Published in final edited form as:

Ecol Appl. 2012 December ; 22(8): 2237–2247.

Cautioning the use of degree-day models for climate change projections in the presence of parametric uncertainty

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Abstract

Developmental models, such as degree-day models, are commonly used to predict the impact of future climate change on the intensity, distribution, and timing of the transmission of infectious diseases, particularly those caused by pathogens carried by vectors or intermediate hosts. Resulting projections can be useful in policy discussions concerning regional or national responses to future distributions of important infectious diseases. Though the simplicity of degree-day models is appealing, little work has been done to analyze their ability to make reliable projections of the distribution of important pathogens, vectors, or intermediate hosts in the presence of the often considerable parametric uncertainty common to such models. Here, a population model of *Oncomelania hupensis*, the intermediate host of *Schistosoma japonicum*, was used to investigate the sensitivity of host range predictions in Sichuan Province, China, to uncertainty in two key degree-day model parameters (t_{min} and K). The intent was to examine the consequences of parametric uncertainty in a plausible biological model, rather than to generate the definitive model. Results indicate that model output, the seasonality of population dynamics, and range predictions, particularly along the edge of the range, are highly sensitive to changes in model parameters, even at levels of parametric uncertainty common to such applications. Caution should be used when interpreting the results of degree-day models used to generate predictions of disease distribution and risk under scenarios of future climate change, and predictions should be considered most reliable when the temperature ranges used in projections resemble those used to estimate model parameters. Given the potential for substantial changes in output with modest changes in parameter values, particular concern is warranted when results will be used to inform policy and management decisions.

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Keywords

degree-day model; parametric uncertainty; climate change; environmental drivers; vector-borne disease

Introduction

Quantitative projections of the response of diseases carried by vectors or intermediate hosts to changes in climate often rely on degree-day models, mathematical models that incorporate temperature dependence into developmental processes. These models have been used since the early 18th century (Reaumur 1735) to study plant and pest development in agriculture, and are increasingly being applied, either singly or coupled with models of population dynamics, to study the effects of climate change on organisms associated with important human infectious disease. In this application, degree-day models are often used to predict changes in the geographic distribution of vectors, intermediate hosts, or pathogens under future climate conditions. Table 1 lists recent examples, with a description of the structural and parametric choices that were made in each case. Considerable uncertainty exists in the estimation of degree-day model parameters, yet in virtually all applications examining a species' response to future climates, the effects of parameter uncertainty have not been considered. Thus, while degree-day models provide a simple tool for projecting how infectious disease systems may respond to climate change, there has been limited critical assessment of whether these models are sufficiently robust to inform management decisions, planning and policy.

Degree-day models express the temperature and time requirements for development in units of degree-days, which accumulate only when the temperature exceeds a minimum threshold. The degree-day model can be expressed as

$$D = \int_{t_1}^{t_2} \left(\frac{T(t)}{K} - \frac{\delta_{\min}}{K} \right) dt, \quad (1)$$

where D is the development that occurs in the interval from time t_1 to t_2 , $T(t)$ is the temperature at time t , and $\delta_{\min}$ is the lower temperature threshold, below which no development occurs. Development begins when $D=0$ and completes when $D=1$. The parameter K is interpreted biologically as the total degree-days necessary for the completion of development. This interpretation becomes clear if Eqn. 1 is rescaled such that

$$k = K \cdot D = \int_{t_1}^{t_2} (T(t) - \delta_{\min}) dt, \quad (2)$$

where k represents the number of degree-day units that accumulate in the given interval. Here, the onset of development occurs when $k=0$, and completes when $D=1$, or, equivalently, when k equals K degree-days. Depending on model implementation and the biology of the organism under study, additional model parameters can be incorporated, such as optimal and maximum temperature thresholds.

Typically, estimates of $\delta_{\min}$ and K are obtained experimentally by measuring the rate of organismal development under a range of constant temperatures. A linear function is then fit to these data and extrapolated, often considerably, outside the experimental temperature range to determine both the minimum temperature at which development can proceed, $\delta_{\min}$, as well as the total number of degree-days necessary for development to complete, K (Campbell et al. 1974). Uncertainty inherent to such a procedure increases the difficulty of

accurately estimating these parameters (Bergant and Trdan 2006). As an example, Kontodimas *et al.* (2004) calculated T_{min} and K for *Nephus bisignatus*, an important natural predator in European agriculture, as 9.39 °C (95% CI: [8.31, 10.46]) and 614.25 degree-days (95% CI: [563.96, 664.54]), respectively. Similarly, Nahrung *et al.* (2008) calculated T_{min} and K for an immature life stage of *Paropsis atomaria*, a pest of eucalypt plantations, as 5.4 °C (95% CI: [-0.28, 11.08]) and 166.7 degree-days (95% CI: [114.17, 219.23]), respectively. These confidence intervals are often sizable (Table 2), and such variance can have a substantial impact on predictions of organism emergence times, or in determining the suitability of specific regions for organism establishment or persistence. However, even when variance estimates are available from previous work, parameter point estimates are often borrowed directly from the literature for use in degree-day model applications, with the influence of parametric uncertainty remaining unexplored (e.g. Yang *et al.* (2006, 2010), Zou *et al.* (2007), Konrad *et al.* (2011)).

Here, the implications of uncertainty in degree-day model parameters are explored through a simple developmental model of *Oncomelania hupensis*, the intermediate snail host of the parasite that causes schistosomiasis. The model is used to generate projections of *O. hupensis* distribution in Sichuan Province, People's Republic of China (PRC), under future climate conditions. Note that the purpose is not to generate highly accurate spatial predictions, nor to develop the definitive model for estimating the distribution of *O. hupensis* in future climatic conditions, but rather to examine the influence of parametric uncertainty on the output of a plausible model following practices common in analogous degree-day model applications. The sensitivity of 1) model-predicted *O. hupensis* density at selected locations within Sichuan, and 2) model-predicted geographic distributions of *O. hupensis*, is explored with respect to changes in the two key model parameters, T_{min} and K . The results are then discussed in the context of the suitability of degree-day models for examining ecological responses to climate change.

Materials and methods

The analysis was structured as follows. First, a temperature-dependent population model for *O. hupensis* was developed to simulate current and future snail populations. Temperature datasets generated for both contemporary and future conditions served as model inputs, and to ensure biological plausibility, the model was fit to historical data on the distribution of *O. hupensis* in Sichuan Province. Finally, to investigate the influence of uncertainty in T_{min} and K , a sensitivity analysis was conducted at selected locations within Sichuan, as well as on the predicted future distribution of *O. hupensis* across Sichuan. The following sections detail each of these steps.

Population model

Schistosoma japonicum, the intestinal trematode that causes schistosomiasis, infects more than 700,000 people in China (Zhou et al. 2007). The presence of the intermediate snail host, *Oncomelania hupensis*, is required for transmission to humans and other mammals (Ross et al. 2001), and thus the geographic distribution of *O. hupensis* restricts transmission in China. In Sichuan Province, *O. hupensis* primarily inhabits irrigation canals and terraces, and environmental factors such as humidity, precipitation, and temperature are all important for survival and reproduction (Ross et al. 2001). Temperature is an especially important variable, and models used to describe the population dynamics and geographic range of *O. hupensis* frequently include the influence of temperature using degree-day formulations (Liang et al. 2002, Liang et al. 2005, Remais et al. 2007, Zhou et al. 2008).

Here, a temperature-dependent, dynamic *O. hupensis* population model was adapted from previous work (Liang et al. 2002), and is expressed as a delay differential equation given by

$$\frac{dS}{dt} = \sum_{\lambda \in N_t} \left[\exp(-\lambda\mu) \exp(-\alpha S_{t-\lambda}) \beta \exp\left(-\kappa(T_{t-\lambda} - \delta_{opt})^2\right) S_{t-\lambda} \right] - \mu S_t \quad (3)$$

where S is the snail density, μ is the snail mortality rate, $T_{t-\lambda}$ is the temperature at time $(t - \lambda)$, and the summation represents the total number of snails that complete development at time t . The value within the summation is determined by the recruitment of snails at time $(t - \lambda)$, given by $\exp(-\kappa(T_{t-\lambda} - \delta_{opt})^2) S_{t-\lambda}$, reduced by a density dependent factor, $\exp(-\alpha S_{t-\lambda})$, and by mortality that occurs between snail birth and the completion of development, $\exp(-\lambda\mu)$. N_t is the set containing all time points prior to time t for which $\int_{t-\lambda}^t (T(t) - \delta_{min}) dt = K$. That is, N_t represents the set of all delays, λ , for which the snails born at time $(t - \lambda)$ complete development at time t . The use of the summation allows for snails born at different time steps to complete development on the same time step, given appropriate temperature conditions.

Mean daily temperature is used here, as in other models (Table 1), but see Paaijmans *et al.* (2009, 2010) for a discussion on the implications of using daily vs. hourly temperature data. The daily average method of calculating daily degree-days (Wilson and Barnett 1983) was used, and no upper threshold was incorporated. Definitions for individual parameters in Eqn. 3 are given in Table 3.

Temperature data

To generate a surface of contemporary and future daily temperature values for Sichuan Province, mean daily temperature data from 1 Jan 1980 to 31 Dec 2009 were obtained from the National Oceanic and Atmospheric Administration National Climatic Data Center (NOAA 2011) for 68 weather stations located within a rectangular region (longitude 97.933 °W and 104.73 °W, latitude 26.367 °N and 34.1 °N) encompassing Sichuan Province. Though *O. hupensis* is an amphibious organism, air temperature was used here rather than water to mimic similar studies (Yang et al. 2006, Zhou et al. 2008). Mean daily temperatures in these datasets were reported in °F and were derived from a minimum of four observations per day. All weather stations within a 200 km buffer distance around the boundary of Sichuan Province were selected so as to ensure accurate temperature interpolation at border regions. Only those weather stations reporting daily mean temperature for more than three years between 1980 and 2009 were included. Weather station locations were geo-coded to Sichuan Province using ArcGIS (ESRI 2008, version 9.2) and overlaid on a digital elevation model (DEM) of the region. Geospatial modeling, described below, was conducted using Spatial Analyst in ArcGIS (version 9.3).

From the station data, an interpolated contemporary temperature dataset was generated at a grid of 90 by 90 meter cells across Sichuan Province using a multiple linear regression model that predicts daily temperature from elevation, latitude and longitude variables (details in Appendix A). This yielded a contemporary temperature dataset consisting of 366 surfaces, each representing one day of interpolated mean temperature. To generate a future temperature dataset for 2050, the original temperature data for all 68 weather stations were entered into a statistical model that incorporates latitude, elevation, and time variables (details in Appendix A), and makes the simple assumption that the rate of temperature increase observed between 1980 and 2009 in Sichuan will continue unchanged into the future. This model was applied at every 90 by 90 meter cell of the spatial domain, yielding a year of daily temperature values at each cell for 2050. For both contemporary and future datasets, all temperatures were converted to °C, and the 366 days of daily temperature were looped to provide three years of simulation input.

Parameter estimation using historical *Oncomelania hupensis* presence in Sichuan Province

Using the parameter ranges in Table 3 as a starting point, the dynamic population model (Eqn. 3) was fit to the historical distribution of *O. hupensis* to generate a set of parameter values for use in the sensitivity analysis (below). Historical data on the presence and absence of *O. hupensis* between 1950–1970 was obtained from routine surveys conducted bi-annually (April–May, September–October) at 63 anti-schistosomiasis stations located throughout counties in Sichuan Province (Qian 1987, Ministry of Health 1992). The data were aggregated such that if any juvenile or adult *O. hupensis* was observed at any time within the range of dates examined, the county in which the snail was observed was marked as a presence. This method leads to a conservative estimate of *O. hupensis* presence (Appendix C: Fig. C1), and is intended to approximate the natural range of *O. hupensis* while being robust to the decades of molluscicidal control measures conducted in the region (Wang et al. 2009).

To narrow the parametric values from the starting ranges given in Table 3, the model in Eqn. 3 was fit to the historic *O. hupensis* presence/absence data as follows. First, to reduce computation time, a subset ($n=365$) of the total number of cells within the spatial grid was chosen at equal intervals within counties in central and eastern Sichuan, with the number of cells per county proportional to county size. At each cell of the subset, a total of 2000 simulations of Eqn. 3 were run using the contemporary temperature dataset as input and parameter values drawn randomly from the ranges in Table 3. The minimum snail density over the three years of simulation time was found at every cell of the subset for each simulation, and this minimum was used to generate a threshold snail density, $s_{\min}$, such that agreement between cells classified as present (minimum snail density $> s_{\min}$) or absent (minimum snail density $< s_{\min}$) and the historical distribution described above was maximized. Simultaneously, simulation performance (i.e. agreement with historical distribution) was evaluated with respect to parameter values drawn. Thus, the constraint on model output provided by the historical distribution data was used to reduce parametric uncertainty, treating the threshold density for “presence” as a parameter, in addition to those listed in Table 3. A full exploration of the multi-dimensional parameter space across the entire spatial domain is computationally prohibitive, and, what is more, the goal is simply to produce a plausible population model (and associated parameter values) that agrees generally with observations, not to produce a definitive model for predicting *O. hupensis* distribution in Sichuan. Thus, parameter sets that met four specified criteria (Appendix B) were selected for further use.

It is important to note that many degree-day models applied in this context perform fitting and validation procedures no more rigorous than those presented here (e.g. Yang *et al.* (2006, 2010), Zhou *et al.* (2008), Craig *et al.* (1999), Konrad *et al.* (2011)). Our purpose is to investigate the influence of parametric uncertainty on degree-day model output using techniques commonly applied, and thus we did not further validate model output. Our analyses, therefore, are not intended to produce a highly accurate spatial model of *O. hupensis* distribution.

Sensitivity analysis

To explore the implications of degree-day model parametric uncertainty, an analysis of the sensitivity of model output to uncertainty in $\min$ and K was carried out at two scales. First, uncertainty was explored intensively at individual locations ($n=6$) within Sichuan Province, examining changes in model output with incremental changes in only $\min$, only K , or both $\min$ and K simultaneously. Second, sensitivity was explored on a broader scale at cells located across the spatial domain ($n=655$), examining how projections of *O. hupensis*

distribution change in response to larger modifications of $s_{\min}$ or K . The following sections discuss these analyses.

Individual location analysis

Simulations were run at six cells representing a range of climate conditions across eastern Sichuan Province (Appendix C: Fig. C2). At each cell, a baseline time-series of snail density was obtained by running a single simulation with the parameter set from the fitting procedure that had the highest overall agreement with historical data and using the contemporary temperature dataset as model input. Next, using the same parameter set, $s_{\min}$ and K were modified by increasing and decreasing the original value from the parameter set by 40%, in increments of 2%. This interval was chosen to capture the wide range of uncertainty often observed in degree-day model parameter estimates (Table 2). Simulations were then run using these modified parameter sets, leading to a total of 1681 simulations per cell. For each simulation, mean snail density and day of first peak in snail density were examined, and their deviation from the baseline simulation was calculated.

Distributional analysis

To investigate how uncertainty in $s_{\min}$ and K affects projections of future *O. hupensis* distribution, simulations were run using the future temperature dataset as input at a subset ($n=655$) of cells chosen at equal intervals across Sichuan Province, with the number of cells per county proportional to county size. For each simulation, the model was applied at every cell of the subset using the parameters sets estimated from the fitting procedure. Each simulation produced a daily snail density at every cell for the three years of simulation input. Daily snail density across the three years of simulation input was averaged to provide an estimate of mean snail density, and then averaged across all parameter sets. This process was repeated to generate a minimum snail density estimate at each cell for use in projecting regions of snail presence. The minimum snail density threshold, $s_{\min}$ (as described above), was used to define snail presence in projected distributions. To investigate the sensitivity of the results to this threshold, the analysis was repeated for several values of $s_{\min}$. Mean and minimum snail density values from the subset grid were spatially interpolated to yield values at all 90×90 meter cells across the spatial domain, yielding a baseline distribution and snail presence estimate for 2050. Finally, sensitivity to changes in $s_{\min}$ and K was investigated by increasing or decreasing the respective parameter in each set by 5%, 15%, 25%, or 35% and generating a new geographic distribution and snail presence estimate that was compared to the future baseline case. All sensitivity analyses were conducted using MATLAB (MathWorks 2009, version R2009a).

Results

Parameter estimation

Among the density thresholds for “presence” explored, a threshold of $s_{\min}=7$ snails per Kuang (a traditional Chinese sampling frame, equal to 0.11 m^2), yielded the greatest number of parameter sets with the highest agreement with historical data, and thus this value was used. However, the simulated distribution of snail presence across Sichuan was approximately the same over a range of threshold values. While this minimum density threshold was found to be the best fit to historical presence/absence data, this does not imply that *O. hupensis* populations require this minimum density to persist. From the 2000 simulations that were run, a total of 73 parameter sets met all four criteria (Appendix B), and were used in subsequent analyses. Appendix B details the agreement between simulated and historical snail presence, and Fig. C3 in Appendix C shows representative simulation output for all parameter sets.

Sensitivity analysis

Individual cell analysis—The sensitivity of model output at two representative cells (locations A, D; see Appendix C: Fig. C2) for the contemporary temperature dataset is shown in Fig. 1, with plots showing the change in mean snail density relative to the baseline simulation given changes in $T_{\min}$ and K . Plots showing the change in the time of the first population peak are given in Fig. C4 in Appendix C. Red colors indicate an increase in these outputs above the baseline value, while blue colors indicating a decrease below the baseline value. Results for locations B, C, E, and F exhibited similar patterns (data not shown). Decreases in $T_{\min}$ and/or K generally lead to increases in mean snail density and an earlier first population peak, and increases in $T_{\min}$ and/or K generally lead to decreases in mean snail density and a delayed first peak time. Note that the diagonal pattern observed in Fig. 1 is due to the inverse relationship between $T_{\min}$ and K , a relationship that can be seen mathematically in Eqn. 1, and indicates a biological trade-off between these two parameters (Trudgill et al. 2005).

Often, the change in model output tends to be gradual, such as at location D. However, in some regions even small changes in $T_{\min}$ and/or K can lead to large changes in model output. For instance, at location A, the baseline snail density using the contemporary dataset is 7.23 snails per 0.11 m², with the first population peak occurring in approximately July of the second year of the simulation. Decreasing either $T_{\min}$ or K by only 5% (such that $T_{\min}=8.075$ or $K=1368$) leads to a mean snail density of approximately 9.8 snails per 0.11 m² and the first population peak now occurring in November of the first year of the simulation. Even a change of 0.2% increases the mean snail density by approximately 24.5% and bumps the first population peak up to November of the first year (data not shown). Cells that exhibit the more gradual sensitivity to $T_{\min}$ and K tend to be in areas with temperatures that are often close to or greater than the minimum temperature threshold (black lines Fig. 2A) and that exhibit a consistent number of population peaks per year (black line Fig. 2B). Alternatively, cells that exhibit a strong sensitivity to $T_{\min}$ and K tend to be those with temperature that often falls below the minimum threshold (grey line Fig. 2A) or that exhibit an inconsistent number of population peaks per year (grey line Fig. 2B).

Mean snail density does not always increase strictly monotonically as $T_{\min}$ and K decrease. Instead, in some cases the mean snail density initially increases as $T_{\min}$ and K decrease, but then a region appears where the mean snail density is less than the baseline snail density, producing the banding pattern shown in the lower left corner of location D (Fig. 1). As $T_{\min}$ and K decrease further, the mean snail density is once again greater than the baseline value. To investigate this pattern further, simulation output at Location D was plotted using parameter values for $T_{\min}$ and K from each of these regions (green symbols, Fig. 1) and then compared to the baseline simulation output (Fig. 3). We see that, following the first year, the baseline population (solid line, Fig. 3) experiences two population peaks per season, one in late spring–early summer, and the second in the fall. However, when the values of $T_{\min}$ and K fall within the range where the unexpected decrease in mean snail density was observed (dotted line, Fig. 3), the seasonal peaks become disrupted as the timing of the completion of snail development no longer fully coincides with suitable temperature conditions. The small population peak observed early in the season is lost, and without this smaller peak to boost the population size, mean snail density decreases. As $T_{\min}$ and K both become much smaller than the baseline values (dashed line, Fig. 3), the seasonal peaks are again disrupted. However, since $T_{\min}$ and K are now very small, population peaks can occur even in the winter months, leading to two large peaks occurring at regular intervals throughout the year, and a subsequent increase in mean snail density.

Distributional analysis—The sensitivity of predicted mean snail density across Sichuan Province to moderate changes in K is shown in Fig. 4 for the 2050 temperature dataset, while results for larger changes in K and changes in $s_{\min}$ are given in Fig. C5 in Appendix C. Comparable to the results at individual cells, mean snail density tends to increase as either $s_{\min}$ or K decreases, and tends to decrease as either $s_{\min}$ or K increases. Importantly, even a 5% change in $s_{\min}$ or K can lead to large changes in snail density, particularly around the edge of the snail distribution.

Additionally, the total area of snail presence (defined using a minimum snail density threshold of $s_{\min}=5, 6, 7$, or 8 snails per 0.11 m²) changes noticeably with changes in $s_{\min}$ or K (Fig. 5), particularly as either of these parameters increases. As $s_{\min}$ decreases by 35%, the total area of snail presence increases modestly by approximately 2%. A similar effect is observed when K decreases. However, as $s_{\min}$ or K increases up to 35%, the area of snail presence decreases, in some cases quite substantially. Using $s_{\min}=7$, a 5% increase in $s_{\min}$ or K yields an approximately 56% and 42% decrease in area of snail presence, respectively (equivalent to a decrease of approximately 94,109 or 70,885 km² from the baseline area of 167,884 km²). Interestingly, this dramatic decrease is much reduced as $s_{\min}$ or K are increased further. The large change in area of snail presence with small changes in $s_{\min}$ or K is not sensitive to the choice of $s_{\min}$ (Fig. 5), although high $s_{\min}$ values tend to exhibit even greater sensitivity to changes in $s_{\min}$ or K .

Discussion

Considerable uncertainty exists in key degree-day model parameters, and even modest uncertainty in a parameter can have a significant effect on model output. The analyses presented here follow methods comparable to other degree-day model forecasting applications, and show that the timing of peak population levels and the total area of snail presence are highly sensitive to even moderate changes in parameters $s_{\min}$ and K . Decreases in these two parameters generally cause simulated snail populations to exhibit higher mean snail densities and an earlier first peak in population size, while increases in these two parameters generally cause simulated snail populations to exhibit lower mean snail densities and a delayed first peak in population size. Importantly, even changes as low as 0.2% can have a striking effect. As common degree-day applications often fail to incorporate uncertainty in estimates of $s_{\min}$ and K (e.g. Nieto *et al.* (2006), Zou *et al.* (2007), Konrad *et al.* (2011)), this result is especially significant.

Failure to include parametric uncertainty can have important consequences for applications of degree-day models, particularly for predictive forecasting. For instance, reliable predictions of peak population levels are necessary to inform vector or host control measures (e.g., predator release, pesticides, chemotherapy), since these measures are often timed to target specific organism densities or life stages. Estimated peak population dates that are off by several weeks or months could thus have severe consequences for the efficacy of timed intervention. In addition, the sensitivity to $s_{\min}$ and K is particularly pronounced in regions where snail populations exhibit inconsistent population cycling, or where the yearly temperature profile often falls below or near the minimum temperature threshold. These regions—which are highly sensitive to parameter error—are likely prevalent along the edges of the existing snail distribution, and are the very regions that are of interest in the context of future climate because of their potential to exhibit the first signs of a range shift. Identifying locations that transition from unsuitable to suitable under climate change conditions is essential for the design of effective disease surveillance systems and for the planning of future control needs. If these regions are misidentified, decisions on where to focus vector or host monitoring activities now, or in the future, will be misinformed.

Another important consequence of parametric uncertainty that arises from the incorporation of a degree-day model into a dynamical population model is the disruption of seasonality. In some cases, a decrease in either T_{min} and K leads to a shift toward a population peak earlier in the season, enabling the population to peak twice per year. This additional peak may imply an increase in disease risk, and thus an increase in the need for control and monitoring activities. In other cases, this shift in the timing of the population peaks disrupts the population cycling, leading to dampening, single peaks over the three year simulation. This predicted decrease in snail density may imply a reduced risk of transmission, or might indicate that control methods being conducted are effective. However, since all three results (declining snail density, one peak per season and two peaks per season) can be generated by altering T_{min} and K , it seems clear that in order for control measures to be effectively implemented, uncertainty in these parameters needs to be better understood and accounted for.

Parametric uncertainty is only one of several factors to be considered when applying degree-day models. Of additional concern is the assumption of a linear relationship between the rate of development and temperature (Kontodimas et al. 2004). Although this assumption simplifies the model and increases its ease of use, organism development (e.g. for poikilotherms or arthropods) is often non-linear (Beck 1983), exhibiting an exponential increase in the rate of development up to a maximum, followed by a declining rate above this value. Portions of the nonlinear response curve can be represented linearly; however, this approximation is only accurate within a limited range of temperatures (Bonhomme 2000). Thus, the application of these models is constrained to temperature ranges that fall within the bounds for which the model was parameterized. In changing environments, or when applied to questions of climate change, temperatures may shift outside the range for which the degree-day model can be reliably applied.

The accuracy of degree-day model predictions is also constrained by the quality and location of temperature data available. Daily temperature extremes, in addition to average temperatures, are expected to change with a changing climate, and this daily temperature variability can influence organism development and ultimately disease transmission (Paaijmans et al. 2009, Paaijmans et al. 2010). Often only mean daily temperature values are available for use, potentially limiting research on the effects of contemporary climate variability. Additionally, it is important to assess the ability of weather station data to accurately represent the microclimate experienced by the organism under study, as differences here can impact the accuracy of degree-day model applications (Dabbs 2010). Finally, other factors such as additional environmental variables (e.g., precipitation, humidity, photoperiod, vegetation, etc.) and anthropogenic effects can impact development, and should be considered when examining the organismal response to changing climates.

Though the focus of this manuscript has been on the consequences of uncertainty in parameters commonly included in degree-day models, it is important to note that many sources of uncertainty are commonly excluded from such analyses. For instance, uncertainty associated with estimating future temperatures (Bergant et al. 2006), individual and population level heterogeneity in response, and variability inherent to temperature and organism data, are all important factors to consider. Indeed, while the simplicity of degree-day models makes them appealing to researchers and others, the complexity of real world systems makes these models poorly suited to understanding, and disentangling, the range of uncertainties inherent in characterizing ecological responses to environmental change.

In summary, care should be used when applying degree-day models to generate projections of organism distribution and dynamics under future climate scenarios. Though the analysis conducted here used a complex dynamical model, the results are relevant for applications of

degree-day models outside of the population dynamics context, as parameter values may have even more influence in purely arithmetic degree-day applications where feedback processes are not present. The use of point estimates for model parameters should be avoided, and full parameter ranges (which are, in many cases, already available) should be explored in model implementations. Where possible, conducting additional laboratory or field experiments could reduce the uncertainty in key parameters identified as especially important in sensitivity analyses. The results of sensitivity analyses should be reported alongside degree-day model results, and at a minimum the impact of parametric uncertainty on specific conclusions and recommendations should be discussed. When sensitivity to model parameters is high, alternate models (e.g. models for nonlinear temperature-dependent development) should be considered. Additionally, the overall ability of the model to capture realistic population dynamics should always be assessed. With these cautions in mind, the degree-day model remains a useful tool for studying temperature-dependent development, and when applied critically to questions of ecological response to climate change, can provide valuable information for managers and decision-makers.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

This work was supported in part by the Ecology of Infectious Disease program of the National Science Foundation under Grant No. 0622743, the National Institute for Allergy and Infectious Disease (K01AI091864) and the Global Health Institute at Emory University. J.L.M. was additionally supported by a training grant from the National Institute for Allergy and Infectious Disease (T32AI055404), and a NSF Graduate Research Fellowship (award number DGE-0940903). S.L. was in part supported by a National Institutes of Health/National Institute of Allergy and Infectious Diseases grant (R01 AI068854) to University of California, Berkeley and Public Health Preparedness for Infectious Disease (PHPID) of The Ohio State University. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. Additionally, we thank Nina Townsend for developing and validating the temperature projection model.

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Figure 1.

Percent deviation from baseline mean snail density given changes in $\delta_{\min}$ and K at two representative locations (Appendix C: Fig. C2) within Sichuan Province. Red colors indicate a value greater than the baseline case, while blue colors indicate a value less than the baseline case. Baseline simulations were run using parameter values of $s_0=22.642$, $\mu=0.0049$, $\beta=0.4648$, $\gamma=0.0195$, $\delta=4.4672$, $\rho_{\text{opt}}=23.08$, $\delta_{\min}=8.5$, and $K=1440$. Percent changes in $\delta_{\min}$ and K are given along the y- and x-axes, respectively. Black lines in the plot of mean snail density at Location D indicate the banding pattern observed (see text), while the green symbols in this same plot correspond to simulation output shown in Fig 3.

Figure 2.

Contemporary temperature and simulation output at two representative locations with no change in $\delta_{\min}$ and K . A) Contemporary temperature data at Locations A (grey line) and D (black line). B) Baseline simulation output at Locations A (grey line) and D (black line), using parameter values of $s_0=22.642$, $\mu=0.0049$, $\alpha=0.4648$, $\beta=0.0195$, $\gamma=4.4672$, $\delta_{\text{opt}}=23.08$, $\delta_{\min}=8.5$, and $K=1440$.

Figure 3. Simulation output at Location D using the baseline parameter values (solid black line), and two modified parameter sets (dashed lines). The first modified parameter set (dashed black line) decreased both $\mu_{\min}$ and K by 26%, while the second modified parameter set (dashed grey line) decreased both $\mu_{\min}$ and K by 38%. Legend symbols corresponding to those found in Fig. 1.

Figure 4.

Predicted mean snail density across Sichuan Province in 2050 given changes in K . Each plot represents the average snail density of the 73 parameter sets, with the center plot using the original parameter values, the top plot increasing K by 5%, and the bottom plot decreasing K by 5%. Regions traced in black indicate areas of snail presence using a minimum snail density threshold of $s_{\min} = 7$.

Figure 5.

Predicted mean area and standard error of snail presence in Sichuan Province in 2050 for $s_{\min}=5$ (dotted-dashed line), $s_{\min}=6$ (dotted line), $s_{\min}=7$ (dashed line), and $s_{\min}=8$ (solid line). A) Predicted area given specified changes in $\delta_{\min}$. B) Predicted area given specified changes in K .

Degree-day model examples

Applications of degree-day models to predict vector or intermediate host responses to climate change.

Table 1

Disease: Vector	Environmental variable(s)	Temperature data	Temperature thresholds	Model type	Citation
Malaria: <i>Anopheles</i> species	temperature	mean daily	minimum developmental temperature	process-based and statistical models	(Lindsay et al. 2010)
Schistosomiasis: <i>Oncomelania hupensis</i>	temperature, rainfall, humidity	mean daily	minimum developmental temperature	process-based and statistical models	(Yang et al. 2010)
	temperature	mean daily	minimum developmental temperature, minimum lethal temperature, maximum lethal temperature	risk mapping	(Zhou et al. 2008)
	temperature	mean monthly	minimum developmental temperature	spatio-temporal statistical model	(Yang et al. 2006)
Lyme disease: <i>Ixodes scapularis</i>	temperature	mean monthly	minimum developmental temperature	dynamic population model	(Ogden et al. 2005, Ogden et al. 2006)
Leishmaniasis: <i>Lutzomyia longipalpis</i>	temperature, surface/soil moisture	mean monthly	minimum developmental temperature	ecological niche models	(Nieto et al. 2006)
West Nile virus: <i>Culex pipiens</i> species	temperature	daily minimum and maximum	minimum developmental temperature	risk mapping	(Zou et al. 2007)
Rift Valley Fever virus: mosquito species	temperature	daily minimum and maximum	minimum developmental temperature	risk mapping	(Konrad et al. 2011)

Table 2
Empirical estimates of degree-day model parameters

Examples of empirically-derived estimates of T_{min} and K for organisms relevant to agriculture and/or infectious disease.

Organism	T_{min} [95% CI] (°C)	K [95% CI] (degree-days)	Citation
<i>Nephus bisignatus</i> predatory coleoptera	9.4 [8.3, 10.5]	614.3 [564.0, 664.5]	(Kontodimas et al. 2004)
<i>Nephus includens</i> predatory coleoptera	10.9 [10.51, 11.35]	490.5 [475.4, 505.6]	(Kontodimas et al. 2004)
<i>Paropsis atomaria</i> eucalyptus pest	5.4 [−0.3, 11.1]	166.7 [114.2, 219.2]	(Nahrung et al. 2008)
<i>Brevicoryne brassicae</i> aphid host	7.1 [6.2, 8.0]	136 [121.9, 150.1]	(Campbell et al. 1974)
<i>Diaeretiella rapae</i> <i>B. brassicae</i> parasite	3.5 [0.7, 6.3]	241 [191.0, 291.0]	(Campbell et al. 1974)
<i>Wuchereria bancrofti</i> Bancroftian filariasis parasite	15.4 [13.1, 17.8]	not provided	(Lardeux and Cheffort 1997)
<i>Schistosoma japonicum</i> schistosome parasite	15.4 [14.2, 16.7]	852.6 [839.5, 865.7]	(Zhou et al. 2008)
<i>Oncomelania hupensis</i> intermediate snail host of <i>S. japonicum</i>	5.8 [5.5, 6.2]	3846.3 [3838.3, 3854.4]	(Zhou et al. 2008)

Table 3
Population Model Parameters

Parameters for the *O. hupensis* population model, with ranges obtained from Liang *et al.* (2005).

Parameter	Definition	Range
s_0	Initial snail density (per Kuang [1 Kuang = 0.11 m ²])	17–35
μ	Snail mortality rate (per day)	0.0023–0.007
	Maximum snail reproduction rate (per day)	0.01–2
	Density dependence	0.001–0.3
	Recruitment kurtosis	1–5.2
opt	Optimum reproduction temperature (°C)	20–25
min	Minimum temperature threshold for development (°C)	7–12
K	Total degree-days required for completion of snail development	1200–1500
	Time delay	varies