Early emergence in a butterfly causally linked to anthropogenic warming

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There is strong correlative evidence that human-induced climate warming is contributing to changes in the timing of natural events. Firm attribution, however, requires cause-and-effect links between observed climate change and altered phenology, together with statistical confidence that observed regional climate change is anthropogenic. We provide evidence for phenological shifts in the butterfly Heteronympha merope in response to regional warming in the southeast Australian city of Melbourne. The mean emergence date for H. merope has shifted −1.6 days per decade over a 65-year period with a concurrent increase in local air temperatures of approximately 0.14°C per decade. We used a physiologically based model of climatic influences on development, together with statistical analyses of climate data and global climate model projections, to attribute the response of H. merope to anthropogenic warming. Such mechanistic analyses of phenological responses to climate improve our ability to forecast future climate change impacts on biodiversity.

Keywords: phenology; biophysical ecology; physiological ecology; climate change; mechanistic model; ecological forecasting

1. INTRODUCTION

There is a strong signal that biological events have happened progressively earlier in spring over the past few decades (Walther et al. 2002; Rosenzweig et al. 2008), including emergence in butterflies, migration in birds and flowering in plants (Hughes 2000; Parmesan & Yohe 2003; Root et al. 2003; Chui et al. 2004; Parmesan 2006; Cleland et al. 2007). These shifts have occurred concurrently with increases in air temperature at regional and global scales and in the direction expected if temperature was playing a causal role (Rosenzweig et al. 2008).

Despite the geographical and taxonomic generality of these signals, the magnitudes and rates of the observed phenological shifts have rarely been tied directly to known physiological responses. This leaves some uncertainty as to the driving forces behind these shifts and also limits the capacity for predictions into the future. Here, we examine historical phenological change in the common brown Heteronympha merope (Nymphalidae) and test whether (i) the phenological shift could be quantitatively explained by the influence of air temperature change on known physiological processes and (ii) the associated climate change could be attributed to human influence.

2. MATERIAL AND METHODS

Heteronympha merope is an annual species that is abundant and widely distributed across southeastern Australia. Males and females emerge and mate in late spring/early summer (November/December) and then the males die and the females become dormant until late summer/early autumn (February/March) after which they begin to oviposit on a wide range of grasses (Edwards 1973). Observed emergence times for H. merope in the vicinity of Melbourne, Victoria, have shifted: mean emergence date for H. merope was 1.6 days per decade over a 65-year period with a concurrent increase in local air temperatures of approximately 0.14°C per decade. We used a physiologically based model of climatic influences on development, together with statistical analyses of climate data and global climate model projections, to attribute the response of H. merope to anthropogenic warming. Such mechanistic analyses of phenological responses to climate improve our ability to forecast future climate change impacts on biodiversity.

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Figure 1. (a) Historical changes in emergence time for *Heteronympha merope* compared with predicted emergence times (solid line with filled circle, observed; dashed line with open square, predicted); (b) corresponding changes in April–October air temperature means; (c) development rate of the immature phases of *H. merope*, in response to temperature; (d) observed April–October average temperature trend over 1944–2007 at Laverton (filled circle) compared with trends owing to the response to anthropogenic climate forcing from four climate model estimates (open symbols). Error bars (99% CI) represent the natural variability of 64-year temperature trends based on model simulations (solid lines) (see also table S2, electronic supplementary material).

3. RESULTS

First spring observations for *H. merope* in the vicinity of Melbourne show a shift in earliest emergence date of −1.6 days per decade over the last 65 years (linear regression: $R^2 = 0.395$, $t_{14} = -2.798$, $p = 0.016$; figure 1a), associated with a regional increase of 0.14°C per decade during the developmentally important period (figure 1b). The thermal response of development rate varies considerably across the life stages (no fifth instars survived at constant temperatures at or above 25°C) (figure 1c). Combining the physiological functions of thermal sensitivity with the microclimate model and historical monthly climate data, we predicted a shift in emergence date of −1.6 days per decade (linear regression: $R^2 = 0.742$, $t_{14} = -3.670$, $p = 0.004$), close and statistically indistinguishable from the observed rate of −1.6 days per decade (heterogeneity of slopes test, $p > 0.05$; figure 1a). While the modelled *H. merope* temperatures are mainly a function of radiation, wind speed and air temperature, sensitivity analyses showed that most (80.6%) of the predicted shift in emergence date was driven by changes in air temperature. Very little (less than 1%) was independently attributable to wind speed and cloud cover, but the predicted effects of the latter two variables were inversely correlated ($r = -0.65$, $p = 0.01$).

Simulations from multi-member ensembles of four different general circulation models for the Melbourne area show that the air temperature trend coincident with the phenological shift in *H. merope* was very unlikely to be a result of natural internal climate fluctuations (figure 1d). Changes in natural external forcing, owing to changes in solar irradiance and volcanic aerosols, are likely to have led to a small cooling...
over this period (Karoly & Braganza 2005) and are very unlikely to explain the observed warming. The observed regional warming trend is consistent with the modelled climate response in this region to increasing greenhouse gases and other anthropogenic climate forcing (figure 1d).

4. DISCUSSION
The immature life stages of *H. merope* differ strongly in their thermal sensitivities, corresponding to seasonal changes in temperature during the immature period. Combining these physiological responses with historical weather records via the microclimate model, we predicted a shift towards earlier emergence of the same magnitude as that observed over the same time period. This very strongly suggests that the observed phenological shift in *H. merope* in the Melbourne area is a direct result of climate change impacts on the development rate.

In our model, egg, caterpillar and pupal temperatures were a function of air temperature and also of radiation (via cloud cover) and wind speed. Cloud cover and wind speed variation did explain part of the predicted shift in emergence date when considered in isolation but had no net effect because they acted in opposite directions. As a consequence, air temperature shifts were seen to dominate the predicted phenological response in this particular case, but it should be clear that this need not necessarily be so. In other cases, concurrent changes in other environmental variables may suppress or exacerbate the effects of air temperature and such complexities can only be considered through a mechanistic analysis of microclimatic impacts on phenology.

The observed shift in air temperature of 0.14°C per decade in the vicinity of Melbourne can very likely be explained through the effects of greenhouse gases emitted by humans (figure 1d). Our analysis thus provides direct causal linkages between the emission of greenhouse gases by humans, a shift in local air temperature, and the physiological response of a butterfly resulting in earlier spring emergence.

Phenological shifts may represent significant environmental challenges, particularly for species of low vagility, or provide opportunities for a species’ persistence (Harrington et al. 1999; Visser & Holleman 2001). Our study illustrates how it is possible to attribute phenological shifts to anthropogenic climate change based on physiological data, a model of how the organism experiences climatic conditions from a microclimatic perspective and the likelihood that locally observed climate change is human-caused. A greater understanding of the physiological links between changes in climate and phenology will strengthen our interpretation of past phenological change. It will also allow better forecasts of future shifts in phenology and their consequences (Ibáñez et al. 2006; Bradshaw & Holzapfel 2008; Kearney & Porter 2009).

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Pearse, F. K. 1978 Geographic variation and natural selection in the common brown butterfly, *Heteronympha merope*. PhD dissertation, La Trobe University, Melbourne, VIC.


