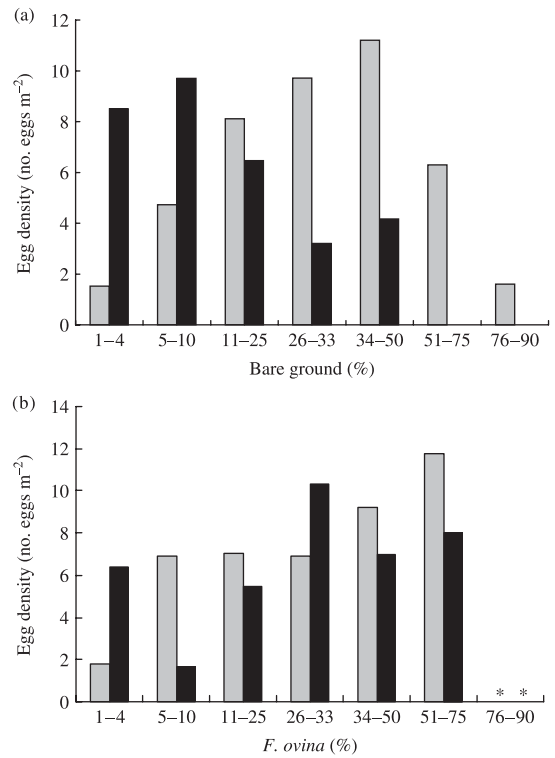When the egg distribution was examined along stratified transects at Old Plantation Banks, Surrey in 1982,

Fig. 1. Egg densities (number of eggs per m²) at different percentages of (a) bare ground, and (b) *Festuca ovina* in 25×25 cm quadrats during 1982 (grey bars) and 2001 (black bars). Percentage cover intervals are the same categories used in the 1982 survey (Thomas *et al*. 1986). A star indicates that the relevant percentage cover category was not available for *Hesperia comma* to utilize.

2001 and 2002, there was no significant difference in the proportion of quadrats containing eggs between years (χ^2-test: $\chi^2 = 0.60$, d.f. = 2, $P > 0.05$; Table 2). Since 1982, there has been a shift towards higher densities of eggs being laid in areas with little bare ground (Fig. 1a; ratio of 2001 to 1982 egg density decreases with increasing percentage bare ground interval; Spearman's rank correlation, $r_s = -0.955$, $n = 7$, $P < 0.001$), but no change in favourable host plant cover between 1982 and 2001 (Fig. 1b; ratio of 2001 to 1982 egg density is not associated with percentage *F. ovina* cover interval; Spearman's rank correlation, $r_s = -0.371$, $n = 6$, $P > 0.05$).

The logistic regression models used to describe the probability of finding an egg within a 25×25 cm quadrat in 1982, 2001 and 2002 were all significant (Table 3). None the less, the overall level of significance, and the number of significant terms within the model, decreased

Table 2. The presence of eggs within quadrats, during surveys in 1982 (Thomas *et al*. 1986), 2001 and 2002, at Old Plantation Banks, Surrey

Year	No. of quadrats (25 cm × 25 cm)	No. and % of quadrats with eggs present	Mean no. of eggs per quadrat	Mean no. of eggs per m²
1982	242	64 (26%)	0·43	6·80
2001	174	43 (25%)	0·37	5·89
2002	180	51 (28%)	0·57	8·98

Table 3. Logistic regression models used to describe the probability of egg presence (P) in 1982 (Thomas *et al.* 1986), 2001 and 2002, where %B and %F represent coefficients for percentage bare ground and percentage *Festuca ovina*, respectively, for Logit (P) = %B + (%B)^2 + %F + (%F)^2 + constant. All coefficients of determination (R^2) quoted in relation to the logistic regression models are consistent with the Nagelkerke (1991) definition. Refer to Table 2 for sample sizes

Year	%B	(%B)^2	%F	(%F)^2	Constant	−2 Log-likelihood	χ^2	R^2	P
1982	0·115*	−0·001*	0·083*	−0·001*	−3·711*	255·20	24·39	0·14	< 0·001
2001	0·083*	−0·002*	0·138*	−0·002	−3·236*	178·74	15·85	0·13	< 0·010
2002	0·047	−0·001	0·100	−0·002	−2·362*	203·42	11·16	0·09	< 0·050

*Significant terms (P < 0·05) within the model.

over time. The combination of bare ground and *F. ovina* that gave the highest probability of finding an egg in 1982, derived from the 1982 model, was 41% bare ground and 46% *F. ovina*. In comparison, the 2001 'optimum' sward composition was only 21% bare ground and 33% *F. ovina*, showing a substantial decrease in the necessity for bare ground (Fig. 2a). The 2002 bare ground and *F. ovina* optima were highly consistent with those in 2001 at 21% and 31%, respectively. When tested on quadrat data collected from independent *H. comma* sites, the 2001 Old Plantation Banks model was a more accurate descriptor of egg locations during 2001 (Logistic regression: P < 0·005 for four of the six sites) than the 1982 model (Logistic regression: P > 0·05 for all six sites) (2001 AUC > 1982 AUC for five of the six sites).

This shift in realized niche results in an increase in habitat availability and quality; most independent patches of habitat within the Surrey network have relatively low percentage cover of bare ground and are predicted to have become more suitable for *H. comma* over this period (Fig. 2b). However, the correlation between adult population density and the 'habitat suitability' of sites within the Surrey network, derived using either the 1982 or 2001 Old Plantation Banks model (applied to the average percentage bare ground and host plant cover at each site), has weakened over time (Fig. 3). Adult density has therefore become harder to predict on the basis of turf composition, suggesting that factors other than the availability of suitable microhabitats for egg-laying are now also limiting butterfly abundance.

EGG-LAYING RATES IN NORTH AND SOUTH-FACING 1 × 1 M MESOHABITAT

Mean daily ambient temperature during the study period was significantly warmer on the south-facing slope than the north-facing slope (day paired *t*-test: t = 2·50, d.f. = 10, P < 0·05). The relationship between the mean daily temperatures on each site was nonlinear; temperatures on the two hillsides were similar on days when the solar energy input was limited and the ambient temperatures were low, but the south-facing slope was increasingly hot compared with the north-facing slope on sunny days when the ambient temperatures were higher (Fig. 4a).
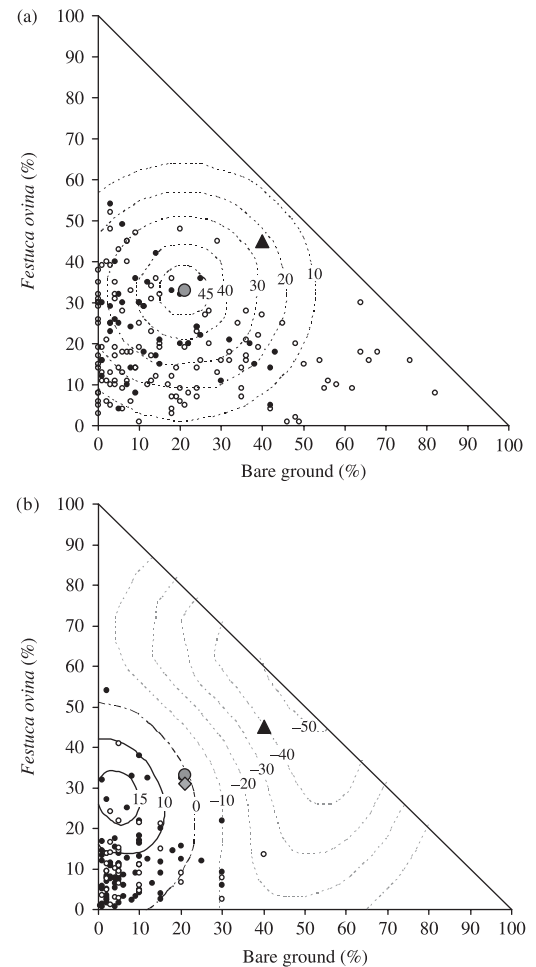

Fig. 2. (a) Percentage chance (dashed lines) of finding an egg in a 25 × 25 cm quadrat in 2001, as a function of the percentage bare ground and *Festuca ovina*, derived from the 2001 model. Grey filled circle, 2001 optimum sward composition; black filled triangle, 1982 optimum sward composition as described by the 1982 model (from Thomas *et al.* 1986); black filled circles, sward composition of quadrats with eggs present in 2001; open circles, sward composition of quadrats with no eggs present in 2001. (b) Changes in the percentage chance of egg presence from 1982 to 2001, derived from the models: black solid lines show increased chance of detecting eggs; grey dashed lines show decreased chance. Black filled triangle, 1982 optimum sward composition; grey filled circle, 2001 optimum sward composition; grey filled diamond, 2002 optimum sward composition described by the 2002 model; open circles, overall turf composition of habitat patches occupied by *Hesperia comma* in the Surrey habitat network in 1982; black filled circles, overall turf composition of habitat patches occupied by *H. comma* in the Surrey habitat network in 2001.
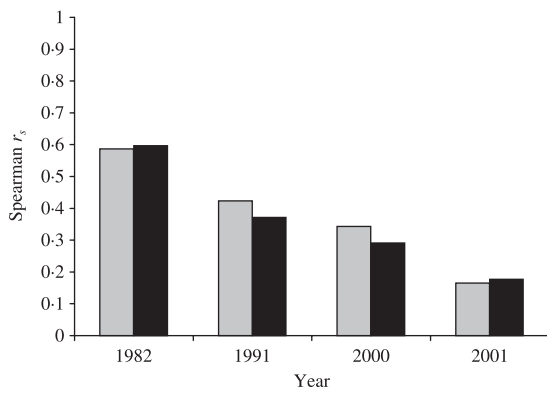
Fig. 3. The Spearman's rank correlation coefficients between adult population density and habitat suitability, as described by the 1982 model (grey bars) and 2001 model (black bars), for habitat patches within the Surrey network over time.

The mean number of eggs laid per fixed quadrat per day was 17·47 on the south-facing site, compared with just 9·71 per quadrat per day on the north-facing site. The daily mean egg-laying rate of *H. comma* females within the fixed quadrats, described by the number of eggs laid per female per hour, was significantly greater on the south-facing site than on the north-facing site (day paired *t*-test: $t = -3.19$, d.f. = 6, $P < 0.05$; Fig. 4b). There was no difference in the way females utilized the mesohabitat available to them on the two sites. Eggs were laid in a variety of microhabitats within the quadrat, and no relationship was found between sward composition surrounding the site of oviposition and mean daily ambient temperature. Egg-laying rate, irrespective of site aspect, increased with rising mean ambient temperatures, although the relationship was weak ($F = 2.98$, $R^2 = 0.06$, $P = 0.09$; Fig. 4c).

EGG-LAYING RATES IN 30 × 30 CM MICROHABITATS

In total, 225 eggs were laid over 7 days. The rate of egg-laying was not related to either the percentage bare ground or the percentage cover of *F. ovina*, suggesting that neither of these 'resources' was limiting oviposition.

The relationship between egg-laying rate and ambient temperature could, as in the mesohabitat investigation, be described by a linear regression equation ($F = 5.08$, $R^2 = 0.11$, $P < 0.05$; Fig. 5). Egg-laying rates at temperatures above 30 °C were excluded from the analysis. Above this threshold, the females within the cages began to suffer from heat stress as they were unable to behave naturally and move away into cooler areas of vegetation (which they were able to do within the larger mesohabitat cages, as in nature).

AMBIENT TEMPERATURE VS. OVIPOSITION SITE TEMPERATURE

One hundred and five egg-laying events were recorded having followed *H. comma* females in August 2001.
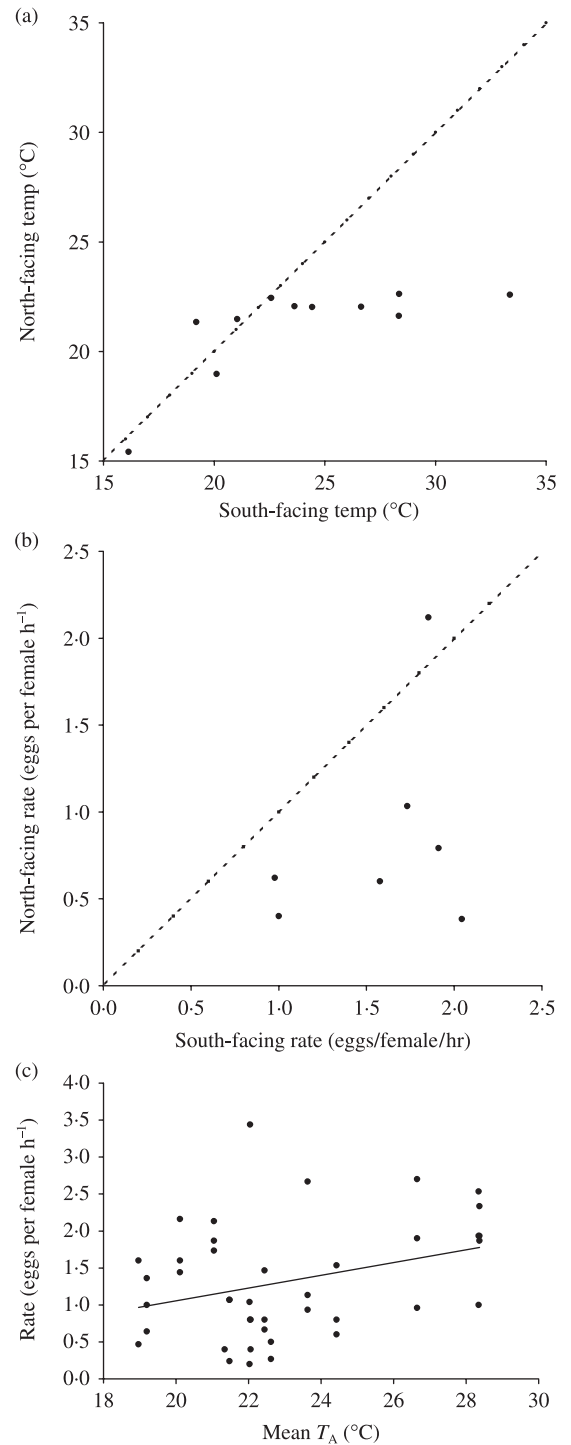
Fig. 4. (a) The relationship between mean ambient temperature (T_A) experienced on the north and south-facing slope. Each point represents the mean temperature between 11.00 and 16.00 BST each day. Dotted line denotes $y = x$. (b) Comparison of mean *Hesperia comma* egg-laying rate on the north and south-facing slope each day. Dotted line denotes $y = x$. (c) Egg-laying rate in mesohabitat investigation, as a function of mean ambient temperature between 11.00 and 16.00 BST. Regression line, $y = 0.061x$ (SE = 0.04)-0.148 (SE = 0.82).

Over the range of ambient temperatures available to *H. comma* throughout the day, the egg-laying rate was much higher above 30 °C (Fig. 6a). None the less, because temperatures were below 30 °C most of the
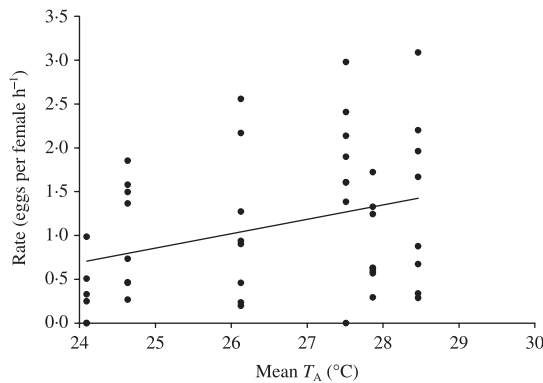
Fig. 5. Egg-laying rate in microhabitat cages, as a function of mean ambient temperature (T_A). Regression line, $y = 0.164x$ (SE 0.07)–3.250 (SE = 1.94).
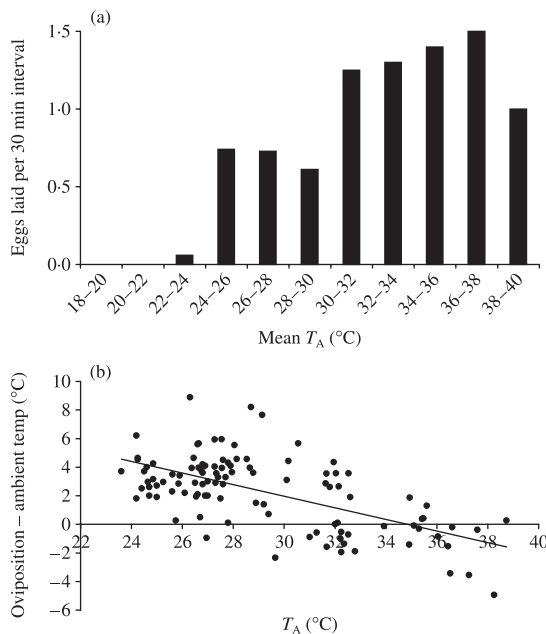

Fig. 6. (a) The number of *Hesperia comma* eggs laid per 30-min period of observation in relation to mean ambient temperature (T_A). (b) The difference in temperature between locations where eggs were laid and ambient temperature at the same point in time, as a function of ambient temperature. Regression line, $y = -0.406x$ (SE = 0.05) +14.155 (SE = 1.51).

time, the majority of individual eggs were laid below this temperature (Fig. 6b). There was a highly significant negative relationship between the microclimate (oviposition site temperature minus ambient temperature) and the ambient temperature when an egg was laid ($F = 63.12$, $R^2 = 0.38$, $P < 0.0005$; Fig. 6b). At lower ambient temperatures, *H. comma* females laid eggs on host plants in relatively hotter areas of sward, whereas at very high temperatures they chose to lay in cool microsites. The slope of the regression (−0.406) is significantly ($P < 0.0005$) shallower than a slope of −1, indicating that females only compensated for about 40% of the variation in ambient temperature, in choice of thermal microhabitat. As with the mesohabitat results, no relationship was found between ambient temperature and the sward composition selected for oviposition.

Discussion

CHANGING HABITAT ASSOCIATIONS 1982–2001

Twenty years ago, *H. comma* females had highly specific ecological requirements, using habitat characterized by high percentages of bare ground for egg-laying, situated on south-facing slopes. In the 19 years (generations) between 1982 and 2001, increasing numbers of populations have established on more northerly facing hillsides (Table 1; Thomas *et al.* 2001) and the optimum sward composition for egg location has shifted from 41% bare ground to 21% bare ground (Figs 1 and 2). This substantial decrease in the requirement for bare ground has resulted in an improvement in the suitability of most habitat patches within the Surrey network. Although there has been a distinctive shift in the optimum values for sward composition, the species has become more catholic in its choice of egg-laying locations; eggs are still laid on 'classic' host plants with characteristics corresponding to those used in 1982, but are also found in swards with no bare ground.

The strength of the relationship of adult population density with habitat suitability, derived by either the 1982 or 2001 models for probability of egg presence, decreased between successive *H. comma* surveys over the 20-year period. Adult density has become harder to predict on the basis of sward composition alone as a wider range of conditions have become available for egg-laying. This suggests that other factors, in addition to the availability of egg-laying locations, may now be limiting butterfly abundance.

The proportion of quadrats with eggs present was consistent between 1982, 2000 and 2001, indicating that the observed changes in habitat associations are not purely a consequence of population effects (i.e. higher egg densities). If population effects were the driving force behind the shift in habitat requirements, the optimum 1982 oviposition locations would still be filled preferentially.

OVIPOSITION RESPONSES TO AMBIENT TEMPERATURES

The mean egg-laying rate of *H. comma* females increased with rising ambient temperatures, indicating that egg-laying is temperature-dependent. The trend was exemplified by the significantly greater egg-laying rate of butterflies on the south-facing site, in comparison with those on the cooler north-facing slope.

At temperatures above 30 °C, butterflies within the microhabitat cages suffered heat stress and did not behave in a natural manner, detrimentally affecting oviposition rates. Under natural conditions, there would indeed be a maximum temperature above which egg-laying rates would decline. However, it is unlikely that this maximum is often or ever exceeded in Britain at present. The response of the butterflies can be attributed

to their confinement, as they were unable to move away into cooler areas of sward to thermoregulate; generally, *H. comma* females can be observed darting between patches of shaded vegetation at the highest ambient temperatures and actively choosing to lay eggs in these cooler environments (Z.G. Davies *et al*. pers. obs.). Females within the larger 1 × 1 m fixed quadrat cages were unaffected as, although restricted to relatively small areas, they could move into cooler patches of sward within the mesohabitat available to them.

The capacity of females for thermal regulation is most clearly demonstrated in Fig. 6(b). Free-flying females chose unusually warm microsites for oviposition during cool ambient conditions, and cool microsites during hot ambient conditions. This adjustment seems to hold the key to understanding the changes in habitat use. At cooler ambient temperatures, and therefore historically, the vast majority of egg-laying would take place at times when females needed to choose particularly warm microhabitats, restricting them to oviposition in warmer vegetation (i.e. short, sparse turf on south-facing sites). In current climatic conditions, *H. comma* females still generally oviposit within warm microsites, but can increasingly utilize cool microhabitats, thereby widening the range of habitat conditions (and number of habitat patches) over which eggs are laid. As a consequence, the association between one specific type of microhabitat and population density has weakened. However, as most eggs are laid under relatively cool ambient conditions and the egg-laying rate increases with temperature, there are often periods of the day, or indeed whole days, which are even now too cool for oviposition.

These results clearly show temperature-dependent variation in egg-laying rate and choice of oviposition location, but they do not fully explain the change in habitat associations that have been witnessed over the past 20 years. Given the traditional use of host plants growing next to bare ground, it might be assumed that on warm days *H. comma* would be more likely to lay eggs in areas consisting of lower percentage bare ground, and that microhabitats comprising of high proportions of bare ground would be more important under cool ambient conditions. Nevertheless, this was not the case: females in the mesohabitat quadrats on the north-facing slope did not choose to lay eggs in microhabitats with more bare ground (see also Davies *et al*. 2005).

This discrepancy might partly arise because we did not investigate the effect of microtopography on habitat choice in ovipositing females. Hollows, which were strongly favoured for egg-laying in 1982 (Thomas *et al*. 1986), are likely to warm up in the sun relatively quickly, and this effect may be stronger when the hollow contains patches of bare ground or shorter areas of turf that are sheltered by surrounding vegetation (Thomas 1983; Thomas *et al*. 1999). In addition, we have only considered changes to the thermal environment itself since 1982, and there is the possibility that selection could have altered aspects of the butterfly's behaviour

or thermal tolerance in the subsequent 19 years (generations). None the less, the thermal microhabitat chosen for egg-laying (Fig. 6b) alters directly in response to changes in ambient temperature at the time of oviposition. This supports the conclusion that *H. comma* was previously limited by ambient temperature to egg-laying within microhabitats characterized by high temperatures, whereas host plants growing within unbroken swards and marginally taller vegetation are now also available for use.

The warmer summers predicted as a consequence of climate warming (UK Climate Impact Programme 2002) are likely to be beneficial to *H. comma* within Britain. The rise in air surface temperatures already experienced by the adult stage of the life cycle, due to the interaction between climate change and phenological advancement, is predicted to have resulted in an increase in fecundity (Davies 2004). Given that failure to lay the full complement of eggs is frequently cited as a key limiting factor in lepidopteran population studies carried out in the north temperate zone (Dempster 1983), changes in oviposition rates within marginal populations may make an important contribution to increasing population growth rates.

IMPLICATIONS FOR CONSERVATION

Hesperia comma populations were traditionally restricted to very sparse vegetation on hot south-facing slopes (Thomas *et al*. 1986). Warmer ambient temperatures have increased *H. comma* egg-laying rates and the species can now utilize a greater variety of *F. ovina* plants for oviposition. These climate-mediated changes in habitat associations and egg-laying rates have facilitated the colonization of an increasingly wide range of aspects and habitats that were previously too cool to be utilized. Since 1982, the species has undergone a vigorous range re-expansion (Thomas *et al*. 2001; Davies *et al*. 2005).

Climate warming has been an important driving force in the recovery of *H. comma* in Britain, on the cool northern edge of the species' geographical range, as the suitable habitats are constrained by temperature. The rise in ambient temperature experienced by the butterfly will have aided the metapopulation re-expansion in a number of ways. First, greater temperatures should increase the potential fecundity of *H. comma* females. If this results in larger populations, for which there is some evidence (e.g. 32 of the 45 habitat patches occupied in the Surrey network experienced site-level increases in population density between 1982 and 2000), they will be less prone to extinction and will result in larger numbers of dispersing migrant individuals being available to colonize unoccupied habitat patches and establish new populations. Secondly, the wider range of thermal and physical microhabitats used for egg-laying increased the potential resource density within each grassland habitat fragment (this could be interpreted either as an increase in effective

area or in patch quality). Again this may increase local population sizes. Thirdly, colonization rates are likely to be greater as a result of the broadening of the species' realized niche; as a larger proportion of the calcareous grassland within the species' distribution becomes thermally suitable, the relative size and connectivity of habitat patches within the landscape increases (Thomas *et al.* 2001). Higher temperatures may directly increase flight (dispersal) capacity, and the greater fecundity of immigrants may improve the likelihood of successful population establishment. Warmer winter temperatures could also allow survival in a wider range of microhabitats (Virtanen *et al.* 1998; Crozier 2004a), although it is not known whether this is the case for this butterfly.

Habitat management for *H. comma* no longer needs to be so intensive and concentrated on the maintenance of sparse tufts of *F. ovina* within broken sward. Instead, conservation efforts should be directed towards maintaining habitat heterogeneity on sites, not just for the benefit of *H. comma*, but for many other calcareous grassland species (Kindvall 1996; Sutcliffe *et al.* 1997). A mosaic of grassland at various sward heights will maximize the choice of microhabitats available to *H. comma* females for oviposition and provide the species with suitable egg-laying locations whatever the ambient temperature and whatever new extremes are experienced (UK Climate Impact Programme 2002). It may even transpire that the temperature of 'classic' oviposition sites will become too hot as a result of continued climate warming, and maintaining heterogeneity within habitat patches will buffer the species against population declines. Finally, ensuring that a wide range of microhabitats is available within unoccupied habitats nearby may increase the probability of colonization. Once a female butterfly has dispersed to a new habitat patch, colonization success may depend on the presence of host plants that match female egg-laying preferences (Hanski & Singer 2001). None the less, maintenance of some areas of 'traditional' habitat is still desirable, as a cool summer could still result in the majority of egg-laying becoming limited to such locations.

From a wider perspective, climate change may in general alter the habitat requirements (realized niche) of many species. The behaviour and physiology of individuals affect the habitat use of a species. At the finest scales, relating to oviposition and larval development, the 'ideal' conditions may change within habitat patches, potentially requiring adjustments to local management actions. At the landscape scale, new habitats may become available for colonization while others deteriorate in suitability or become uninhabitable. When documenting the impacts of climate change on species, examining population trends only at historically 'optimal' locations is likely to generate erroneous conclusions with regard to regional trends. This is because the 'ideal' conditions are likely to have shifted, both within habitat patches and among patches within the landscape; studies using fixed sample points located only in initially high-density / optimal habitats are predisposed to detect deterioration in density / conditions.

Conservation practitioners need to be aware that habitat choice in some species will undoubtedly be influenced by climate warming, most evidently in poikilothermic species; the changing requirements of species must be considered so that habitat is not managed on the basis of a prescription that is out of date. Just as we know that the habitat requirements of species vary geographically, we cannot assume that they will be constant through time.

References

Asher, J., Warren, M.S., Fox, R., Harding, P., Jeffcoate, G. & Jeffcoate, S. (2001) *The Millennium Atlas of Butterflies in Britain and Ireland*. Oxford University Press, Oxford.

Blaustein, A.R., Root, T.L., Kiesecker, J.M., Belden, L.K., Olson, D.H. & Green, D.M. (2002) Amphibian phenology and climate change. *Conservation Biology*, **16**, 1454–1455.

Bourn, N.A.D. & Thomas, J.A. (2002) The challenge of conserving grassland insects at the margins of their range in Europe. *Biological Conservation*, **104**, 285–292.

Crick, H.Q.P. & Sparks, T.H. (1999) Climate change and egg-laying trends. *Nature*, **399**, 423–424.

Crozier, L.G. (2004a) Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology*, **85**, 231–241.

Crozier, L.G. (2004b) Field transplants reveal summer constraints on a butterfly range expansion. *Oecologia*, **141**, 148–157.

Davies, Z.G. (2004) *Conservation biology of silver-spotted skipper* (Hesperia comma) *metapopulations*. PhD Thesis, University of Leeds, Leeds.

Davies, Z.G., Wilson, R.J., Brereton, T.M. & Thomas, C.D. (2005) The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. *Biological Conservation*, **124**, 189–198.

Dempster, J.P. (1983) The natural control of populations of butterflies and moths. *Biology Reviews of the Cambridge Philosophical Society*, **58**, 461–481.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.

Hanski, I. & Singer, M.C. (2001) Extinction-colonisation dynamics and host plant choice butterfly metapopulations. *American Naturalist*, **158**, 341–353.

Kindvall, O. (1996) Habitat heterogeneity and survival in a bush cricket metapopulation. *Ecology*, **77**, 207–214.

Met Office (2001) *Automatic Weather Measurements: Observing – Whatever the Weather*. Met Office, Bracknell.

Nagelkerke, N.J.D. (1991) A note on a general definition of the coefficient of determination. *Biometrika*, **78**, 691–692.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Pollard, E. (1977) A method for assessing changes in the abundance of butterflies. *Biological Conservation*, **12**, 115–134.

Roy, D.B. & Sparks, T.H. (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6**, 407–416.

Roy, D.B. & Thomas, J.A. (2003) Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologia*, **134**, 439–444.

Sutcliffe, O.L., Thomas, C.D., Yates, T.J. & Greatorex-Davies, J.N. (1997) Correlated extinctions, colonisations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia*, **109**, 235–241.

Thomas, C.D. & Jones, T.M. (1993) Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: lessons for conservation in a fragmented landscape. *Journal of Animal Ecology*, **62**, 472–481.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. & Conradt, L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577–581.

Thomas, J.A. (1983) The ecology and conservation of *Lysandra bellargus* (Lepidoptera: Lycaenidae) in Britain. *Journal of Applied Ecology*, **20**, 59–83.

Thomas, J.A., Thomas, C.D., Simcox, D.J. & Clarke, R.T. (1986) Ecology and declining status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain. *Journal of Applied Ecology*, **23**, 365–380.

Thomas, J.A., Rose, R.J., Clarke, R.T., Thomas, C.D. & Webb, N.R. (1999) Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology*, **13**, 55–64.

Trout, R.C., Tapper, E.C. & Harradine, J. (1986) Recent trends in the rabbit population in Britain. *Mammal Review*, **19**, 153–173.

Trout, R.C., Ross, J., Tittensor, A.M. & Fox, A.P. (1992) The effect on a British wild rabbit population (*Oryctolagus cuniculus*) of manipulating myxomatosis. *Journal of Applied Ecology*, **29**, 679–686.

UK Climate Impact Programme. (2002) *Climate Change Scenarios for the United Kingdom: the UKCIP02 Briefing Report* (eds M. Hulme, J.R. Turnpenny, G.J. Jenkins). Tyndall Centre for Climate Change Research. University of East Anglia, Norwich.

Virtanen, T., Neuvonen, S. & Nikula, A. (1998) Modelling topoclimatic patterns of egg mortality of *Epirrita autumnata* (Lepidoptera: Geometridae) with a Geographical Information System: predictions for current climate and warmer climate scenarios. *Journal of Applied Ecology*, **35**, 311–322.

Warren, M.S. & Bourn, N.A.D. (1997) The impact of grassland management on threatened butterflies in ESA's. *Grassland Management in the Environmentally Sensitive Areas* (ed. R.D. Sheldrick), pp. 138–143. British Grassland Society Occasional Symposium No. 32. Arrowhead Books, Reading.

Warren, M.S., Thomas, J.A. & Wilson, R.J. (1999) *Management Options for the Silver-Spotted Skipper Butterfly: a Study of the Timing of Grazing at Beacon Hill NNR, Hampshire, 1983–98*. Butterfly Conservation, Wareham, Dorset.

Wells, T.C.E., Sheail, J., Ball, D.F. & Ward, L.K. (1976) Ecological studies on the Porton Ranges: relationships between vegetation, soils and land-use history. *Journal of Ecology*, **64**, 589–629.