Exploring the universal ecological responses to climate change in a univoltine butterfly

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Running title: Temperature effects on body size, phenology, and geographic range

Summary

1. **1.** Animals with distinct life stages are often exposed to different temperatures during each stage. Thus, how temperature affects these life stages should be considered for broadly understanding the ecological consequences of climate warming on such species. For example, temperature variation during particular life stages may affect respective change in body size, phenology, and geographic range, which have been identified as the “universal” ecological responses to climate change. While each of these responses has been separately documented across a number of species, it is not known whether each response occurs together within a species. The influence of temperature during particular life stages may help explain each of these ecological responses to climate change.
2. **2.** Our goal was to determine if monthly temperature variation during particular life stages of a butterfly species can predict respective changes in body size and phenology. We also refer to the literature to assess if temperature variability during the adult stage influences range change over time.
3. **3.** Using historical museum collections paired with monthly temperature records, we show that changes in body size and phenology of the univoltine butterfly, *Hesperia comma*, are partly dependent upon temporal variation in summer temperatures during key stages of their life cycle. June temperatures, which are likely to affect growth rate of the final larval instar, are important for predicting adult body size (for males only; showing a positive relationship with temperature). July temperatures, which are likely to influence the pupal stage, are important for predicting the timing of adult emergence (showing a

negative relationship with temperature). Previous studies show that August temperatures, which act on the adult stage, are linked to range change.

4. Our study highlights the importance of considering temperature variation during each life stage over historic time-scales for understanding intraspecific response to climate change. Range edge studies of ectothermic species that have annual life cycles, long time-series occurrence data, and associated temperature records (ideally at monthly resolutions), could be useful model systems for intraspecific tests of the universal ecological responses to climate change and for exploring interactive effects.

Key-words: body size, climate change, global warming, *Hesperia comma*, Lepidoptera, museum collections, phenology, range change, Silver-spotted Skipper, temperature variation

Introduction

Ecologists are increasingly reporting responses to climate change that appear to be ubiquitous across taxa and habitat types. Notably, some studies suggest that warming may be causing widespread body size declines (Gardner *et al.* 2011; Sheridan & Bickford 2011) while others show that many aquatic and terrestrial species are experiencing earlier phenological events and range expansions (Walther *et al.* 2002; Parmesan & Yohe 2003; Hickling *et al.* 2006; Miller-Rushing & Primack 2008; Diamond *et al.* 2011). Collectively, these are thought to be the three “universal” ecological responses to climate change (Daufresne, Lengfellner & Sommer 2009; Ohlberger 2013). Yet if such universal responses indeed exist, then each of these responses should be observable within and between species and at varying temporal scales (i.e. not just recently). At the century scale for example, one could hypothesize that years with warm temperatures could result in a species (i) reducing its body size, (ii) emerging, flowering, or spawning earlier (or other phenological events), and (iii) expanding its range. Yet despite empirical support for each response interspecifically across some groups, it is not known whether each response may occur within a species. Intraspecific tests of each response are important, in part, because responses to warming are likely to be interactive, which may be easier to explain at the intraspecific scale. For example, body size is thought to influence dispersal ability (linked to range expansion) and the timing of phenological events within species (Ozgul *et al.* 2010; McCauley & Mabry 2011). Moreover, organisms with complex life cycles experience different temperatures during each life stage. How different life stages separately and collectively respond to temperature is essential for understanding intraspecific response to climate change (Kingsolver *et al.* 2011;

Buckley *et al.* 2015), including changes in body size, phenology, and geographic range.

Species that complete their life cycles in one year (such as univoltine insects) may be useful for testing intraspecific response to temperature change; particularly if studied populations are near a range edge, where they may be approaching the limits of their thermal tolerance. For some such species, it may be possible to link temperature variation of particular months during key life stages to respective changes in body size, phenology, and probability of range change. In holometabolous insects, for example, adult body size is a direct result of growth rate during the larval stages (Shingleton 2011). Thus, if temperature is a factor influencing larval growth rate, then temperatures during the particular month(s) of the larval phase are likely to be important for predicting adult body size. Temperature should be especially important during the final larval instar, which is a critical period when holometabolous insects attain the critical size needed to initiate metamorphosis (Shingleton 2011). Similarly, the timing of phenological events and range changes may be partly dependent upon respective temperatures during the subsequent pupal and adult stages of holometabolous insects (see below).

Though rarely discussed in tandem, the timing of phenological events and range changes have often been linked to temperature variability across multiple taxa and habitat types using time-series data (see first paragraph references), but these trends have not generally been examined alongside temporal analyses of temperature-size responses. There is a particular need for such studies using invertebrates given that they represent the majority of animal biodiversity, live in all habitat types, are of fundamental ecological importance, and perhaps most importantly, they are exclusively ectothermic; thus, they are highly sensitive to changes in temperature (Bickford, Sheridan & Howard 2011; Ohlberger 2013). Until recently, the prevailing hypothesis was that adult body sizes of invertebrates will get smaller with increasing temperature (Sheridan & Bickford 2011), but the direction of the temperature-size response may depend upon a number of factors, such as habitat, food quality, sexual size dimorphism, season length, voltinism, and others (Diamond & Kingsolver 2010; Stillwell *et al.* 2010; Forster, Hirst & Atkinson 2012; Ghosh, Testa & Shingleton 2013; Horne, Hirst & Atkinson 2015).

A recent meta-analysis of intraspecific temperature-size responses of arthropods under laboratory conditions and across latitude revealed an interesting dichotomy of response between multivoltine (more than two broods or generations per year) and univoltine (one brood or generation per year) terrestrial species (Horne, Hirst & Atkinson 2015). Multivoltine species tend to get smaller with increasing temperature and at lower latitudes, whereas univoltine species show the opposite response, suggesting that univoltine arthropods exhibit a converse Bergmann cline (Horne, Hirst & Atkinson 2015). These differences are thought to be due to evolutionary adaptations to variation in season length such that univoltine species take advantage of a longer growing season (i.e. at lower latitudes and/or higher temperatures) by growing larger, whereas multivoltine species may use a longer growing season by maturing earlier at smaller sizes to produce more generations per year (Horne, Hirst & Atkinson 2015). However, the studies used for the meta-analysis were restricted to laboratory and spatial comparisons, it is therefore unknown if the body sizes of univoltine species respond to variations in seasonal temperature from year to year.

Specifically, do the adults of univoltine species within the same region reach larger sizes in years with warm temperatures during the final larval instar stage (i.e. an effectively longer growing season) compared to relatively cool years?

A key step for testing intraspecific ecological responses to temperature change is the establishment of a historical baseline of trends, at the highest feasible spatial and temporal resolution, before the recent (1970s onwards) onset of rapid climate warming. This requires copious amounts of historical data (such as body size and phenological records) to be paired with historic temperature records (ideally at monthly or daily resolutions). Natural history collections, which often consist of thousands of specimens with detailed information on collection date and locality, can provide invaluable datasets for such studies (Johnson *et al.* 2011). In Britain, for example, both monthly temperature data and natural history collections of butterfly specimens, dating back over a century, are available. When paired, Brooks *et al.* (2014) showed that a number of British butterfly adults emerge earlier (using specimen collection date as a proxy for emergence date) during years with warm spring temperatures and later in cool, wet springs. Likewise, Kharouba *et al.* (2014) found that the timing of flight season of Canadian butterflies was related to spring temperatures (also using museum collections), but the strength of response varied according to taxon specific ecological traits (i.e. species with shorter flight seasons and shorter wingspan were more sensitive). Unlike adult body size change in holometabolous insects, where it is hypothesized that temperature during the final instar larval stage will be an important predictor, phenological responses (in this case, adult emergence from the pupa) are more likely to be dependent upon temperature just before adults emerge, during the pupal stage.

Predictors of range change, on the other hand, should be partly dependent on temperature during the adult phase of the life cycle of winged holometabolous insects, when individuals are reproductive and capable of longer dispersal. For example, years with warm August temperatures have been linked with high local abundances and range expansion of the univoltine Silver-spotted Skipper (*Hesperia comma*, Linnaeus, 1758) in southeastern England since the early 1980s (see Davies *et al.* 2005; Davies *et al.* 2006 for full descriptions of recent range dynamics). Alternatively, years with comparatively cool August temperatures have reduced populations and are expected to contribute to range contractions/local extinctions (Lawson *et al.* 2012; Lawson *et al.* 2013). Alongside improved habitat management, the range expansion of *H. comma* is thought largely to be a result of increased availability of thermally suitable habitat due to recent climate warming (Thomas *et al.* 2001; Davies *et al.* 2006; Lawson *et al.* 2012). Specifically, egg-laying rates are temperature dependent and females adjust oviposition based on the relative temperature of the larval foodplant (the grass - *Festuca ovina*; Davies *et al.* 2006). Warm August temperatures are correlated with higher egg-laying rates and the number of microhabitats available for optimal oviposition (Thomas *et al.* 2001; Davies *et al.* 2006). Interestingly, the recently expanded portions of the *H. comma* range are generally comprised of individuals with larger relative investment in body size (as measured by relative thorax size), suggesting that larger individuals are capable of longer distance dispersal (Hill, Thomas & Lewis 1999).

Given the apparent sensitivity of *H. comma* population sizes and range dynamics to August temperature variation, one may expect that body size and phenology would also be highly sensitive to temperature in this species, particularly for monthly temperatures prior to August when individuals are either in the larval or pupal stage. As such, we hypothesize that (i) years with warm temperatures during the final larval instar stage (June) will lead to larger adults and (ii) years with warm months during the pupal stage (July) will lead to earlier adult emergence (phenology). We use wing length measurements (as a proxy for body size) and collection date (as a proxy for adult emergence date) of digitized Natural History Museum (NHM, London) specimens paired with historic monthly temperature records to test these hypotheses.

Materials and methods

TEMPERATURE RECORDS

Mean monthly air temperature data are available from two sources: the central England temperature records (CET; http://www.metoffice.gov.uk/hadobs/hadcet/) and regional monthly records from the UK MET Office (http://www.metoffice.gov.uk/climate/uk/summaries/datasets). The CET covers a region triangulated by Lancashire, London, and Bristol and dates from 1659 (Manley 1974; Parker, Legg & Folland 1992; Perry & Hollis 2005). For central England, mean monthly minimum and maximum temperature data are available from 1878 (Parker & Horton 2005) and monthly precipitation data from 1873 (Alexander & Jones 2001). However, this area is slightly outside most of the southern England chalk grasslands range of *H. comma*. Alternatively, monthly records for the England southeast and central south region encompasses the modern range of *H. comma*, yet are only available from 1910 onwards. Previous researchers have shown that CET data are representative of the UK as a whole (Croxton *et al.* 2006), and paired monthly correlations between the regional and CET data for the years between 1910-1981 (encompassing the overlap in CET and regional temperature data for all years of NHM specimen collection) justify this conclusion (all Pearson's correlations > 0.96). In addition, pairwise comparisons of mean monthly air temperatures between the two record types are not significantly different (Wilcoxon signed-rank test; $p > 0.05$) except for August temperatures ($p = 0.02$) where the regional data are warmer than CET data by 0.42ºC on average. Although August air temperature records are slightly warmer in the regional dataset, this is the month when the vast majority of *H. comma* individuals are adults, and are thus past the growth and emergence stages of their life cycle (the focus of our analysis). Given the broad similarity between CET and regional monthly temperature records, we have chosen to focus our analysis using the CET data since it covers the entire temporal range of collected specimens useful for body size and phenology analyses (1880-1973; see below).

STUDY SYSTEM

Hesperia comma adults spend much of their time basking or feeding on a variety of nectar sources while staying inactive during overcast days. The species' life cycle is one generation per year (univoltine) and it is one of the last butterflies to emerge as an adult in southern England. Individuals generally spend September to March in the ovum stage, mid to late March through June as larvae (the final instar occurs in June) and approximately one month as a pupa (~July). Their life cycle culminates with the adult flight period from late July to early September (UK Butterfly Monitoring Scheme). The vast majority of field counts of adults of this species are recorded in August (Lawson *et al.* 2013). Like other British butterflies, *H. comma* has been well collected by amateur and professional naturalists, particularly from the mid-19th century through the 1960s (Brooks *et al.* 2014). The NHM houses a very large collection of British butterflies (65 species) comprising ~180,000 specimens, which have been digitized, geo-referenced, and databased. 863 of these specimens are *H. comma*, collected from 1860-1981, about half of which are useful for body size and/or phenology analysis (see below). As with abundance counts in the field, the vast majority of specimens were collected in August (84%). Importantly, the NHM data are restricted to counties within southern England (particularly southeast England: >50% of specimens are from Hertfordshire, Surrey, Kent, and Dorset), thus keeping the geographic scope of the study comparable to modern field studies (e.g. Davies *et al.* 2006; Lawson *et al.* 2012; Lawson *et al.* 2013).

WING LENGTH DATA

Forewing length was chosen as a proxy for body size (the point of wing attachment on the thorax to the apex of each forewing; Fig. 1) using digitized NHM specimens and Image-J software. We chose forewing length as opposed to other metrics of body size (i.e. body length) because it is less prone to shrinkage over time due to specimen drying. To confirm that forewing length scales with another potential metric of body size, we correlated forewing surface area by forewing length for a subset of specimens ($n=43$). The correlation is very high ($r = 0.97$), supporting the use of forewing length as a proxy for overall wing size, and by extension, body size.

Because we are interested in the relationship between monthly temperature variation and wing length, we only measured the forewing lengths of specimens that were field caught and labeled with a collection month. We averaged the measurements of left and right forewing lengths for each specimen with relatively un-damaged wings. For each sex, we calculated the median value of our wing length measurements across specimens per year for years that contain three or more specimens.

We have focused our wing-size analysis and discussion based on specimens collected in August as they represent the overwhelming majority of specimens (see above) and August coincides with the peak period of adult abundance (UK Butterfly Monitoring Scheme). However, including specimens collected in June (2% of specimens), July (11% of specimens), or September (3% of specimens) did not qualitatively change our results (see below). As a result, the wing length dataset of August collected individuals consists of 331 specimens collected from 58 years from 1880 to 1973. 158 of these specimens are female, collected over 30 years from 1880-1971. 173 specimens are male, collected over 28 years from 1892-1973. These data were paired with the associated monthly mean, minimum, and maximum CET temperature values for each year, and total monthly precipitation for each year (mm).

WING LENGTH ANALYSIS

We performed a multiple linear regression analysis to model the relationship between forewing length and nine variables: mean monthly temperatures from March through September (i.e. the months spanning the larval, pupal, and adult life stages), year of collection, and sex as a factor variable (after confirming that assumptions for running a linear model are met). Variable selection for final models was performed using stepwise regression in both directions using the MASS package in R (Venables & Ripley 2002). Variance inflation factors (VIF) were determined using the car package (Fox & Weisberg 2011). We repeated the above analyses using minimum and maximum monthly temperatures and total monthly precipitation (mm) as predictors of wing-length.

We repeated the analysis using an information-theoretic (IT) approach. Models were selected using (IT) model selection, with model averaging based on Akaike Information Criterion (AIC) to linearly relate wing length to the explanatory variables listed above (following Burnham & Anderson 2002). We applied the *dredge* function of the R package *MuMIn* (Barton 2013) to fit models for all possible combinations of explanatory variables and then ranked them based on AICc. We then extracted the model-averaged coefficient for each variable that was present in at least one candidate model. The set of candidate models was defined as those with ΔAIC ≤ 7 (Burnham, Anderson & Huyvaert 2011). We identified the importance of each variable based on its frequency in the candidate models. An importance score of 1.0 indicates that a variable was present in all candidate models. The importance scores and the model-averaged coefficients were used to determine the main variables for explaining wing length. Specifically, if a variable had an importance score of 1.0 and did not have a coefficient (slope) estimate that included zero, then we were confident that it is a main variable for explaining wing length (or collection date, see below). We further identified the most important variables by determining which are retained after nested models were removed (Richards, Whittingham & Stephens 2011) using the nested function in *MuMln* (Barton 2013). The removal of nested models reduces the chance of selecting overly complex models (i.e. those that include variables which add little or no predictive power) while not affecting the selection of the very best models (Richards, Whittingham & Stephens 2011). In practice, variables with the highest importance scores are the best predictors and will be retained regardless of whether nested models are removed. For presentation purposes, we show the importance scores and coefficient estimates for all variables (calculated from the nested and un-nested candidate models) while highlighting which variables are retained when nested models are removed (Tables 1-3 and SI tables 1-15).

PHENOLOGY DATA

For phenological analysis, we included records in the analysis only if i) the data labels specified the location of collection to at least vice-county level (see Fig. S1 for a map of collection locations), ii) the day of collection was recorded and iii) if the specimens were field caught. Dates that varied by more than three standard deviations from the mean collection date were treated as outliers and excluded from further analysis, as were specimens with unreliable locality data (i.e. locations remote from the known 20th century distribution). Collection dates were converted to day number after December 31st. The median and 10th percentile collection dates were calculated for each year in which there were five or more records.

PHENOLOGY ANALYSIS

Following the methods outlined above for wing-length, we performed a multiple linear regression analysis using stepwise regression to examine the relationship between 10th percentile and median collection dates with the explanatory variables of mean monthly temperature (March through September) and year of collection. We repeated analyses using minimum and maximum monthly temperatures and total monthly precipitation (mm). Further, we used IT-AIC model selection as described above to relate collection dates to the explanatory variables.

Results

WING LENGTH

The stepwise multiple linear regression analysis (March-September mean temperature; none with a VIF >2) was significant (adjusted $R^2 = 0.74$; $p<0.0001$), with sex (factor) and June temperatures as the most important variables ($p<0.0001$) for predicting wing-length. These results do not change if we re-run the analysis while using collection locality as a factor variable (at the county scale) to predict wing-lengths across all specimens (i.e. not just those collected in years with three or more specimens; adjusted $R^2=0.57$; $p<0.0001$; factor (county) not significant). Thus, locality at the county scale does not appear to influence wing-size in our dataset and was therefore excluded from subsequent analyses.

Due to the importance of sex for predicting wing length, we subsequently ran the stepwise multiple linear regression analyses for males and females separately. Males are significantly smaller than females (t-test, $p<0.0001$) and can be easily recognized by their scent scales, which form a distinct dark line on their dorsal forewings (Fig. 1). Mean June temperature was the only significant variable for predicting male wing lengths (showing a positive relationship), for both August collected individuals (adjusted $R^2=0.43$; $p<0.001$) and for those collected across all summer months (June – September; adjusted $R^2=0.24$; $p=0.01$). Likewise, June was the only significant variable for analyses using minimum (adjusted $R^2=0.33$; $p=0.002$) and maximum (adjusted $R^2=0.38$; $p<0.001$) monthly temperature values. Mean June temperature alone can explain 39% of the variability in male wing lengths (Fig. 2c). There was no significant relationship between female wing lengths and mean monthly temperatures for August collected individuals ($p=0.07$) or for females collected across all summer months ($p=0.09$). Likewise, female wing lengths were not significantly related to minimum and maximum monthly temperatures. In addition, there was no significant relationship between male or female wing lengths and total monthly precipitation. Figure 2 shows that mean June temperature is a good predictor of male wing lengths, but female wing lengths cannot be well predicted by any of the variables.

The above results from the stepwise multiple linear regression analyses were reflected by the model selection analyses performed using the IT-AIC approach. Sex (factor) and mean June temperatures were the most important variables (importance scores of 1.0) to predict wing lengths for the overall dataset (both males and females; Table 1). After nested models were removed, the only variables retained were sex (factor), June, and April (Table 1). Mean June temperature was the most important variable for predicting male wing lengths (importance score of 1.0; Fig. 2a; after nested models were removed, only June and May were retained; Table 2). Likewise, June was the most important variable (importance scores of 1.0) when models were run using minimum and maximum monthly temperatures. For females, April temperature (mean, minimum, maximum) was the most important variable for predicting wing length, but it was not present in all models (importance score 0.72 or lower; Fig. 2b; after nested models were removed, only April and June were retained; Table 2), nor is it significantly related to female wing length using ordinary linear regression ($p>0.05$). For analyses relating precipitation to male and female wing length, July was the most important variable - but it was not present in all candidate models (importance scores of 0.49 and 0.35 respectively) nor was it significantly related to male or female wing lengths using ordinary linear regression ($p>0.08$). Overall, monthly precipitation is a poor predictor or wing lengths. All results relating wing lengths to minimum/maximum monthly temperature and rainfall using the IT-AIC analyses can be found in SI tables 1-9.

To deal with potential scaling effects caused by the sexual size dimorphism, we calculated the slope of the natural log of wing lengths versus June temperatures, which was then transformed into a percentage change in wing length per ºC using the formula: $(\exp^{(\text{slope})}-1)*100$ (Forster, Hirst & Atkinson 2012; Horne, Hirst & Atkinson 2015). There was a 2.20% increase in male wing length per ºC compared with a 0.90% increase in female wing length (though the regression itself is not significant, Fig. 2d), further showing that male wing sizes are more sensitive to change in June temperatures than female wing sizes.

PHENOLOGY

Between 1892 and 1973 sufficient specimens were available for analysis (i.e. five or more records in one year) in 40 of those years, providing a total of 437 useable records. The stepwise multiple linear regression analysis (no variables with a VIF >2) shows that mean July temperature was the only significant variable to predict median collection dates (a negative relationship; adjusted $R^2 = 0.42$; $p<0.0001$). For 10th percentile collection dates, mean July temperature and year were both significant (adjusted $R^2=0.46$; $p<0.0001$), though year only was only weakly significant (p=0.04), indicating no long-term phenological trend in the response of *H. comma* to temperature. 10th percentile collection date advanced 3.8 days per 1°C increase mean July temperature (ordinary linear regression: $R^2 = 0.36$; $p < 0.0001$; Fig. 3c) and median collection date advanced by 5.1 days per 1ºC increase in mean July temperature (ordinary linear regression: $R^2 = 0.43$; $p < 0.0001$; Fig3d). We found weak positive relationships between 10th percentile and median collection dates with April rainfall (ordinary linear regression: $R^2 = 0.11$; $p = 0.034$ and $R^2 = 0.20$; $p = 0.004$ respectively). There were also significant negative relationships between 10th percentile and median collection date with minimum and maximum July temperatures as well as a slight positive relationship with July rainfall, but these variables were strongly correlated with mean July temperature.

These results were also evident from the IT-AIC model selection analysis. Mean July temperature is the most important variable for predicting both10th percentile and median collection dates (importance scores of 1.0; Fig. 3a,b; Table 3). When nested models were removed, July, year, April and September were retained for analyses predicting 10th percentile collection date; whereas only July was retained to predict median collection dates (Table 3). Likewise, July was the best predictor of collection dates when models were run with minimum and maximum monthly temperatures (importance scores of 1.0). For rainfall, July was the most important month for predicting 10th percentile collection dates (importance score = 0.98) and April was the most important variable for predicting median collection dates (importance score = 0.98), closely followed by July rainfall (importance score = 0.86); but as described above, April and July rainfall are only weakly related to collection date. All results relating collection dates to minimum/maximum monthly temperature and rainfall using the IT-AIC analyses can be found in SI tables 10-15.

Discussion

Determining how different life stages of a species separately and collectively respond to temperature is essential for understanding the ecological and evolutionary consequences of climate change (Kingsolver *et al.* 2011; Buckley *et al.* 2015). Here, we show that changes in wing length and phenology of the univoltine butterfly, *Hesperia comma*, are partly dependent upon temporal variation in monthly summer-time temperatures during key stages of their life cycle (Fig. 4). June temperatures, when larvae are in the final larval instar, are important for predicting adult wing length (but only for males). July temperatures, during the pupal stage, are important for predicting timing of adult emergence (phenology). Finally, August temperatures, during the adult stage, have recently been shown to be important for predicting geographic range expansion during years with warm August temperatures and localized extinction during years with cooler August temperatures (Lawson *et al.* 2012; Lawson *et al.* 2013). Our study would not be possible without long time-series data from digitized natural history collections paired with monthly temperature records (for wing length and phenology), previously published data from field surveys over recent decades (for range change), and extensive prior knowledge of the life cycle and natural history of *H. comma* (Thomas *et al.* 1986; Thomas *et al.* 2001; Davies *et al.* 2006; Lawson *et al.* 2012; Lawson *et al.* 2013).

Advancement in adult emergence dates and range expansion has commonly been reported for northern temperate butterfly species in recent years (Parmesan *et al.* 1999; Breed, Stichter & Crone 2013; Brooks *et al.* 2014; Kharouba *et al.* 2014), but these responses have not been examined alongside body size change. Until recently, it was thought that warming will cause widespread declines in body size of ectotherms because they burn more metabolic energy when it is warmer and thus, need more food to achieve and maintain large body sizes at higher temperatures (Bickford, Sheridan & Howard 2011; Ohlberger 2013). If increased consumption is not sustainable, then a shift towards smaller individuals over time is predicted with warming (Sheridan & Bickford 2011). While this may be true for a number of ectotherms (particularly for aquatic species; Forster, Hirst & Atkinson 2012), we now know that voltinism is also an important factor influencing the direction of the temperature-size response, at least among terrestrial arthropods (Horne, Hirst & Atkinson 2015). Univoltine species (e.g. some butterflies) appear to get larger with increasing temperatures, whereas multivoltine species show the opposite response. Our study mirrors this result, which we believe to represent the first support of the ‘converse Bergmann cline’ (Blanckenhorn & Demont 2004) using a temporal rather than a spatial or laboratory dataset in insects (see Teplitsky & Millien (2014) for an endothermic study).

Interestingly, our results suggest that male wing sizes are more responsive than females to temperature, also noticed in field studies of other butterfly species (Gilchrist 1990). Males are significantly smaller than females as adults (Fig. 1), which is common across insects and largely due to longer female development times (Teder 2014). Assuming that the relative size difference between male and female adults is also found in their respective final larval instar, then variation in June temperatures will affect growth of male caterpillars more than females simply due to differences in surface area to volume ratio (smaller individuals lose heat faster than large individuals). Thus, cold June temperatures should disproportionally restrict the growth of smaller caterpillars (males) compared to larger caterpillars (females), though possible differences in microhabitat may also be an important, yet largely untested variable (Kingsolver *et al.* 2011). In addition, field surveys indicate that males tend to emerge earlier than females (Hill, Thomas & Lewis 1999), though this was not evident in our dataset. Earlier emergence (and shorter developmental time) could mean that males experience different temperatures (and/or more extreme temperatures) than females for some portion of their life cycle, which may also contribute to our findings. Furthermore, warmer June temperatures may improve larval food quality (*Festuca ovina*) and increase rate of feeding (Higgins *et al.* 2014), leading to larger adult sizes. Finally, and in line with predictions from Horne, Hirst & Atkinson (2015), years with warm June temperatures are, on average, likely to have more days of sunshine, effectively producing a longer larval growing season leading to increased size of the final instar and subsequent adult size. But why this would affect males and not females remains unclear. One possibility is that the upper range of female body sizes is more constrained compared to males given that they are the larger sex and maximum body size should be set within physiological limits; suggesting that females are already near their upper size limits whereas males have more scope for change. Interestingly, years with the warmest average June temperatures in our dataset (16.4ºC) have males with relatively small wing sizes, indicating that the upper limit to male wing size may occur just below this temperature threshold (Fig. 2c). Although it requires further study, our results provide further support that climate variability may contribute to the magnitude of sexual size dimorphism (Stillwell *et al.* 2010).

Incorporating the interactive effects of each response (body size, phenology, range change) will be a key, yet challenging, step towards a comprehensive understanding of the ecological effects of climate change (Kingsolver *et al.* 2011; McCauley & Mabry 2011). In *H. comma* for example, Hill, Thomas & Lewis (1999), found that the most rapidly expanded portions of its range in Britain were composed of individuals that had a higher relative investment in thorax size, which is primarily composed of muscles used in flight. While we did not measure thorax size (due to the probability of shrinkage for old specimens) and the temporal scope of our study (1880-1973) is prior to the more recent range expansion, we do show that male wing sizes get larger during years with warm June temperatures. Across butterfly species, larger wings (and other life history traits) are often associated with longer dispersal distances (Hughes, Dytham & Hill 2007; Stevens *et al.* 2013). Thus, if wing sizes scale positively with seasonal temperature across univoltine species, then range expansions (assuming habitat is available) would be more likely during years with warm temperatures during both the final larval instar and adult stages. This scenario implies an interactive effect of body size on distribution, but an interaction of distribution on body size should also be apparent. *Hesperia comma* adults are smallest at the very northern edge of the range in Scandinavia, where summer temperatures are cool (Dennis & Shreeve 1989; though they did not distinguish between males and females), which we would predict based on the positive relationship between temperature and male wing size (Fig. 2). There are likely to be other interactive effects (distribution and phenology, e.g. Diamond *et al.* 2011; body size and phenology; e.g. Kharouba *et al.* 2014) but the current lack of long-term *H. comma* studies outside of southern England precludes much discussion (but see Karlsson 2014). Further, the influence of microhabitat (e.g. slope and aspect of chalk hills, sward height) on the temperature experienced by the larval, pupal, and adult stages, which is often a key component of field based ecological studies of *H. comma* (Thomas *et al.* 2001; Davies *et al.* 2006), may have caused some of the unexplained variation in our results.

We have used historical data and previous research to link monthly summer temperature variation during key stages of the life history of *H. comma* to respective changes in body size, phenology, and range change. Historically however, years with warm June temperatures did not necessarily also have both warm July and August temperatures. Yet in the near future, one may expect it will be more common to have years when these months are collectively warmer than they were in the past. Based on our results, this would result in relatively large males, earlier emergence, and continued range expansion (Fig. 4). However, the possibility of further range expansion will be highly dependent upon habitat availability and appropriate habitat management for this species.

Where available, natural history collections paired with associated meta-data can be used to establish a baseline of ecological response to temperature variation before the onset of modern climate warming. Such studies are needed in conjunction with continued long-term monitoring of relevant traits (e.g. body size, phenology, abundance, distribution) and sustained specimen collection deposited in natural history museums (Johnson *et al.* 2011) as a part of the greater goal of understanding the ecological and evolutionary consequences climate change. Moreover, studies assessing the consequences of climate change for organisms with complex life cycles, where different environments are experienced during different life stages, must take into account the differing responses of each life stage (Kingsolver *et al.* 2011). We show that changes may be predictable at the intraspecific scale if long-term data are integrated with knowledge of the life history and ecology of a species. But scaling up predictions established for single species to the community level and across varying spatial scales will be a greater challenge (but see Hinks *et al.* 2015). General patterns may emerge once each "universal" ecological response to climate change and their interactions are explored intraspecifically, followed by comparative analyses across taxonomic groups with different modes of life and habitat requirements.

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Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.r2250

Fig. 1

Boxplots of all August collected male (n=217) and female (n=202) forewing lengths of *H. comma* specimens. Males have significantly smaller forewing lengths than females and can be distinguished by a dark band of scent scales on each forewing. The white dotted lines illustrate specimen forewing lengths.

Fig. 2

Coefficient (slope) estimates for each variable (March – September mean monthly temperature and year) to predict a) male wing lengths and b) female wing lengths using the IT-AIC approach. June is the only variable that was found in all candidate models (importance score of 1.0) for predicting male wing lengths, with slope estimates not including zero. For females, none of the variables were found in all candidate models and all had slope estimates that include zero. The bottom panels show the significant linear regression of c) male wing lengths and d) the non-significant regression of female wing lengths versus June temperature. Each point represents the median value of forewing lengths for years with at least three specimens (n=28 years from 1892-1973 for males; n=30 years from 1880-1971 for females).

Fig. 3

Coefficient (slope) estimates for each variable (March – September mean monthly temperature and year) to predict a) 10th percentile collection day and b) median collection day using the IT-AIC approach. July was the only variable present in all candidate models (importance scores of 1.0) for predicting both 10th percentile and median collection days, with slope estimates not including zero. All of the slope estimates for non-July variables include zero. The bottom panels show the significant linear regressions of c) 10th percentile and d) median collection days versus July temperature. Each point represents values for years with at least five specimens (n=40 years, spanning from 1892-1973).

Fig. 4

Climate change affects the body size, phenology and geographic range of a species. In the Silver-spotted Skipper (*Hesperia comma*) in Britain, male body size is correlated with June temperatures during the final larval instar, adult emergence is correlated with July temperature during the pupal stage, and geographic range change is linked with August temperature during the adult stage.

Table 1. Parameter estimates for the candidate models using information criteria (ΔAIC < 7) for predicting wing lengths of all individuals (males and females). In addition to sex, predictor variables include year and mean monthly temperatures (March-September) when *H. comma* individuals are in the larval through adult stages of their life cycle in southern England. An importance score of 1.0 means that a variable was present in all candidate models. Columns are ordered in descending order by importance score. Coefficient estimates (slope) are averaged over all the candidate models. Variables in bold are those that were retained when nested models were removed.

	Factor (sex)	**JUN**	**APR**	SEP	MAY	MAR	AUG	Year	JUL
Importance scores	1.0	1.0	0.68	0.42	0.42	0.37	0.31	0.25	0.24
N containing models	102	102	60	50	48	47	43	42	43
Coefficient estimate	-1.32	0.22	0.11	0.10	-0.09	-0.05	-0.06	0.00	0.04
Std. Error	0.12	0.06	0.06	0.07	0.07	0.05	0.06	0.00	0.06
Adjusted Std. Error	0.12	0.06	0.06	0.08	0.07	0.05	0.07	0.00	0.07
Lower CI	-1.55	0.10	-0.01	-0.05	-0.22	-0.15	-0.19	-0.01	-0.09
Upper CI	-1.08	0.35	0.22	0.25	0.05	0.04	0.07	0.00	0.17

Table 2. Importance scores and number of candidate models containing each variable (mean monthly temperatures and year) when analyses are separately run to predict male and female wing lengths using information criteria ($\Delta AIC < 7$). Columns are ordered in descending order by importance score. The predictor variables include year and mean monthly temperatures (March-September) when *H. comma* individuals are in the larval through adult stages of their life cycle in southern England. Coefficient estimates with confidence intervals are shown graphically in Figs 2a and b. Variables in bold are those that were retained when nested models were removed.

Males	**JUN**	**MAY**	SEP	APR	AUG	MAR	JUL	Year
Importance scores	1.0	0.65	0.18	0.18	0.18	0.16	0.15	0.15
N containing models	43	22	12	12	12	12	11	11
Females	**APR**	**JUN**	SEP	MAR	AUG	JUL	Year	MAY
Importance scores	0.67	0.51	0.31	0.28	0.22	0.21	0.19	0.15
N containing models	69	57	49	45	42	39	36	31

Table 3. Importance scores and number of candidate models containing each variable (mean monthly temperatures and year) when analyses are separately run to predict 10th percentile collection day and median collection day using information criteria (ΔAIC < 7). Columns are ordered in descending order by importance score. An importance score of 1.0 means that a variable was present in all candidate models. The predictor variables include year and mean monthly temperatures (March-September) when *H. comma* individuals are in the larval through adult stages of their life cycle in southern England. Coefficient estimates with confidence intervals are shown graphically in Figs 3a and b. Variables in bold are those that were retained when nested models were removed.

10th percentile collection day	**JUL**	**Year**	**APR**	**SEP**	MAY	JUN	MAR	AUG
Importance scores	1.0	0.88	0.61	0.35	0.27	0.19	0.17	0.16
N containing models	53	40	27	28	19	16	15	15
Median collection day	**JUL**	Year	APR	JUN	MAY	SEP	MAR	AUG
Importance scores	1.0	0.44	0.32	0.27	0.24	0.18	0.18	0.18
N containing models	69	31	29	27	26	22	21	22

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