Early emergence in a butterfly causally linked to anthropogenic warming

Michael R. Kearney^{1,*}, Natalie J. Briscoe¹, David J. Karoly², Warren P. Porter³, Melanie Norgate⁴ and Paul Sunnucks⁴

¹Department of Zoology, and ²School of Earth Sciences, The University of Melbourne, Victoria 3010, Australia

³Department of Zoology, The University of Wisconsin, Madison, WI 53706, USA

⁴School of Biological Sciences, Australian Centre for Biodiversity, Monash University, Clayton, Victoria 3800, Australia

*Author for correspondence (mrke@unimelb.edu.au).

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 –1.5 days per decade over a 65-year period with a concurrent increase in local air temperatures of approximately 0.16°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 over the past few decades (Walther *et al.* 2002; Rosenzweig *et al.* 2008), including emergence in butterflies, migration in birds and fruiting and flowering in plants (Hughes 2000; Parmesan & Yohe 2003; Root *et al.* 2003; Chuine *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 butterfly *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), the males then 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 (37.60–38.54° S, 144.17–145.48° E) were based on opportunistically collected museum records and privately collected data courtesy of Kelynn L. Dunn. We used the 10-year average of the earliest observed record per year from 1941–2005 as the emergence date. While the use of opportunistically collected data probably adds considerable noise to any signal of phenological shift, we accounted for any chronological bias by including the number of museum records as a covariate in the analysis of the trend through time.

The thermal dependence of development rate for eggs, larvae and pupae was determined from the offspring of 10 field-collected females, raised individually on the grass *Ehrharta erecta* (Poaceae) from egg to emergence in glass vials (height 130 mm, diameter 25 mm) sealed with a moistened foam stopper. Temperature was controlled at 8°C, 12°C, 15°C, 25°C or 30°C with a 12:12 light:dark photoperiod. We observed the animals daily and recorded time to completion of each life cycle stage, the inverse of this being the developmental rate. We then fitted polynomial regressions to the relationship between development rate and temperature for each life stage, using the adjusted r^2 method (Quinn & Keough 2002).

We used historical weather data for 1945–2007 (Bureau of Meteorology, Australia) from Laverton (37.86° S, 144.76° E), a rural site close to Melbourne, to model the physiological response of *H. merope* to temperature. This station is a ‘high-quality’ site, unaffected by changes in exposure, urbanization, instrumentation, etc., during the study period. Weather records (mean monthly maximum and minimum air temperature, wind speed and cloud cover) were translated into microclimates experienced by immature *H. merope* using biophysical modelling software (NICHE MAPPER, <http://www.zoology.wisc.edu/faculty/Porter/Porter.html#niche>; Porter & Mitchell 2006). This software includes a microclimate model that translates weather-station records into near-surface air temperature and wind speed profiles and a soil surface energy balance (Porter *et al.* 1973). The model includes a first-principles model of solar radiation (McCullough & Porter 1971) and uses cloud cover records to predict long- and short-wave radiation loads. Individuals were assumed to be 3 cm above the ground in grass tussocks (75% shade), based on our observations of larval behaviour. Microclimate model predictions compared well with field microclimate measurements (figure S1, electronic supplementary material).

Animals were assumed to be at the 3 cm air temperature. Predicted daily cycles in animal body temperature were converted to constant temperature equivalents (CTEs) (as implemented in Mitchell *et al.* 2008), which were then used as independent variables in the fitted equations for thermal dependence of development rate. There was a good agreement between modelled CTE-based development times and the development times measured under natural, fluctuating thermal conditions in grass tussocks in Melbourne over the winter of 2007 (table S1, electronic supplementary material). We encoded the equations for development rate and CTE calculations into the Ectotherm model of NICHE MAPPER. The Ectotherm program tracked developmental stage on an hourly basis given a specified laying date (11 April—females lay from around March to April in Melbourne; Pearse 1978) and outputted the time of completion of development based on observed meteorological data from 1944 to 2005. We calculated separate emergence dates for each year and then took the average value for each 10-year window as the final emergence date. Note that we did not solve an energy balance specifically for the caterpillars with the Ectotherm model but rather assumed that they were at the shaded 3 cm air temperature.

We compared observed temperature trends from the high-quality weather station in Laverton with output from extended climate model simulations, both including and excluding anthropogenic

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2010.0053> or via <http://rsbl.royalsocietypublishing.org>.

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).

climate forcing for the single-model grid box overlying Melbourne and Laverton. Anthropogenic climate forcing included observed increases in greenhouse gases and estimated variations of anthropogenic aerosols, whereas natural external climate forcing included estimated changes in solar irradiance and volcanic aerosols. Multi-member ensembles of simulations from four different climate models with prescribed changes in both anthropogenic and natural external climate forcing were used to provide regional temperature data for 1944–2007 (table S2, electronic supplementary material). The range of possible trends owing to natural internal climate variability was estimated using the variability of regional temperature from extended control model simulations (including only natural climate variation with no changes in external forcing).

3. RESULTS

First spring observations for *H. merope* in the vicinity of Melbourne show a trend in earliest emergence date of -1.4 days per decade over the last 65 years (figure 1a). This trend is statistically significant (linear regression: $R^2 = 0.766$, year $p = 0.022$, museum record number $p = 0.046$) and occurs coincident with a regional air temperature increase of 0.16°C per decade during the developmentally important period ($R^2 = 0.893$, $p = 0.001$; 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 -1.5 days per decade ($R^2 = 0.866$, $p = 0.024$), close and statistically indistinguishable from the observed rate of -1.4 days per decade (heterogeneity of slopes test, $p > 0.944$; figure 1a). Importantly, the physiological model provided a better prediction of emergence date ($R^2 = 0.652$, $p = 0.028$) than did air temperature ($R^2 = 0.426$, $p = 0.112$). 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 0.16°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).

We thank Chris Thomas, Lesley Hughes, K. McClellan, Cheryl O'Dwyer, Nigel Stork, Anna Lister and Neil Murray for discussion/comments on the manuscript. We especially thank Mark Hendrickx whose critique of a previous version of the article significantly improved the final version. This study was supported by the Australian Research Council grants DP0772837 and FF0668679, Parks Victoria and Department of Sustainability and Environment, and by an Australian Department of Climate Change grant to N.J.B.

- Bradshaw, W. E. & Holzapfel, C. M. 2008 Genetic response to rapid climate change: it's seasonal timing that matters. *Mol. Ecol.* **17**, 157–166. (doi:10.1111/j.1365-294X.2007.03509.x)
- Chuine, I., Yiou, P., Viovy, N., Seguin, B., Daux, V. & Ladurie, E. L. R. 2004 Historical phenology: grape ripening as a past climate indicator. *Nature* **432**, 289–290. (doi:10.1038/432289a)
- Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A. & Schwartz, M. D. 2007 Shifting plant phenology in response to global change. *Trends Ecol. Evol.* **22**, 357–365. (doi:10.1016/j.tree.2007.04.003)
- Edwards, E. D. 1973 Delayed ovarian development and aestivation in adult females of *Heteronympha merope merope* (Lepidoptera: Satyriinae). *J. Aust. Entomol. Soc.* **12**, 92–98. (doi:10.1111/j.1440-6055.1973.tb01642.x)
- Harrington, R., Woiwod, I. & Sparks, T. 1999 Climate change and trophic interactions. *Trends Ecol. Evol.* **14**, 146–150. (doi:10.1016/S0169-5347(99)01604-3)
- Hughes, L. 2000 Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evol.* **15**, 56–61. (doi:10.1016/S0169-5347(99)01764-4)
- Ibáñez, I., Clark, J. S., Dietze, M. C., Feeley, K., Hersh, M., LaDeau, S., McBride, A., Welch, N. E. & Wolosin, M. S. 2006 Predicting biodiversity change: outside the climate envelope, beyond the species area curve. *Ecology* **87**, 1896–1906. (doi:10.1890/0012-9658(2006)87[1896:PBCOTC]2.0.CO;2)
- Karoly, D. J. & Braganza, K. 2005 Attribution of recent temperature changes in the Australian region. *J. Climate* **18**, 457–464. (doi:10.1175/JCLI-3265.1)
- Kearney, M. & Porter, W. P. 2009 Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* **12**, 334–350. (doi:10.1111/j.1461-0248.2008.01277.x)
- McCullough, E. C. & Porter, W. P. 1971 Computing clear day solar radiation spectra for the terrestrial ecological environment. *Ecology* **52**, 1008–1015. (doi:10.2307/1933806)
- Mitchell, N. J., Kearney, M., Nelson, N. J. & Porter, W. P. 2008 Predicting the fate of a living fossil: how will global warming affect sex determination and hatching phenology in tuatara? *Proc. R. Soc. B* **275**, 2185–2193. (doi:10.1098/rspb.2008.0438)
- Parnesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* **37**, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)
- Parnesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)
- Pearse, F. K. 1978 Geographic variation and natural selection in the common brown butterfly, *Heteronympha merope*. PhD dissertation, La Trobe University, Melbourne, VIC.
- Porter, W. P., Mitchell, J. W. 2006 *Method and system for calculating the spatial-temporal effects of climate and other environmental*

- conditions on animals*, vol. 1 (eds U. P. Office). Madison, WI: Wisconsin Alumni Research Foundation. See <http://www.patentstorm.us/patents/7155377-fulltext.html>.
- Porter, W. P., Mitchell, J. W., Beckman, W. A. & DeWitt, C. B. 1973 Behavioral implications of mechanistic ecology—thermal and behavioral modeling of desert ectotherms and their microenvironment. *Oecologia* **13**, 1–54. (doi:10.1007/BF00379617)
- Quinn, G. P. & Keough, M. J. 2002 *Experimental design and analysis for biologists*. Cambridge, UK: Cambridge University Press.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. 2003 Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60. (doi:10.1038/nature01333)
- Rosenzweig, C. *et al.* 2008 Attributing physical and biological impacts to anthropogenic climate change. *Nature* **453**, 353–357. (doi:10.1038/nature06937)
- Visser, M. E. & Holleman, L. J. M. 2001 Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. R. Soc. Lond. B* **268**, 289–294. (doi:10.1098/rspb.2000.1363)
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395. (doi:10.1038/416389a)