

Thermal performance under constant temperatures can accurately predict insect development times across naturally variable microclimates

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Abstract

External conditions can drive biological rates in ectotherms by directly influencing body temperatures. While estimating the temperature dependence of performance traits such as growth and development rate is feasible under controlled laboratory settings, predictions in nature are difficult. One major challenge lies in translating performance under constant conditions to fluctuating environments. Using the butterfly *Pieris napi* as model system, we show that development rate, an important fitness trait, can be accurately predicted in the field using models parameterized under constant laboratory temperatures. Additionally, using a factorial design, we show that accurate predictions can be made across microhabitats but critically hinge on adequate consideration of non-linearity in reaction norms, spatial heterogeneity in microclimate and temporal variation in temperature. Our empirical results are also supported by a comparison of published and simulated data. Conclusively, our combined results suggest that, discounting direct effects of temperature, insect development rates are generally unaffected by thermal fluctuations.

KEY WORDS

degree-days, development rate, fluctuations, insect, Jensen's inequality, microclimate, predictions, rate summation, temperature, thermal performance

INTRODUCTION

Many ecological processes are fundamentally dependent on temperature and its variability. Yet, predicting thermal responses in the field is notoriously difficult, since it requires a mechanistic understanding of how traits respond to the range of temperatures organisms experience throughout their life cycles (Sinclair et al., 2016). One central challenge when predicting ectotherm

thermal responses in nature is the potential discrepancy between trait values under constant and fluctuating thermal environments. While constant temperatures are unnatural for most ectothermic terrestrial animals, they are commonly used when estimating temperature dependent trait performance. However, whether predictive models of temperature-sensitive performance traits parameterized under constant temperatures generally yield correct predictions under natural fluctuations is an

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unsolved question in thermal biology (see Colinet et al., 2015; Ma et al., 2021).

Certain mechanisms can cause differences between performance under constant and fluctuating temperatures, such as thermal stress accumulation (MacMillan & Sinclair, 2011; Williams et al., 2015), thermal acclimation (Angilletta, 2009; Sgrò et al., 2016), repair during favourable temperatures of damage sustained under adverse ones (Colinet et al., 2006; Lalouette et al., 2011), or ontogenetic shifts in thermal performance (Berger et al., 2011; Bowler & Terblanche, 2008). These mechanisms cause temperature-induced or time-dependent changes in thermal reaction norms, making it difficult to bridge the gap between thermal performance under constant and fluctuating conditions. We hereby refer to such eco-physiological effects as inherent effects of thermal fluctuations. Moreover, other environmental cues may influence how temperature affects performance (Gotthard, 2008), complicating predictions—particularly under fluctuating temperature regimes. These hurdles are well-known and have been discussed in the literature (Chown & Terblanche, 2006; Colinet et al., 2015; Dowd et al., 2015; Sinclair et al., 2016).

Although linear models (such as degree-day models) are used extensively for predicting thermal responses (Rebaudo & Rabhi, 2018), both theory and empirical data have shown that biological thermal reaction norms are generally not linear. They are usually unimodal and left skewed, with both convex and concave parts (Angilletta, 2006; Huey & Kingsolver, 1989). Therefore, non-linear models that capture the typical shape of thermal reaction norms (hereafter thermal performance curves [TPCs]) are increasingly used in favour of linear models (Rebaudo et al., 2018).

These non-linear responses have made Jensen's inequality (Jensen, 1906)—which shows that the mean value of a predictor variable fluctuating along a curvilinear part of the reaction norm inaccurately predicts the mean of the response variable (Figure 1)—a much discussed topic in thermal biology (Colinet et al., 2015; Denny, 2017; Dowd et al., 2015; Martin & Huey, 2008; Ruel & Ayres, 1999; Vasseur et al., 2014). Indeed, Jensen's inequality is a necessary null hypothesis for identifying mechanisms that lead to inherent effects of thermal fluctuations (e.g. acclimation). It highlights that it is not enough simply to compare average performance under fluctuating and constant temperatures of corresponding means. Instead, it is sensible first to estimate performance under constant temperatures and then to use rate summation (or equivalent methods; see Bernhardt et al., 2018; Liu et al., 1995) for predicting the performance under fluctuating temperatures. If the prediction fails, it implies that there are inherent effects of thermal fluctuations at play.

Alternatively, if thermal variability does *not* inherently influence trait performance, these general patterns should follow when predicting non-linear thermal responses using rate summation:

1. The predictive accuracy of non-linear thermal performance models significantly exceeds that of linear degree-day models when temperatures fluctuate over highly non-linear regions of the thermal reaction norm, but both model types perform similarly when temperatures fluctuate over approximately linear regions.
2. The benefit from the higher complexity of non-linear models critically hinges on adequate sampling of the prediction model's input data. When temperatures fluctuate over non-linear regions of the thermal reaction norm, the superior accuracy of non-linear models is only apparent if the resolution of input temperatures, both temporal and spatial, is high enough to capture such fluctuations.

Here, we study development rate, a key life history trait (Chown et al., 2002; Nylin & Gotthard, 1998), under natural temperature fluctuations. Using the butterfly *Pieris napi* as a model species, we parameterized development time prediction models under constant laboratory conditions. We validated the models through field transplantations stretching across two life stages (eggs and larvae) and multiple microclimates and designed our experiments to meet several important methodological assumptions (Box 1; Havird et al., 2020).

Moreover, to explore the patterns described above in bullet points 1 and 2 the study was expanded to include comparisons of multiple prediction models with varying complexity and resolution of input data in a factorial design. Non-linear development rate models fitted separately for each life stage were contrasted against a degree-day model fitted for the full ontogenetic period (the typical approach; Rebaudo et al., 2018). Different sampling frequencies of environmental temperatures were compared, covering a gradient from 15-min point measurements to daily mean temperatures. The potential importance of microclimate variation for predictive modelling of ectotherm responses has long been recognized and still constitutes a challenge (Higley et al., 1986; Rebaudo et al., 2016; Woods et al., 2015). In fact, weather station data are still used extensively (e.g. Kingsolver & Buckley, 2017; Lehmann et al., 2020; Sunday et al., 2012). Therefore, we also compared predictions using temperatures measured by a nearby weather station to predictions using microclimate data measured on-site.

Results were concordant with the expected patterns, and non-linear TPCs accurately predicted average development times under well-sampled field conditions. Development rates appear unaffected by thermal fluctuations when direct effects of temperature are accounted for. The generality of these results was further explored using simulated and published data comparing development times under fluctuating and constant temperatures. In agreement with our experimental findings, our

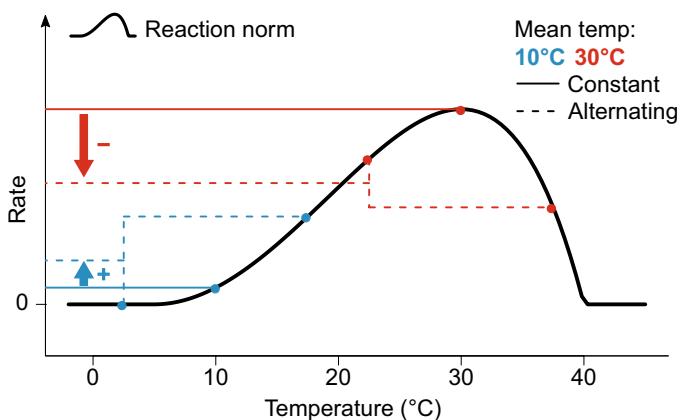


FIGURE 1 A visualization of the consequences of Jensen's inequality when using mean temperatures to predict mean performance in a variable thermal environment, and the response is non-linear. Here, performance is represented by an arbitrary rate process whose thermal reaction norm has a minimum, optimum and maximum temperature for performance of 5, 30 and 40°C, respectively. Four hypothetical temperature treatments are illustrated: constant (solid coloured lines) and alternating (i.e. abruptly fluctuating, dashed coloured lines) temperatures, each with a mean of both 10°C (blue) and 30°C (red). The temperature range of the alternating treatments is 15°C, and alternations are assumed to be symmetrical. The upwards arrow represents a positive effect of thermal fluctuations on average performance, and the downwards arrow represents a negative effect. This demonstrates that, when compared to a constant thermal environment of the same mean, (1) temperature fluctuations over a mainly convex portion of the thermal reaction norm increase average performance, and (2) temperature fluctuations over a mainly concave portion of the thermal reaction norm decrease average performance. Because of the typical thermal reaction norm shape, fluctuations should generally have a negative influence on average performance under warm conditions, and a positive effect under cold conditions. This figure demonstrates the general direction of the effect of temperature variance on average thermal performance under a simplified scenario. In reality, the absolute effect will vary greatly depending on the interaction between thermal regimes and reaction norms. For details, see Colinet et al. (2015); Dowd et al. (2015) and Denny (2017); Martin and Huey (2008); Ruel and Ayres (1999); and Vasseur et al. (2014).

BOX 1 Methodological assumptions for successfully implementing development rate summation

1. The thermal performance curve (TPC) under constant temperatures is adequately described (e.g. TPCs are not fitted to data from only a few temperatures; Dowd et al., 2015; Howe, 1967; Liu et al., 1995).
2. If used for extrapolation, the TPC is meaningful outside of the sampled range (e.g. linear degree-day models with no upper developmental threshold are avoided, as they assume a potentially infinite increase in trait performance with temperature; Colinet et al., 2015; Ruel & Ayres, 1999).
3. Mortality is not used to infer performance in other traits (e.g. 100% end mortality under constant temperatures is not assumed to imply a development rate of 0; Khelifa et al., 2019; Liu et al., 1995).
4. Differences in thermal performance among life stages are accounted for (e.g. by fitting separate TPCs; Kingsolver & Buckley, 2020; Sinclair et al., 2016).
5. The sampling resolution is adequate for the temporal scales of interest (e.g. interpolation methods which might miss prolonged periods at adverse conditions are avoided; Irvine, 2011; Rabinovich et al., 2006; Simonet & Davenport, 1981).
6. The sampling resolution is adequate for the spatial scales of interest (e.g. behavioural thermoregulation that cause discrepancies between operative body temperatures and measured temperatures is reduced by fine-scale sampling; Abram et al., 2017; Tattersall et al., 2012; Woods et al., 2015).
7. When using artificial thermal regimes, thermal ramping and decline, or other discrepancies between actual and programmed temperatures, are accounted for (Petavy et al., 2001).
8. When fluctuations span relatively long time periods, and treatment is carried out over the full development, differences in thermal sums depending on starting temperature are accounted for (Franke et al., 2014).
9. Potential confounding effects are avoided (e.g. the use of different host plants or genetic populations in constant and fluctuating treatments is avoided; Rabinovich et al., 2006; Zhao et al., 2014).

simulation showed that the general pattern of development time differences found in the published data could arise from Jensen's inequality alone. As such, this study

provides valuable theoretical insights for disentangling the intricate network of thermal effects on insect fitness, and our results have practical implications for ectotherm

phenology, distribution and population dynamics modelling, providing useful guidance for parameterization and sampling effort.

MATERIALS AND METHODS

Study organism

Pieris napi L. (Lepidoptera: Pieridae) is a widespread, circumboreal butterfly that feed on plants from the Brassicaceae family (Chew & Watt, 2006; Friberg et al., 2015; Friberg & Wiklund, 2019; Petersen, 1949). It is a pupal diapauser with latitudinal variation in voltinism, bivoltine in the areas sampled here (ArtDatabanken, 2020). Females lay eggs directly on the larval host plants. Prior to pupation, larvae attach to the substrate by spinning a girdle of silk, spending roughly 1 day as pre-pupae.

Thermal performance 2018

Mated *P. napi* females were sampled from the Stockholm area, Sweden (WGS84 decimal: Lat. 59.368, Lon. 18.061), during the first flight peak in May. F2 individuals from five families were treated at six different temperatures (10–35°C) under 23-h day lengths. For details on the rearings, see Appendix S1. We estimated the effects of temperature not only on eggs and larvae separately but also for the egg and larval stage in succession (from oviposition to pupation, hereafter referred to as the ontogeny treatment).

Egg treatments were started immediately (1–15 min) after oviposition on *Armoracia rusticana*. Leaves were moved to a climate chamber once 5–15 eggs had been laid, resulting in sample sizes between 41 and 77 per treatment ($n_{\text{tot}} = 344$). Eggs were checked for hatchings twice daily (morning/afternoon). Dead eggs were visually identified and kept under treatment conditions for 2 weeks after hatching had ceased.

For the larval treatments, eggs were first kept under ambient (22L:2D, 23°C) conditions until the day of hatching, when treatment was initiated. Larvae from the same family were kept in containers housing only four to six larvae each. Sample sizes were 46–50 per treatment ($n_{\text{tot}} = 292$).

The ontogeny treatments were started simultaneously as the egg treatments using the same method. Leaves were moved to separate containers, each housing four to six eggs. Sample sizes were 46–53 per treatment ($n_{\text{tot}} = 294$).

Sex was determined in the pupal stage and therefore only recorded for individuals in the ontogeny and larval treatments. All larvae were fed *ad libitum* with *A. rusticana*. Development times and mortality were recorded for subsequent model fitting.

Thermal performance 2019

As the 35°C treatment resulted in 100% mortality, additional mated females were sampled 2019 (from the same location as 2018), and two additional temperature treatments at 28 and 32°C were added using previous methodology. Matings yielded six families, and sample sizes per temperature treatment were 65–96 for eggs ($n_{\text{tot}} = 161$), 45–63 for larvae ($n_{\text{tot}} = 108$), and 86–112 for ontogeny ($n_{\text{tot}} = 182$).

Field transplantations

Mated *P. napi* females were sampled from the Stockholm area, Sweden (59.368, 18.061) during the first flight peak in May 2019. For details on the rearings, see Appendix S1. When four to seven F1 eggs had been laid on an *Armoracia rusticana* leaf, it was moved to a separate container (Figure S1, modified with small holes at the bottom to allow for drainage of potential rainwater during the transplantation period). Roughly 25 females contributed to the experimental population. None of the families used for the transplantations were used in previous thermal performance experiments.

Containers were immediately placed in a 15°C climate cabinet (Panasonic MLR-352; PHC Europe B.V., Etten-Leur, The Netherlands) to lower development rate, while ensuring that a minimal and estimable proportion of the total development was completed in the lab. Eggs spent 4–49 h at 15°C before being moved to field conditions.

On 28 June 2019, the eggs were transplanted to nine different sites across a heterogeneous field area, Kronängen, in Södermanland, Sweden (58.972, 17.158, Figure 2d,e). The sites covered a wide variety of microhabitats (Appendix S1, Figure S12, and Table S2). In each site, five containers were placed in a cage of 80 × 80 × 50 cm³, with coarse-meshed netting protecting against potential predators while allowing for wind and rain to pass through (Figure S1). In each cage, temperature loggers with internal sensors (EL USB-1; Lascar Electronics, Salisbury, UK) were placed in two containers in opposing corners of the cage. Temperatures were logged every 15 min, and measurements from the two loggers were averaged (average absolute differences between the loggers did not exceed 0.4°C within any cage). The relatively small size of the containers causes homogeneous temperatures within, minimizing the potential for larval behavioural thermoregulation. Additionally, comparisons with sun shielded loggers in the same study area show that effects caused by radiative heating are likely negligible (Appendix S1; Figure S13). Consequently, temperatures logged within containers should accurately reflect the temperatures experienced by the individuals.

Transplanted individuals were fed *ad libitum* with *A. rusticana*, and host plants were monitored daily. Host plants were watered when water levels were anticipated

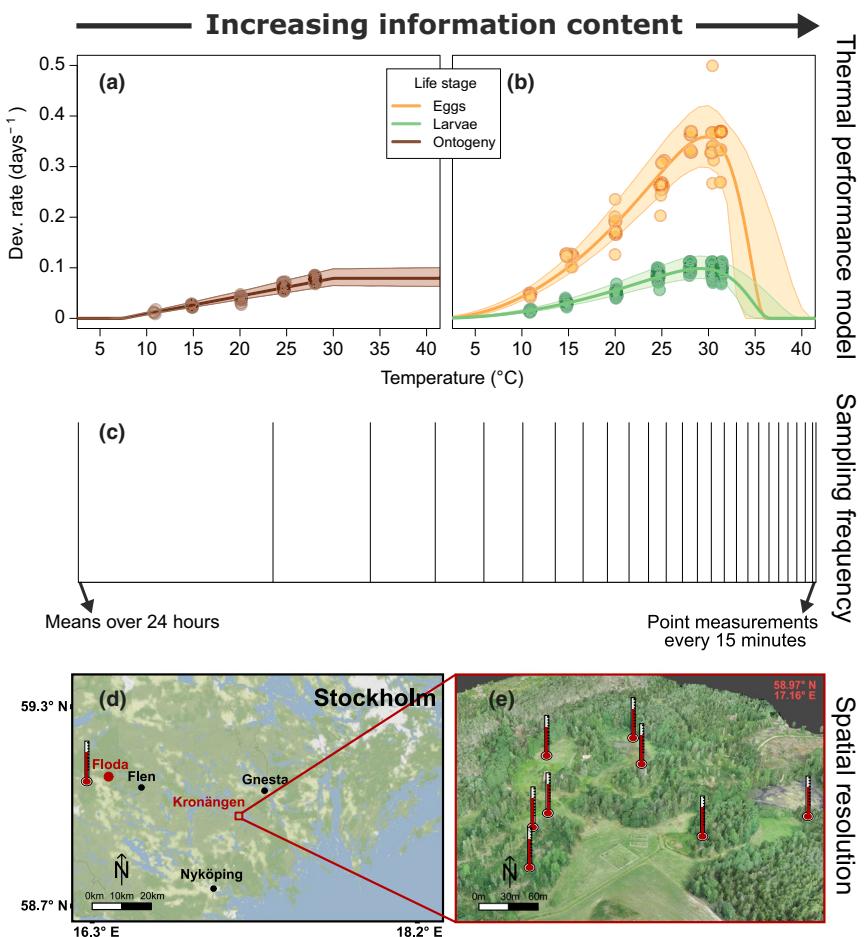


FIGURE 2 Demonstration of different complexity levels in the components of the prediction models. Information content increases from left to right, going from simplified to more complex thermal performance models, low to high temperature sampling frequency, and macroclimate to microclimate temperature measurements. Two approaches for modelling development rate as a function of temperature were used: (a) a degree-day model with a horizontal cut-off at 30°C and a linearly extrapolated lower developmental threshold, fitted for the full ontogenetic development (climate cabinet settings from 10 to 28°C) and (b) empirical non-linear models, fitted separately for the egg and larval stage. (c) Different sampling intervals were used for the temperature input data, ranging from daily to bihourly means (based on hourly point measurements), as well as hourly and 15-min point measurements. Temperature measurements were gathered from both (d) the nearest inland weather station with hourly measurements, Floda, and (e) each of the eight different sites. In (a) and (b), measured temperatures (by calibrated temperature loggers) are used instead of the pre-programmed climate cabinet settings (10–32°C), and points represent real, experimental data (polygons represent 95% prediction intervals)

to reach below the cut plant stems before the next inspection. One of the cages suffered from drought, causing high mortality and completely synchronous pupation of the five individuals left, indicating earlier pupations at suboptimal sizes as a response to adverse conditions (see Shafiei et al., 2001). Therefore, it was removed from the subsequent analyses. In all other cages, the watering was adequate (i.e. never below the cut plant stems), and high host plant quality was maintained.

Pupations were recorded daily until 1 August 2019. At that date, pre-pupae and large, wandering fifth-instar larvae were recorded. If those individuals were later found to have pupated, pre-pupae were recorded as having pupated 1 day later, and larvae 2 days later. These assumptions are consistent with observed patterns in all stages of the experiment. The total sample size of surviving individuals for which pupation date could be

determined was 93 out of 96 total (for more information on this and mortality, see Appendix S1, Figure S14, and Table S2).

Thermal performance models

Bayesian models were fitted using Stan (Carpenter et al., 2017) through the package brms (Bürkner, 2017) in R (R Core Team, 2020). Development rate (days^{-1}) was modelled as a function of the average temperature experienced by each individual during the treatment.

Two types of models were fitted: a linear degree-day model, and non-linear models (Figure 2a,b, respectively). The linear degree-day model was fitted to data from the linear part of the reaction norm in the ontogeny treatment (10–28°C) with a horizontal cut-off at 30°C

(where the reaction norm deviates from linearity) and a linearly extrapolated lower threshold. The Ratkowsky function (Ratkowsky et al., 1983) was used for the non-linear TPCs. This function has several desirable properties described in Appendix S1. Separate non-linear TPCs were fitted for the egg and larval development rates. For details on how the concept of degree-day modelling relates to thermal reaction norms and an explanation on the horizontal cut-off, see Appendix S1.

Experiment year was treated as an intercept effect centred on 0, essentially averaging the main function between the years. As we expect a 50/50 sex ratio, a similar approach was used for the effect of sex, but this effect was additionally allowed to vary with temperature. Family and container were modelled as group-level effects with random intercepts. Family effects were allowed to vary among temperature treatments.

For detailed information on the models used, the model fitting process, prior specifications, and posterior predictive checks (see Appendix S1, Table S1, and Figure S3). Model fittings and subsequent predictions were for validation purposes repeated using non-linear least squares (through the ‘nls’ function in R) on marginal means (Figure S2). To ensure that model choice did not have a major impact on our results, this was repeated for nine different commonly used non-linear thermal performance models (Figure S5). Additionally, degree-day models with horizontal cut-offs were fitted separately for eggs and larvae, and typical degree-day models without horizontal cut-offs were fitted for both the ontogeny treatments and the separate life stages (Figure S4). Subsequent predictions were made to ensure that neither the cut-off nor the separation of life stages influenced the conclusions (Figure S4).

Prediction models

Microclimate temperatures were measured at 15-min intervals in each of the field transplantation sites. Together with the estimated TPCs, field temperatures were used to predict development times of the transplanted *P. napi* eggs and larvae. Predictions were made using rate summation (for details, see Appendix S1) based on temperatures from 15-min point measurements, 1-h point measurements (every fourth 15-min measurement), and means over 1–24 h, resulting in a gradient of temperature sampling frequencies (Figure 2c). Hourly point measurements were used for calculating mean temperatures. We used linear degree-day models to predict total development time from egg to pupa (Figure 2a), and non-linear models to predict egg and larval development times separately (Figure 2b). These two approaches represent two complexity levels of the prediction model's thermal performance component (Figure 2a,b).

The procedure above was repeated using temperature data from the nearest inland weather station with hourly

point measurements (Floda, 59.056, 16.395; Figure 2d; SMHI, 2020). The weather station and microclimate measurements represent two levels of spatial resolution in the input data of the prediction models (Figure 2d,e). Consequently, a full factorial design was used, testing the predictive accuracy of each combination of prediction model parameters (e.g. high environmental temperature sampling frequency, high model complexity and high spatial resolution), with the only exception being that 15-min temperature point measurements were not available in the weather station data.

Percentage errors in development time predictions were calculated as $(\text{Time}_{\text{observed}} - \text{Time}_{\text{predicted}})/\text{Time}_{\text{observed}}$ for each prediction model (i.e. each unique combination of sampling frequency, model complexity, and spatial resolution) and individual. Prediction model-specific average percentage error was estimated using a multivariate analysis in the aforementioned Bayesian framework. Prediction errors within each prediction model were treated as a separate response variable, and the average error was modelled as a population-level intercept effect. Cage and container were treated as group-level effects with random intercepts. Cage-specific prediction error can be caused by both the interaction between the prediction model and the site-specific thermal regime, as well as other, random, cage effects. While the former depends on which prediction model is used, the latter is shared among all prediction models. As such, cage (i.e. site) effects were modelled as correlated among prediction models. Residual variance was allowed to vary among sites, as it is expected to vary with thermal regime. Model uncertainty in average percentage prediction error is presented using 90% highest density intervals (HDIs). A Gaussian error distribution and default priors for the brms package were used. Posterior predictive checks are presented in Figure S3.

Comparing published and simulated data

To expand our results, we calculated logarithmic (\log_2) fold change in development time between fluctuating and constant temperatures of corresponding means for 98 insect species from seven orders and multiple life stages, using data from 101 published studies (Table S3). Temperature treatments encompassed a wide range of mean temperatures and fluctuation ranges. The published data were graphically compared to data simulated under similar thermal conditions. Simulations included statistical noise and temperature-dependent effects on mortality but assumed no inherent effects of temperature fluctuations on development time. The simulated TPC parameters, the mean and fluctuation range of temperature treatments, and mortality rates were based on distributions of data from the present and previously published studies. For details on the simulation procedure, see Appendix S1 and Figures S6–S11.

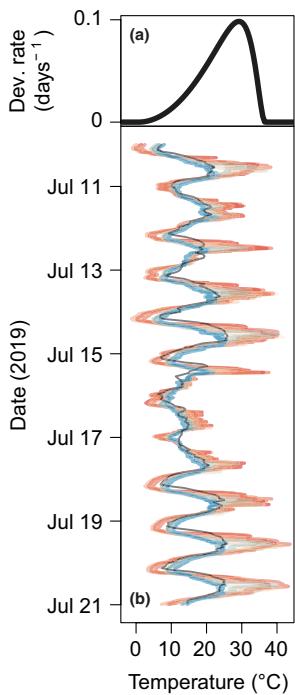


FIGURE 3 Demonstration of how (a) the thermal performance curve (TPC) for *Pieris napi* larval development rate relates to (b) the actual temperatures experienced by the transplanted individuals, here shown as temperature fluctuations over 10 days during the middle of the field experiment. Each line represents one of the eight transplantation sites. Lines are coloured by temperature variance, with red lines representing sites with high temperature variance, and blue lines sites with low temperature variance. The black line represents weather station data for the same time period. Although sites do not vary drastically in mean temperature, they clearly sample different regions of the TPC, with temperatures in some sites fluctuating over the full range and in other sites only over the approximately linear region. The weather station data poorly represent the sites with large temperature variance

RESULTS

Field transplantations and model predictions

For the TPC parameter estimates, see Table S1. Some transplantation sites had wide temperature fluctuations, covering the full thermal breadth (as estimated by the non-linear models). Other sites had narrow fluctuations, mainly within the approximately linear regions of the TPC (Figure 3). Similarly, the weather station only recorded temperatures in the approximately linear range of the curve, highlighting the disparity between weather station data and many microclimates (Figure 3). The proportions of surviving individuals suggest that mortality might be correlated with the magnitude of heat extremes (Appendix S1; Figure S14). The average development time from oviposition to pupation for the transplanted individuals was 33.5 days. Although sites showed a large variation in thermal regimes, differences in site means were relatively small, but variation in development times noticeably differed among sites (Figure 4a).

Predictions using linear degree-day models yielded unrealistically low development time estimates, and accuracy was relatively unaffected by sampling frequency (Figure 4b,d). As sampling intervals shrink and temperatures are averaged over shorter time periods, variance in input temperatures increases. However, as long as the variation in input temperatures does not reach above the horizontal threshold, or below the estimated minimum temperature for development (i.e. remains within the region of linear increase, see Figure 2a), this will not influence predictions. As sampling intervals become short enough to cause input temperatures to fluctuate over these thresholds, the horizontal upper cut-off counteracts the *increase* in error that would result if no horizontal cut-off was used (c.f. Figure S4). Thus, linear degree-day models consistently overestimate the average rate of development under fluctuating conditions. Average error in development time predictions was estimated to -10.2% and -9.0% when using microclimate and weather station measurements, respectively.

The effects of sampling frequency on prediction error are more complex when non-linear TPCs are employed (see Figure 4c,e). When using weather station temperature data, accuracy decreases as sampling frequency increases. When using microclimate data, accuracy first decreases as sampling frequency increases. It then increases steeply, until 90% HDIs for the average prediction error overlap 0% at the two shortest sampling intervals (Figure 4c). This high predictive accuracy when using non-linear models and high-resolved environmental sampling is concordant with a lack of inherent effects of temperature fluctuations. At 15-min sampling intervals, the average error in development time predictions was estimated to -1.9% when using microclimate data and non-linear TPCs. Contrastingly, when using weather station data, the average prediction error was estimated to -8.0% at the highest sampling frequency. The (initial) decrease in accuracy of the non-linear models is merely a consequence of Jensen's inequality when thermal regimes are artificially distorted by temperature averaging (for details, see Appendix S1).

When microclimate temperatures and non-linear TPCs are used, informative differences in prediction error among sites become apparent (Figure 4c). In sites with low temperature variance, predictive accuracy was relatively high and invariant across different sampling frequencies. Contrastingly, in the highly variable sites, low environmental sampling frequency (i.e. averaging temperatures over long periods of time) caused overestimations of development rate. As environmental sampling frequency increases, the systematic overestimation of development rate in high-variance sites disappears (Figure 4c). This is because temperatures in high-variance sites fluctuated over highly non-linear regions of the TPC, whereas temperatures in low-variance sites did not (Figure 3). Differentiating development time

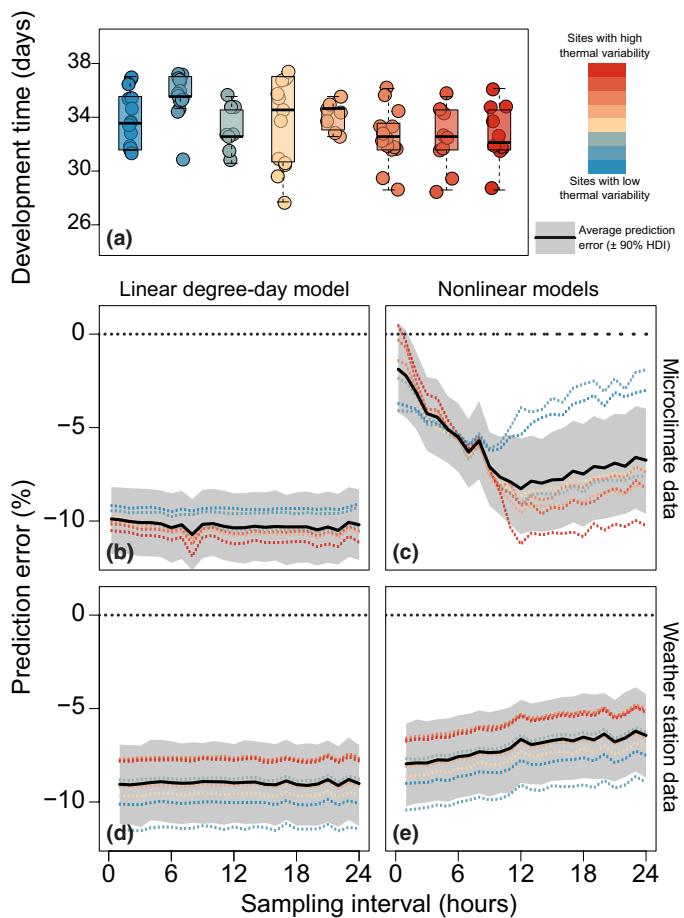


FIGURE 4 (a) Development times (to pupation) of transplanted individuals in each of the eight sites. Sites are coloured by their temperature variance. (b–e) Predictive accuracies for each prediction model, measured in percentage error (y-axis). Values on the x-axis represent the sampling frequency of the input temperature data, ranging from 15-min and 1-h point estimates, and bihourly to daily means. Short sampling intervals correspond to a high sampling frequency. The dotted line represents an average percentage prediction error of 0. Thick black lines represent estimates of average prediction error, and grey shading represents the 90% highest density interval (HDI). Site-specific errors (posterior medians for their estimated random intercepts) are represented by coloured lines. Coloured lines in (b–e) represent sites of corresponding colour in (a)

predictions between microhabitats is not possible when using weather station data. In that case, variation in prediction error only reflects the variation in development times observed in the field (Figure 4a,d,e).

The combined results follow the expected patterns under the null hypothesis and suggest that rate summation only yields accurate predictions across a wide range of microclimates when non-linearity, temporal variation and spatial variation are accounted for. Estimated prediction errors were 4.7–5.4 times higher when using weather station data or linear degree-day models compared to when using non-linear TPCs in combination with microclimate measurements.

The main results did not change when examining raw prediction errors, using non-linear least squares for curve fitting, fitting life stage-specific linear degree-day models or changing TPC function (Figures S2, S4 and S5). The latter indicates a robustness to errors associated with extrapolation using non-linear TPCs in this study system.

Comparing published and simulated data

Most reviewed studies did not contain enough information for a standardized reanalysis using rate summation. Indeed, in light of both Jensen's inequality and the assumptions outlined in Box 1, we found that evidence for inherent effects of thermal fluctuations on insect development rate is surprisingly sparse.

Because of the typical shape of development rate TPCs, Jensen's inequality predicts that fluctuations will tend to lower development times at cold mean temperatures but increase them as mean temperatures approach the optimal constant temperature (Figure 1; Colinet et al., 2015). The strength of the effect should generally be dependent on the range of the fluctuations. This is apparent from the simulated and published data, which both follow this pattern in a very similar manner (Figure 5). When considering statistical noise and time-dependent effects on mortality, the general relationship between development time under constant and fluctuating temperatures of

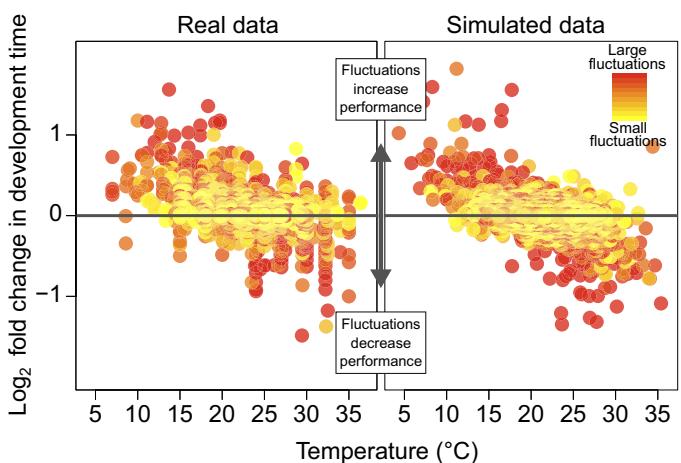


FIGURE 5 Log₂ fold change (y-axis) in development time between fluctuating and constant temperatures of corresponding means (x-axis) in published data and simulations. A value of 1 means that the development time under fluctuating temperatures is half of that under constant temperatures (i.e. performance is doubled), and vice versa for -1. The colour shows the range of the thermal fluctuations, highlighting the interaction between mean temperature and fluctuation range. Red indicates relatively large fluctuations for the given mean temperature, and yellow indicates relatively small fluctuations

corresponding means can, over a wide range of temperatures, be adequately described using Jensen's inequality alone (Figure 5).

DISCUSSION

The use of degree-day models, averaged environmental temperatures and weather station measurements all lead to a 'linearized' temperature response in the prediction model. This should be of relatively little detriment when making predictions in environments where temperatures rarely vary beyond the approximately linear regions of the reaction norm. However, such situations could be rare for insects and other small ectothermic animals that frequently occupy scales where microclimate variation is substantial. Microclimatic effects can either amplify or buffer temperatures (Woods et al., 2015; Zhu et al., 2019), and as seen in our data, a linearized prediction model is not generalizable across microhabitats (Lembrechts et al., 2020; Lembrechts & Nijs, 2020; Rebaudo et al., 2016).

During warm seasons, as in this study, temperatures vary more over the concave region of the TPC, causing linearized temperature responses to overestimate performance (vice versa during cold seasons; see Figure 1). This pattern has previously been identified when using degree-day models (and error potential is even larger without an upper cut-off; see Figure S4) or daily average temperatures for making predictions (Maiorano et al., 2012). Our results align with these expectations, but they also highlight the important role of micro-macroclimate decoupling in such linearization, as well as the gradual effects of decreasing temporal resolution in the form of temperature averaging (Figure 4). For example, Khelifa et al. (2019) successfully employed rate summation in

five species of *Scatophaga* flies under fluctuating temperatures in well-controlled laboratory conditions. However, they overestimated development time when applying the method in the field using weather station data—particularly when temperatures often fell below the estimated minimum for development. In light of our findings, these results are in accordance with Jensen's inequality. Weather stations are unlikely to fully reflect microclimatic thermal fluctuations, potentially causing an underestimation of performance during cold periods. We emphasize that non-linear reaction norms are 'data-hungry': without spatially *and* temporally high-resolved sampling of environmental conditions, ecological consequences may be misinterpreted. Consequently, the gains from investing in parameterization and sampling for prediction models are relative. In environments with temperature variation primarily in the approximately linear region of the TPC, average temperatures or linear degree-day models could be sufficient. However, variation in highly non-linear regions of the reaction norm calls for highly resolved environmental sampling and well-estimated TPCs. The effort put into estimating the TPC should scale proportionally with the probability of environmental temperatures varying along highly non-linear regions. For example, to reduce error caused by extrapolation and model choice (see Appendix S1 for more information), sampling the right side of the TPC should be prioritized when environmental temperatures frequently approach the maximum temperature for development.

Still, despite theory showing that linear temperature responses are generally unrealistic, linear degree-day models are used extensively for insect phenology modelling (Rebaudo & Rabhi, 2018). Perhaps this stems from the assumption that temperatures fluctuate mainly in the left region of the thermal reaction norm (see Campbell et al.,

1974). We here show that this general assumption must be re-evaluated at microclimatic scales. Without data on temperature fluctuation ranges at relevant spatial scales, the performance of linear degree-day models will likely suffer from errors associated with unwanted extrapolation.

In our model species, *P. napi*, the rate summation approach accurately predicted average development time under naturally fluctuating temperatures across multiple microclimates, but, as hypothesized, only when the appropriate conditions are met (Figure 4; Box 1). Additionally, cage-specific prediction errors (Figure 4c) followed the expected pattern under the null hypothesis: using linear degree-day models or mean temperatures is most detrimental when temperatures fluctuate over highly non-linear regions of the TPC. These findings imply that fluctuations themselves do not have a major effect on performance, and each infinitesimal step in time can be successfully modelled as a constant temperature. The concept of development rate summation is old and has previously been scrutinized (Kaufmann, 1932; Liu et al., 1995). Liu et al. (1995) identified and avoided many of its methodological pitfalls and suggested that, in general, the rate summation approach is appropriate. Since then, this approach has been criticized; for example, Colinet et al. (2015) and Ma et al. (2021) conclude that constant temperatures poorly predict performance under thermal fluctuations. While this general assumption seems justified for some processes, such as mortality (Rezende et al., 2014), and perhaps growth (Kingsolver et al., 2015), it appears to be unwarranted for insect development rates. This also highlights that our results should not naively be assumed to extend to other processes.

Although a multitude of biological responses to fluctuating environmental conditions have been identified (Bernhardt et al., 2020), such responses should not by default be confounded with inherent effects of temperature fluctuations. For example, behavioural thermoregulation could superficially cause deviations from the null hypothesis (given Jensen's inequality) by creating a discrepancy between measured temperatures and actual body temperatures (Ma et al., 2021; Woods et al., 2015). Indeed, with robust methodology (see Box 1), inherent effects of thermal fluctuations (Milosavljević et al., 2020) stand out as the exception rather than the rule (Khelifa et al., 2019; Ludwig & Cable, 1933; Martínez-García et al., 2018). This is corroborated by the similarities between simulated and observed differences in development times between fluctuating and constant temperatures across a large number of studies, species and thermal regimes (Figure 5). Our conclusion from these comparisons is that Jensen's inequality sufficiently explains the general dynamics in the published data. The only example where insect development rate summation *generally* seems misguided, we have found, is in overwintering or dormant phenotypes—presumably due to proactive responses (Bradshaw & Holzapfel, 2001; Gotthard et al., 2000; Lehmann et al., 2016; Salis et al., 2016). Still, the

mechanistic basis for why development rate stands out as being particularly robust to time-dependent effects (see Xing et al., 2014) is a topic for future studies.

As climate changes, the importance of predictive ecological modelling of thermal performance increases (Sunday et al., 2011). In insects, climate warming is linked to macroecological shifts, such as range margin expansions (Chen et al., 2011) and can continue causing profound insect-related ecosystem disturbances (Seidl et al., 2017), as well as economic damage from insect pest species in many scenarios (Lehmann et al., 2020). Sinclair et al. (2016) dissect and challenge the use of TPCs for approximating fitness, and present the goal of putting ‘the Humpty-Dumpty of TPCs’ back together again, highlighting the need for field validation. Here, we present data on an important fitness trait, development rate, from such a field validation experiment. Though challenges remain (e.g. predictions in nature being complicated by spatial microclimate complexity within the foliage; Pincebourde & Woods, 2012), we suggest that it is reasonable to assume no inherent effects of temperature fluctuations on insect development rates in absence of evidence of the contrary. Importantly, such evidence must also be carefully scrutinized, since confounding effects (e.g. on other life history traits or on trophic interactions through parasitoids, predators or host plants) could lead to incorrect conclusions (Box 1). Fortunately, the necessary methodological assumptions are increasingly achievable, even in ecological contexts, for example, through recent advances in microclimate modelling or high-resolution monitoring (Bramer et al., 2018; Kearney et al., 2020). For instance, Rezende et al. (2020) successfully predicted mortality in 11 species of *Drosophila* under rising temperatures, using a method akin to rate summation that resets during prolonged exposure to benign temperatures. Its generality across taxa and predictive accuracy under field conditions have yet to be tested, but it holds promise for future ecological modelling. Hopefully, these previous and our current findings suggest that, although many pieces remain missing, the Humpty-Dumpty of insect thermal performance is slowly coming together.

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AUTHOR CONTRIBUTIONS

LvS, PL, KG and KHG designed the study. LvS, KHG and PL conducted the experiments. LvS and JN

performed the modelling. LvS drafted the manuscript, and PL and KG contributed substantially to the final version. All authors have approved the final manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data used in this study have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.gth76hm5>).

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REFERENCES

- Abram, P.K., Boivin, G., Moiroux, J. & Brodeur, J. (2017) Behavioural effects of temperature on ectothermic animals: Unifying thermal physiology and behavioural plasticity. *Biological Reviews*, 92, 1859–1876.
- Angilletta, M.J. (2006) Estimating and comparing thermal performance curves. *Journal of Thermal Biology*, 31, 541–545.
- Angilletta, M.J. (2009) *Thermal adaptation: A theoretical and empirical synthesis*. New York, NY: Oxford University Press.
- ArtDatabanken. (2020). *Artportalen (species observation system)*. SLU, Uppsala. Available at: <http://www.artportalen.se> [Accessed 30th October 2020].
- Berger, D., Friberg, M. & Gotthard, K. (2011) Divergence and ontogenetic coupling of larval behaviour and thermal reaction norms in three closely related butterflies. *Proceedings of the Royal Society B: Biological Sciences*, 278, 313–320.
- Bernhardt, J., O'Connor, M., Sunday, J. & Gonzalez, A. (2020) Life in fluctuating environments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1814), 20190454.
- Bernhardt, J.R., Sunday, J.M., Thompson, P.L. & O'Connor, M.I. (2018) Nonlinear averaging of thermal experience predicts population growth rates in a thermally variable environment. *Proceedings of the Royal Society B: Biological Sciences*, 285(1886), 20181076.
- Bowler, K. & Terblanche, J.S. (2008) Insect thermal tolerance: What is the role of ontogeny, ageing and senescence? *Biological Reviews*, 83, 339–355.
- Bradshaw, W.E. & Holzapfel, C.M. (2001) Genetic shift in photoperiodic response correlated with global warming. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 14509–14511.
- Bramer, I., Anderson, B.J., Bennie, J., Bladon, A.J., De Frenne, P., Hemming, D. et al. (2018) Advances in monitoring and modelling climate at ecologically relevant scales. *Advances in Ecological Research*, 58, 101–161.
- Bürkner, P.C. (2017) brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80, 1–28.
- Campbell, A., Frazer, B.D., Gilbert, N., Gutierrez, A.P. & Mackauer, M. (1974) Temperature requirements of some aphids and their parasites. *Journal of Applied Ecology*, 11, 431–438.
- Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M. et al. (2017) Stan: A probabilistic programming language. *Journal of Statistical Software*, 76, 395–411.
- Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026.
- Chew, F.S. & Watt, W.B. (2006) The green-veined white (*Pieris napi* L.), its Pierine relatives, and the systematics dilemmas of divergent character sets (Lepidoptera, Pieridae). *Biological Journal of the Linnean Society*, 88, 413–435.
- Chown, S.L., Addo-Bediako, A. & Gaston, K.J. (2002) Physiological variation in insects: Large-scale patterns and their implications. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, 131, 587–602.
- Chown, S.L. & Terblanche, J.S. (2006) Physiological diversity in insects: Ecological and evolutionary contexts. *Advances in Insect Physiology*, 33, 150–152.
- Colinet, H., Renault, D., Hance, T. & Vernon, P. (2006) The impact of fluctuating thermal regimes on the survival of a cold-exposed parasitic wasp, *Aphidius colemani*. *Physiological Entomology*, 31, 234–240.
- Colinet, H., Sinclair, B.J., Vernon, P. & Renault, D. (2015) Insects in fluctuating thermal environments. *Annual Review of Entomology*, 60, 123–140.
- Denny, M. (2017) The fallacy of the average: On the ubiquity, utility and continuing novelty of Jensen's inequality. *Journal of Experimental Biology*, 220, 139–146.
- Dowd, W.W., King, F.A. & Denny, M.W. (2015) Thermal variation, thermal extremes and the physiological performance of individuals. *Journal of Experimental Biology*, 218, 1956–1967.
- Franke, K., Heitmann, N., Tobner, A. & Fischer, K. (2014) Fitness costs associated with different frequencies and magnitudes of temperature change in the butterfly *Bicyclus anynana*. *Journal of Thermal Biology*, 41, 88–94.
- Friberg, M., Posledovich, D. & Wiklund, C. (2015) Decoupling of female host plant preference and offspring performance in relative specialist and generalist butterflies. *Oecologia*, 178, 1181–1192.
- Friberg, M. & Wiklund, C. (2019) Host preference variation cannot explain microhabitat differentiation among sympatric *Pieris napi* and *Pieris rapae* butterflies. *Ecological Entomology*, 44, 571–576.
- Gotthard, K. (2008) Adaptive growth decisions in butterflies. *BioScience*, 58, 222–230.
- Gotthard, K., Nylin, S. & Wiklund, C. (2000) Individual state controls temperature dependence in a butterfly (*Lasiommata maera*). *Proceedings of the Royal Society B: Biological Sciences*, 267, 589–593.
- Havird, J.C., Neuwald, J.L., Shah, A.A., Mauro, A., Marshall, C.A. & Ghalambor, C.K. (2020) Distinguishing between active plasticity due to thermal acclimation and passive plasticity due to Q10 effects: Why methodology matters. *Functional Ecology*, 34, 1015–1028.
- Howe, R. W. (1967) Temperature effects on embryonic development in insects. *Annual Review of Entomology*, 12, 15–42.
- Higley, L.G., Pedigo, L.P. & Ostlie, K.R. (1986) DEGDAY: A program for calculating degree-days, and assumptions behind the degree-day approach. *Environmental Entomology*, 15, 999–1016.
- Huey, R.B. & Kingsolver, J.G. (1989) Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology & Evolution*, 4, 131–135.
- Irvine, P.M. (2011) *Using a logistic phenology model with improved degree-day accumulators to forecast emergence of pest grasshoppers*. B.Sc. Thesis, University of Lethbridge.
- Jensen, J.L.W.V. (1906) Sur les fonctions convexes et les inégalités entre les valeurs moyennes. *Acta Mathematica*, 30, 175–193.
- Kaufmann, O. (1932) Einige bemerkungen über den einfluss von temperaturschwankungen auf die entwicklungsdauer und streuung bei insekten und seine graphische darstellung durch kettenlinie und hyperbel. *Zeitschrift für Morphologie und Ökologie der Tiere*, 25, 353–361.
- Kearney, M.R., Gillingham, P.K., Bramer, I., Duffy, J.P. & Maclean, I.M.D. (2020) A method for computing hourly, historical, terrain-corrected microclimate anywhere on earth. *Methods in Ecology and Evolution*, 11, 38–43.

- Khelifa, R., Blanckenhorn, W.U., Roy, J., Rohner, P.T. & Mahdjoub, H. (2019) Usefulness and limitations of thermal performance curves in predicting ectotherm development under climatic variability. *Journal of Animal Ecology*, 88, 1901–1912.
- Kingsolver, J.G. & Buckley, L.B. (2017) Quantifying thermal extremes and biological variation to predict evolutionary responses to changing climate. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1723), 20160147.
- Kingsolver, J.G. & Buckley, L.B. (2020) Ontogenetic variation in thermal sensitivity shapes insect ecological responses to climate change. *Current Opinion in Insect Science*, 41, 17–24.
- Kingsolver, J.G., Higgins, J.K. & Augustine, K.E. (2015) Fluctuating temperatures and ectotherm growth: Distinguishing non-linear and time-dependent effects. *Journal of Experimental Biology*, 218, 2218–2225.
- Lalouette, L., Williams, C.M., Hervant, F., Sinclair, B.J. & Renault, D. (2011) Metabolic rate and oxidative stress in insects exposed to low temperature thermal fluctuations. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, 158, 229–234.
- Lehmann, P., Ammuné, T., Barton, M., Battisti, A., Eigenbrode, S.D., Jepsen, J.U. et al. (2020) Complex responses of global insect pests to climate warming. *Frontiers in Ecology and the Environment*, 18, 141–150.
- Lehmann, P., Pruischer, P., Posledovich, D., Carlsson, M., Käkelä, R., Tang, P. et al. (2016) Energy and lipid metabolism during direct and diapause development in a pierid butterfly. *Journal of Experimental Biology*, 219, 3049–3060.
- Lembrechts, J.J., Aalto, J., Ashcroft, M.B., De Frenne, P., Kopecký, M., Lenoir, J. et al. (2020) SoilTemp: A global database of near-surface temperature. *Global Change Biology*, 26, 6616–6629.
- Lembrechts, J.J. & Nijs, I. (2020) Microclimate shifts in a dynamic world. *Science*, 368, 711–712.
- Liu, S.S., Zhang, G.M. & Zhu, J. (1995) Influence of temperature variations on rate of development in insects: Analysis of case studies from entomological literature. *Annals of the Entomological Society of America*, 88, 107–119.
- Ludwig, D. & Cable, R.M. (1933) The effect of alternating temperatures on the pupal development of *Drosophila melanogaster* Meigen. *Physiological Zoology*, 6, 493–508.
- Ma, C.-S., Ma, G. & Pincebourde, S. (2021) Survive a warming climate: Insect responses to extreme high temperatures. *Annual Reviews in Entomology*, 66, 1–22.
- MacMillan, H.A. & Sinclair, B.J. (2011) The role of the gut in insect chilling injury: Cold-induced disruption of osmoregulation in the fall field cricket, *Gryllus pennsylvanicus*. *Journal of Experimental Biology*, 214, 726–734.
- Maiorano, A., Bregaglio, S., Donatelli, M., Fumagalli, D. & Zucchini, A. (2012) Comparison of modelling approaches to simulate the phenology of the European corn borer under future climate scenarios. *Ecological Modelling*, 245, 65–74.
- Martin, T.L. & Huey, R.B. (2008) Why “Suboptimal” is optimal: Jensen’s inequality and ectotherm thermal preferences. *The American Naturalist*, 171, 102–118.
- Martínez-García, H., Aragón-Sánchez, M., Sáenz-Romo, M.G., Román-Fernández, L.R., Veas-Bernal, A., Marco-Mancebón, V.S. et al. (2018) Mathematical models for predicting development of *Orius majusculus* (Heteroptera: Anthocoridae) and its applicability to biological control. *Journal of Economic Entomology*, 111, 1904–1914.
- Milosavljević, I., McCalla, K.A., Morgan, D.J.W., Hoddle, M.S. & Bextine, B. (2020) The effects of constant and fluctuating temperatures on development of *Diaphorina citri* (Hemiptera: Liviidae), the Asian citrus psyllid. *Journal of Economic Entomology*, 113, 633–645.
- Nylin, S. & Gotthard, K. (1998) Plasticity in life-history traits. *Annual Review of Entomology*, 43, 63–83.
- Petavy, G., David, J.R., Gibert, P. & Moreteau, B. (2001) Viability and rate of development at different temperatures in *Drosophila*: A comparison of constant and alternating thermal regimes. *Journal of Thermal Biology*, 26, 29–39.
- Petersen, B. (1949) On the evolution of *Pieris napi* L. *Evolution*, 3, 269–278.
- Pincebourde, S. & Woods, H.A. (2012) Climate uncertainty on leaf surfaces: The biophysics of leaf microclimates and their consequences for leaf-dwelling organisms. *Functional Ecology*, 26, 844–853.
- R Core Team. (2020) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at <https://www.R-project.org/> [Accessed 30th October 2020].
- Rabinovich, J., Pietrokovsky, S. & Wisnivesky-Colli, C. (2006) Temperature and development rate of *Triatomata guasayana* (Hemiptera: Reduviidae) eggs under laboratory conditions: Physiological and adaptive aspects. *Physiological Entomology*, 31, 361–370.
- Ratkowsky, D.A., Lowry, R.K., McMeekin, T.A., Stokes, A.N. & Chandler, R.E. (1983) Model for bacterial culture growth rate throughout the entire biokinetic temperature range. *Journal of Bacteriology*, 154, 1222–1226.
- Rebaudo, F., Faye, E. & Dangles, O. (2016) Microclimate data improve predictions of insect abundance models based on calibrated spatiotemporal temperatures. *Frontiers in Physiology*, 7, 1–12.
- Rebaudo, F. & Rabhi, V.B. (2018) Modeling temperature-dependent development rate and phenology in insects: Review of major developments, challenges, and future directions. *Entomologia Experimentalis et Applicata*, 166, 607–617.
- Rebaudo, F., Struelens, Q. & Dangles, O. (2018) Modelling temperature-dependent development rate and phenology in arthropods: The devRate package for r. *Methods in Ecology and Evolution*, 9, 1144–1150.
- Rezende, E.L., Bozinovic, F. & Santos, M. (2020) Predicting temperature mortality and selection in natural *Drosophila* populations. *Science*, 369, 1242–1245.
- Rezende, E.L., Castañeda, L.E. & Santos, M. (2014) Tolerance landscapes in thermal ecology. *Functional Ecology*, 28, 799–809.
- Ruel, J.J. & Ayres, M.P. (1999) Jensen’s inequality predicts effects of environmental variation. *Trends in Ecology & Evolution*, 14, 361–366.
- Salis, L., Lof, M., van Asch, M. & Visser, M.E. (2016) Modeling winter moth *Operophtera brumata* egg phenology: Nonlinear effects of temperature and developmental stage on developmental rate. *Oikos*, 125, 1772–1781.
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G. et al. (2017) Forest disturbances under climate change. *Nature Climate Change*, 7, 395–402.
- Sgrò, C.M., Terblanche, J.S. & Hoffmann, A.A. (2016) What can plasticity contribute to insect responses to climate change? *Annual Reviews in Entomology*, 61, 433–451.
- Shafiei, M., Moczek, A.P. & Nijhout, H.F. (2001) Food availability controls the onset of metamorphosis in the dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). *Physiological Entomology*, 26, 173–180.
- Simonet, D.E. & Davenport, B.L. (1981) Temperature requirements for development and oviposition of the carrot weevil. *Annals of the Entomological Society of America*, 74, 312–315.
- Sinclair, B.J., Marshall, K.E., Sewell, M.A., Levesque, D.L., Willett, C.S., Slotsbo, S. et al. (2016) Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters*, 19, 1372–1385.
- SMHI (2020) *Swedish Meteorological and Hydrological Institute*. Available at: <http://www.smhi.se> [Accessed 30th October 2020].
- Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, 278, 1823–1830.

- Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, 2, 686–690.
- Tattersall, G.J., Sinclair, B.J., Withers, P.C., Fields, P.A., Seebacher, F., Cooper, C.E. et al. (2012) Coping with thermal challenges: Physiological adaptations to environmental temperatures. *Comprehensive Physiology*, 2, 2151–2202.
- Vasseur, D.A., DeLong, J.P., Gilbert, B., Greig, H.S., Harley, C.D.G. & McCann, K.S. et al. (2014) Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20132612.
- Williams, C.M., Henry, H.A.L. & Sinclair, B.J. (2015) Cold truths: How winter drives responses of terrestrial organisms to climate change. *Biological Reviews*, 91, 214–235.
- Woods, H.A., Dillon, M.E. & Pincebourde, S. (2015) The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. *Journal of Thermal Biology*, 54, 86–97.
- Xing, K., Hoffmann, A.A. & Ma, C.S. (2014) Does thermal variability experienced at the egg stage influence life history traits across life cycle stages in a small invertebrate? *PLoS ONE*, 9, 1–8.
- Zhao, F., Zhang, W., Hoffmann, A.A. & Ma, C.S. (2014) Night warming on hot days produces novel impacts on development, survival and reproduction in a small arthropod. *Journal of Animal Ecology*, 83, 769–778.
- Zhu, L., Ives, A.R., Zhang, C., Guo, Y. & Radeloff, V.C. (2019) Climate change causes functionally colder winters for snow cover-dependent organisms. *Nature Climate Change*, 9, 886–893.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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