

Biomechanics meets the ecological niche: the importance of temporal data resolution

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In Figs 4–6, some of the bars were incorrectly assigned as daily data instead of monthly data and *vice versa*. The corrected figures appear below.

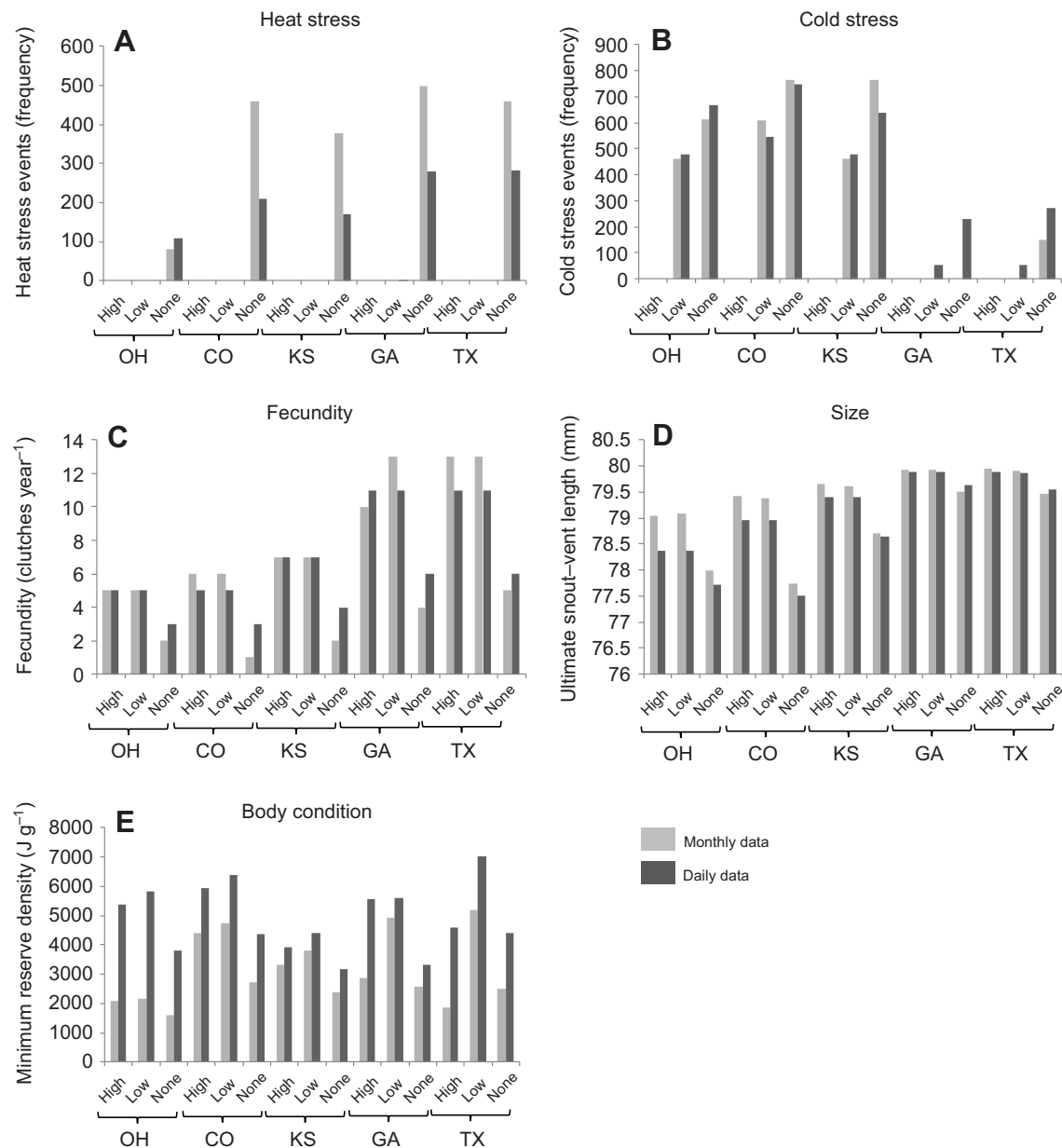


Fig. 4. Summaries of physiological metrics from simulations at sites in Ohio (OH), Colorado (CO), Kansas (KS), Georgia (GA) and Texas (TX). All results are for 5 year simulations as depicted in Figs 1–3, and all represent the years 1973–1978, except for Ohio, which represents the years 2004–2009 (1973–1978 was not available for this site). In each plot, results are shown for simulations driven by daily data (pale-grey bars) and monthly averages (dark-grey bars) over the 5 year blocks. Results are presented for the three behavioural buffering scenarios – high (100% maximum shade, 2 m maximum burrow depth), low (50% maximum shade, 10 cm burrow depth) and none (sessile, on the surface in 0% shade).

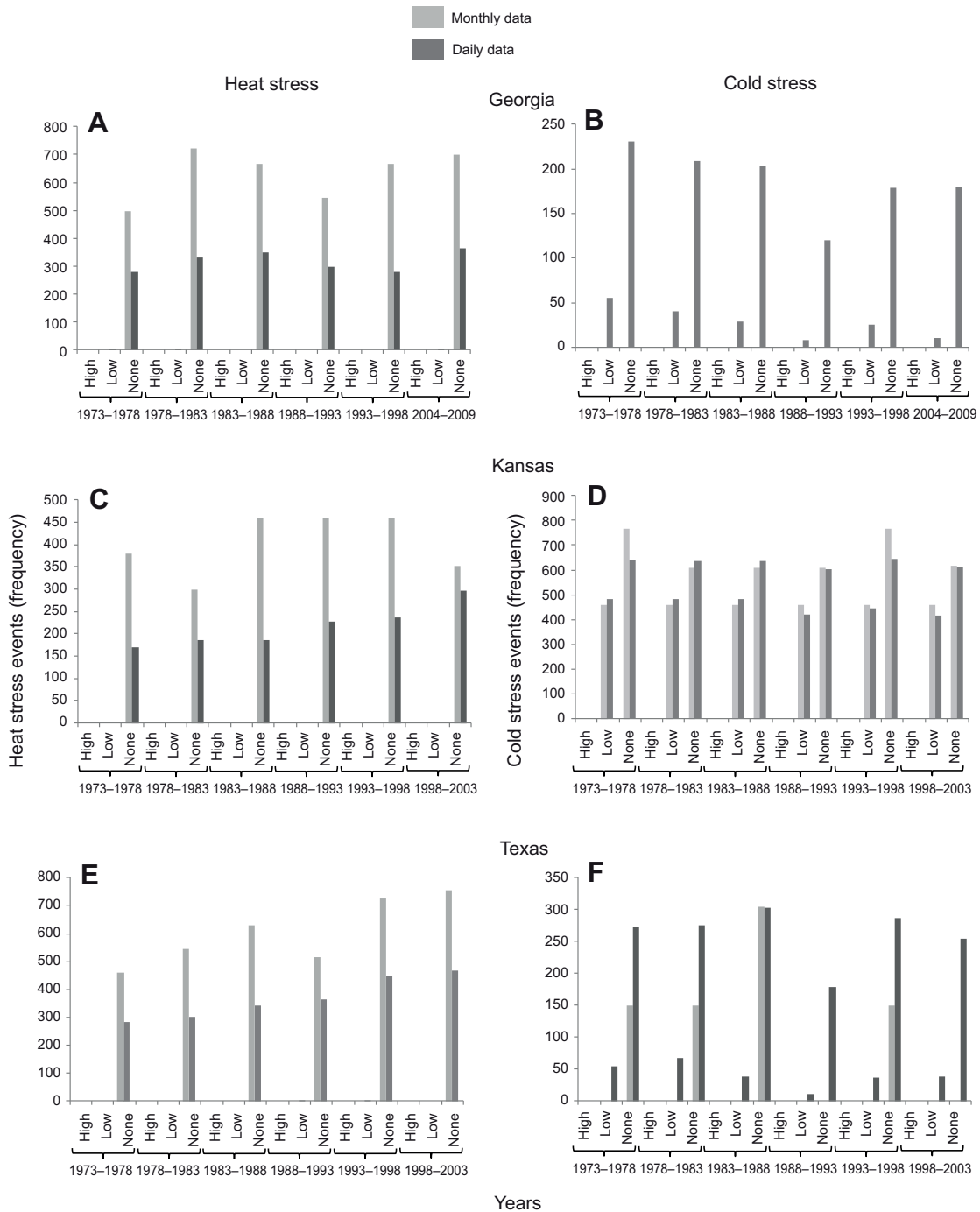


Fig. 5. Summaries of physiological metrics (heat and cold stress events) from simulations at three sites where climate data for 30 years were available. All results are for 5 year simulations, as depicted in Figs 1-3. In each plot, results are shown for simulations driven by daily data (pale-grey bars) and monthly averages (dark-grey bars) over different 5 year blocks. Results are presented for the three behavioural buffering scenarios – high (100% maximum shade, 2m maximum burrow depth), low (50% maximum shade, 10cm burrow depth) and none (sessile, on the surface in 0% shade).

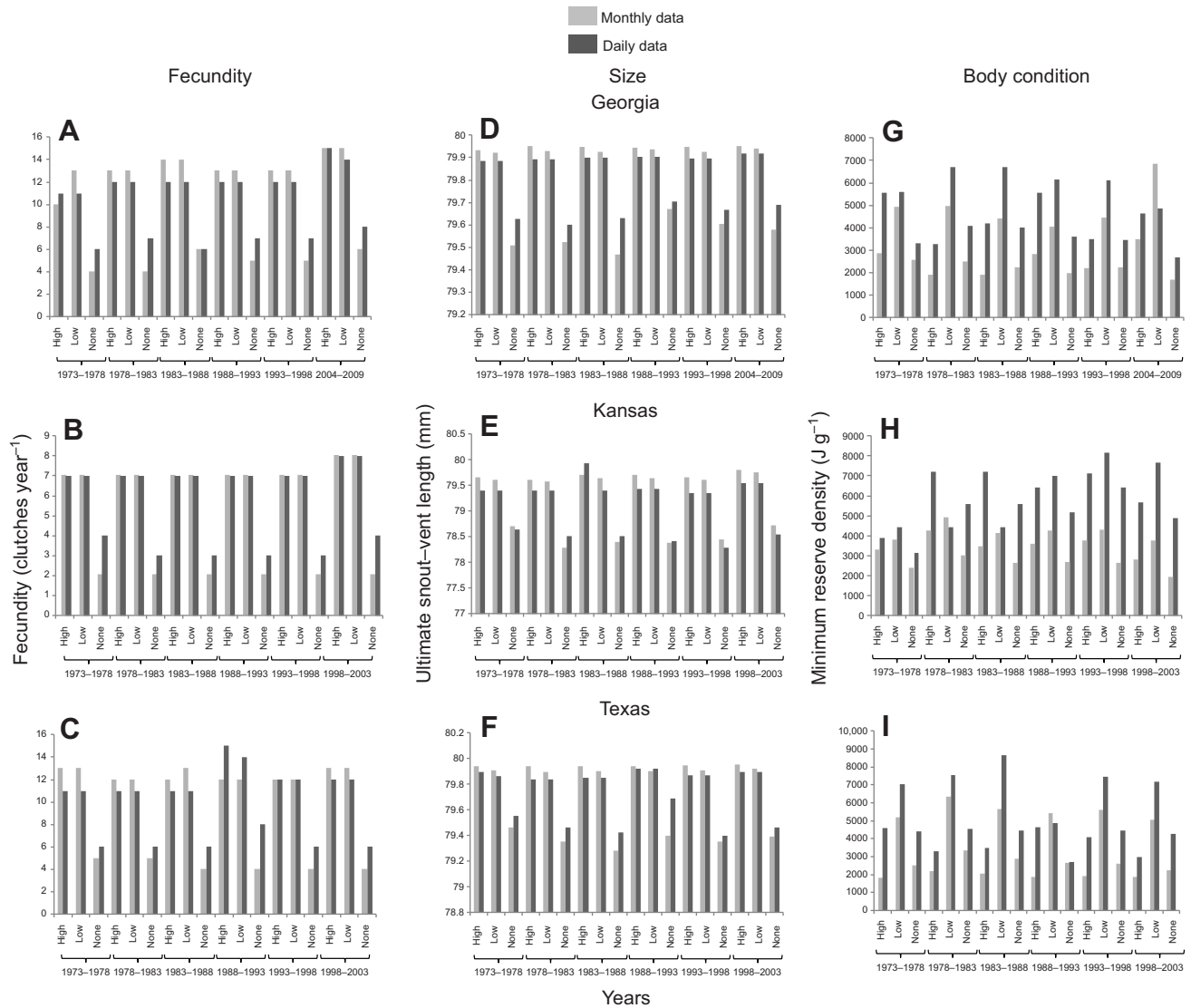


Fig. 6. Summaries of physiological metrics (fecundity, maximum body size and minimum reserve density) from simulations at three sites where climate data for 30 years were available. All results are for 5 year simulations, as depicted in Figs 1–3. In each plot, results are shown for simulations driven by daily data (pale-grey bars) and monthly averages (dark-gray bars) over different 5 year blocks. Results are presented for the three behavioural buffering scenarios – high (100% maximum shade, 2 m maximum burrow depth), low (50% maximum shade, 10 cm burrow depth) and none (~sessile, on the surface in 0% shade).

The authors apologise for any inconvenience that this error may have caused but assure readers that this doesn't affect the results, interpretations or conclusions of the paper.

RESEARCH ARTICLE

Biomechanics meets the ecological niche: the importance of temporal data resolution

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Summary

The emerging field of mechanistic niche modelling aims to link the functional traits of organisms to their environments to predict survival, reproduction, distribution and abundance. This approach has great potential to increase our understanding of the impacts of environmental change on individuals, populations and communities by providing functional connections between physiological and ecological response to increasingly available spatial environmental data. By their nature, such mechanistic models are more data intensive in comparison with the more widely applied correlative approaches but can potentially provide more spatially and temporally explicit predictions, which are often needed by decision makers. A poorly explored issue in this context is the appropriate level of temporal resolution of input data required for these models, and specifically the error in predictions that can be incurred through the use of temporally averaged data. Here, we review how biomechanical principles from heat-transfer and metabolic theory are currently being used as foundations for mechanistic niche models and consider the consequences of different temporal resolutions of environmental data for modelling the niche of a behaviourally thermoregulating terrestrial lizard. We show that fine-scale temporal resolution (daily) data can be crucial for unbiased inference of climatic impacts on survival, growth and reproduction. This is especially so for species with little capacity for behavioural buffering, because of behavioural or habitat constraints, and for detecting temporal trends. However, coarser-resolution data (long-term monthly averages) can be appropriate for mechanistic studies of climatic constraints on distribution and abundance limits in thermoregulating species at broad spatial scales.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/215/6/922/DC1>

Key words: biophysical ecology, dynamic energy budget theory, temporal resolution, ectotherm, thermoregulation, habitat quality.

Introduction: mechanistic niche models and why we need them

The niche concept captures the interaction of an organism with its biotic and abiotic environment. Early applications of niche models focused on biotic interactions and what they mean for population dynamics and community structure (MacArthur and Levins, 1967; Maguire, 1973; Roughgarden, 1972). A major focus of these kinds of niche studies was population dynamics models that were modified to represent the effects of inter- and intra-specific competition on carrying capacity. The long-term potential of this approach was criticised by Schoener (Schoener, 1986) for being too descriptive, with its basis in ‘megaparameters’ (e.g. competition coefficients) that could not be decomposed into processes. Schoener (Schoener, 1986) argued that much could be gained in ecology by following a more mechanistic path where theory and models could be constructed on the basis of individual-level processes – that is, those of behavioural ecology, physiological ecology and ecomorphology, and going from such a foundation to population- and community-level phenomena.

Other more physiologically based approaches have correlated species-range boundaries with large-scale environmental parameters such as air or water temperature. For example, Hutchins (Hutchins, 1947) compared several metrics of surface water temperature [monthly mean, minimum monthly mean (winter), maximum monthly mean (summer)] against the worldwide distributions of marine organisms such as mussels and barnacles

and used these relationships to argue that physiological limitations determined the broad geographic range-limits of these species. Subsequently, numerous studies have correlated species-range edges with environmental data such as air or sea-surface temperature, often measured using remote sensing or other large spatial-scale methods (Britton et al., 2010; Fodrie et al., 2010; Jones et al., 2009; Peacock, 2011; Root, 1988). Indeed, contrary to Schoener’s call, the field of ‘ecological niche modelling’ is now dominated by descriptive studies of how the occurrence records of species (presence or absence, abundance) are associated with environmental gradients, as captured by spatial abiotic data such as climate and terrain (Soberón, 2007). Although biotic interactions, and the influence of abiotic parameters on these interactions, are assumed to occur, they are almost never explicitly modelled.

Ultimately, the processes of coexistence, population growth and geographic range limits are the outcome of different rates of birth, death, immigration and emigration. Occurrence records reflect the outcome of these processes, biased to varying degrees by the observation process (Wintle et al., 2004). Such observations can be statistically related to spatial habitat data using regression [e.g. generalized linear models (GLMs), generalized additive models (GAMs)] or machine-learning (e.g. Maxent) methods (Elith and Leathwick, 2009). These ‘correlative’ models are often highly predictive and constitute, by far, the majority of ‘ecological niche models’ applied at present. This is in part because occurrence data

are widely available for many taxa, as are environmental data collected and modelled over large geographic scales, albeit at fairly coarse spatial resolution.

However, correlative models represent the processes that affect birth and death rates only in an implicit manner; although the correlative modeller inevitably has underlying processes driving observed and future patterns of distribution in mind, the parameters of correlative models have no meaningful dimensions or interpretation such that they could be independently observed in nature (Dormann et al., 2012). It is also debatable whether such models can be said to represent niches, which should ideally be defined with respect to the environments actually experienced by an organism rather than by static depictions of the habitats in which they are observed (Kearney, 2006).

Such concerns are particularly relevant when making predictions of the likely impacts of climate change, where future, novel predictions will likely fall outside of the range of parameters that originally trained the model (Elith et al., 2010). Moreover, many of the initial impacts of environmental change might not simply occur as the result of mortality and thus changes in species-range boundaries but also might be reflected in changes in physiological performance (e.g. Beukema et al., 2009) and the subsequent impacts on ecological services that precede large-scale population- or ecosystem-scale collapse (Mumby et al., 2011). Such effects can only be predicted using approaches that are able to relate changes in the environment to sublethal responses of organisms (Monaco and Helmuth, 2011), including the potential for behavioural buffering of changing climatic impacts (Bogert, 1949; Kearney et al., 2009b; Williams et al., 2008). Thus, many of Schoener's arguments (Schoener, 1986) still apply, but for somewhat different reasons. His sentiments were recently (apparently independently) reiterated by McGill and colleagues (McGill et al., 2006), with an appeal to develop individual-level mechanistic models of the niche that connect to environmental gradients.

There has been a growing effort to achieve the goals to which Schoener and McGill and associates appealed, namely to develop mechanistic niche models that explicitly and formally capture the processes connecting functional traits to environmental gradients and determining their outcome for survival, growth, development, reproduction and dispersal (Buckley, 2008; Buckley, 2010; Buckley et al., 2010; Dunham, 1993; Kearney and Porter, 2004; Kearney and Porter, 2006; Kearney and Porter, 2009; Kearney et al., 2010a; Porter et al., 1973; Violle et al., 2007). Such models are attractive because of the theoretical insight they can offer about environmental constraints on organisms. In a more applied sense, however, they have advantages over correlative models in forecasting the impact of novel environmental change and predicting the outcome of habitat or trait manipulations – for example, under altered fire regimes or genetic manipulation (Helmuth, 2009; Helmuth et al., 2005).

The relative trade-offs between correlative and mechanistic models have yet to be fully explored. For example, Buckley and colleagues (Buckley et al., 2010) recently compared the ability of correlative and mechanistic models to predict the ranges of a lizard and a butterfly. However, they used very coarse environmental input data, thus potentially negating any advantage of the mechanistic approach. Few studies have compared the effect of varying temporal resolution of forcing data on model predictions of physiological parameters directly relevant to reproduction and survival (Dillon et al., 2010; Savage, 2004). Thus, a key aim of the present study is to explore further the issue of temporal data resolution and its impact on the output of mechanistic niche models aimed at predicting distribution and abundance.

Integrating metabolic theory with biophysical ecology: how mechanistic can we get?

Mechanistic niche models vary in the extent to which they combine formalized theory and empirical description. For example, recent attempts to predict climatic constraints on species distributions have applied the principles of biophysical ecology to model body temperature, water loss and metabolic heating requirements as a function of environmental variables such as air temperature, wind speed, humidity and radiation. These biophysical principles come from the general theory of transport phenomena (Bird et al., 2002), which are firmly grounded in the principles of thermodynamics. These same models have additionally been linked to more empirically based models of metabolism – that is, growth, development and reproduction. For instance, Kearney and colleagues (Kearney et al., 2010b) modelled the reproductive potential of leaf-eating possums by combining biophysically modelled energy (heating) and water (cooling) costs with empirical allometric functions of maintenance metabolic costs and food intake rates. This latter example represents an example of phenomenological energy budgets, which are typically parameter rich and more taxon specific in formulation.

In recent years, there has been a strong focus on the development of mechanistic models of metabolism (van der Meer, 2006). Dynamic energy budget (DEB) theory is particularly attractive in the context of mechanistic niche models because it uniquely captures the dynamics of development, growth, body condition and reproduction as an explicit function of temperature and food intake in a comparatively parameter-sparse manner (Kearney and Porter, 2006; Kearney et al., 2010a). The integration of DEB theory with biophysical models of the 'climatic niche' provides an extremely general approach to modelling the niche that can capture complex environmental interactions. We refer the reader to Nisbet et al. (Nisbet et al., 2012) for a more detailed discussion of the differences between energy budgets derived from formal metabolic theory *versus* more traditional, empirically based energy budgets.

In this study, we build on an integration of DEB theory with biophysical principles that was developed to model variation in life history and distribution limits in the North American lizard *Sceloporus undulatus* (Kearney, 2012). We use it to consider important issues arising from the nature and resolution of the environmental data required to drive mechanistic niche models. Specifically, we address the potentially important role of the temporal resolution of input data in driving biophysical models of body temperature, which are then used to predict patterns of mortality, growth and reproduction. This question has significant practical implications as environmental data are increasingly more available to the research community, but often in summarized form: when data are collapsed into temporal averages (e.g. monthly means or extremes), is the variability that is removed simply 'noise' or does it contain information that fundamentally changes our predictions of current, past and future responses of populations to the physical environment (Helmuth et al., 2010)?

Data requirements of mechanistic niche models

Mechanistic niche models are highly prescriptive in their data requirements, especially when compared with correlative models. First, estimates of the functional traits of the study species that form the parameters of the model must often be derived from costly experimental or observational studies of organisms in the field or in the laboratory. Second, the requisite environmental variables come directly from the equations of state (i.e. the energy balance equations), which are solved on a fixed time-step. A biophysical

model of heat exchange, for instance, requires data on air temperature, solar and infrared radiation, wind speed and humidity as experienced by the organism (e.g. near to the ground). Moreover, to capture thermoregulatory behaviour, or in environments such as intertidal zones where environmental conditions change extremely rapidly (e.g. Helmuth et al., 2011), these data might be required on an hourly time-step or shorter. This inflexibility in data requirements potentially hampers the application of mechanistic niche models in many instances because suitable data are often unavailable except at point locations.

As a result, mechanistic niche modellers must often resort to simplifying assumptions and ‘workarounds’ to deal with these data-requirement issues. For biophysical modelling of heat exchange, many of these solutions were pioneered by Porter and colleagues (Grant and Porter, 1992; McCullough and Porter, 1971; Porter, 1989; Porter et al., 2000; Porter and Mitchell, 2006; Porter et al., 1973; Porter et al., 2002). For example, weather-station records of temperature, wind speed and humidity are made 1–2 m above the ground (specifically to minimize microclimatic effects!). However, empirically derived velocity and temperature profiles can be used to estimate conditions experienced by organisms at different heights above the ground (Porter et al., 1973). In addition, coarse approximations of diurnal cycles in temperature, humidity and wind speed can be made through sinusoidal or step-functions fitted to daily observations of maxima and minima (Porter et al., 1973). Finally, the homeostatic mechanisms of organisms themselves can be modelled explicitly such that one only needs to know the extremes of environments available in a given habitat. For example, one could assume that an animal can and will choose any shade level between the maximum and minimum available. Some modellers are beginning to take advantage of reanalysed data, for example those made available by NASA Modern Era Retrospective-Analysis (MERRA), the North American Regional Reanalysis (NARR) (Mesinger et al., 2006) and the FCC Integrated Surface Hourly Database, which provide data on a 1–3 h basis, but such approaches have been used only rarely (e.g. Dillon et al., 2010; Mislán and Wethey, 2011).

A key issue that we focus on here is the temporal resolution of climatic data needed for mechanistic niche modelling. The field of species distribution modelling has been revolutionized by the availability of spatially interpolated climatic data, with global gridded data now available for a wide range of climatic variables. The kinds of data needed for biophysical models of the climatic niche are available in gridded form for many parts of the world, but mostly this consists of long-term (30 year) averages per month of daily maximum and minimum values. Although some studies have used high-resolution data from weather stations to examine patterns in physiological stress at single locations (e.g. Denny et al., 2006; Gilman et al., 2006; Helmuth et al., 2011), most mechanistic models of species distributions have been based on long-term average conditions (i.e. climate) rather than real weather, using a sine wave to convert data expressed as maximum/minimum to hourly data (Buckley, 2008; Buckley, 2010; Buckley et al., 2010; Kearney et al., 2008; Kearney and Porter, 2004; Kearney et al., 2009a; Kearney et al., 2009b; Kearney et al., 2010b; Natori and Porter, 2007; Porter et al., 2002; Porter et al., 2006).

Case study: the energy budget of the lizard *Sceloporus undulatus*

Study system

Sceloporus undulatus (Bosc and Daudin 1801) is a small, insectivorous lizard broadly distributed across the USA and

Mexico. It has become a model species for studies of ectotherm thermal biology (e.g. Angilletta, 2001; Angilletta et al., 2002), life history (e.g. Adolph and Porter, 1993; Niewiarowski et al., 2004; Tinkle and Dunham, 1986) and distribution constraints (Buckley, 2008; Buckley et al., 2010; Parker and Andrews, 2007).

The integrated DEB–biophysical model of *S. undulatus* has been described in detail previously (Kearney, 2012). Briefly, DEB parameters for *S. undulatus* were estimated using the ‘covariation method’ (Lika et al., 2011a; Lika et al., 2011b) by using the MATLAB package ‘DEBtool’ (<http://www.bio.vu.nl/thb/deb/deblab/debtool/>). In DEB theory, a distinction is made between ‘core’ parameters and ‘auxiliary’ parameters. The core DEB parameters are intimately linked to the underlying assumptions of DEB theory and relate directly to processes controlling state-variable dynamics. However, the DEB parameters are not directly observable because they relate to the abstracted state variables of structure, reserve and maturity. Auxiliary parameters combine with the core DEB parameters and state variables to define mapping functions from the abstract quantities such as structural volume to real-world observations such as wet mass. In the covariation method, empirical observations are obtained for a given species (entered in the ‘mydata.m’ DEBtool script), mapping functions are specified using auxiliary theory (contained in the ‘predict.m’ DEBtool subroutine) that relates the given set of empirical data to the DEB core parameters and state variables, and the set of core and auxiliary parameters that best reflects the empirical data is obtained inversely through a regression procedure. The general idea behind the covariation method is to let all available information compete to produce the best-fitting parameter set, and to this end it is necessary to estimate all parameters from all data sets simultaneously. The covariation method applies the Nelder–Mead simplex method for estimating parameters, using either a maximum likelihood (ML) or weighted least squares (WLS) criterion for model fit.

A FORTRAN script implementing the DEB model was integrated with the ‘Niche Mapper’ system for biophysical predictions of body temperature and activity as a function of climatic or weather data (e.g. Kearney et al., 2009b). The Niche Mapper system calculates hourly steady-state body temperatures (T_b) from actual or interpolated weather-station records given the properties of the animal and its microhabitat. It incorporates a microclimate model of above- and below-ground conditions (described further below) and an animal model that solves coupled heat- and mass-balance equations for core temperature given the behaviour of the animal (e.g. shade seeking, burrowing, nocturnal or diurnal), its physical properties (e.g. shape, size, solar reflectance) and the available microclimates. The DEB script was called every hour within the Niche Mapper system to estimate structural volume, reserve density and reserve allocated to reproduction, given the body temperature estimate. It then fed back the new body size for the biophysical calculations in the next time interval.

Weather data

We obtained near-continuous hourly-interval historical data for air temperature, wind speed, relative humidity and cloud conditions from 1973 to 2010 from the Hourly Surface Data and Quality Controlled Local Climatological Data products of the National Climatic Data Center (<http://gis.ncdc.noaa.gov/maps>). We attempted to obtain these data for the weather station nearest to each of the 11 *S. undulatus* life-history study sites, and at a comparable elevation, but were only able to achieve this for five of these sites

Table 1. Summary of weather stations used in the present study, including the years for which data were obtained and the mean temperature of the periods used to construct Fig. 4

Station	Name	State	Latitude	Longitude	Elevation	Years	Mean temperature (°C)
4855	Marion Municipal	Ohio	40.616	-83.064	301.8	2004–2009	10.67
23066	Grand Junction/Walk	Colorado	39.134	-108.538	1474.9	1973–1978	11.73
13996	Topeka/Billard Municipal	Kansas	39.073	-95.626	269.7	1973–2003	12.88
13869	Albany Municipal	Georgia	31.536	-84.194	58.8	1973–1998, 2004–2009	18.84
23034	San Angelo/Mathis	Texas	31.351	-100.494	576.7	1973–2003	18.94

(Table 1). For two of these sites, we had continuous data from 1973 to 2003, and, for one of the five, we had data from 1973–1998 and then from 2004–2009, enabling us to assess the impact of temporal climatic variation within a site. For the other two sites, we only considered a single 5 year block of continuous climatic data.

Cloud conditions were represented in the dataset as ‘ceiling height dimension’, which is the number of metres above ground level to the lowest cloud with five-eighths or more summation total (opaque) sky cover. Because we know of no empirical function to relate cloud base height to percentage cloud cover, we converted

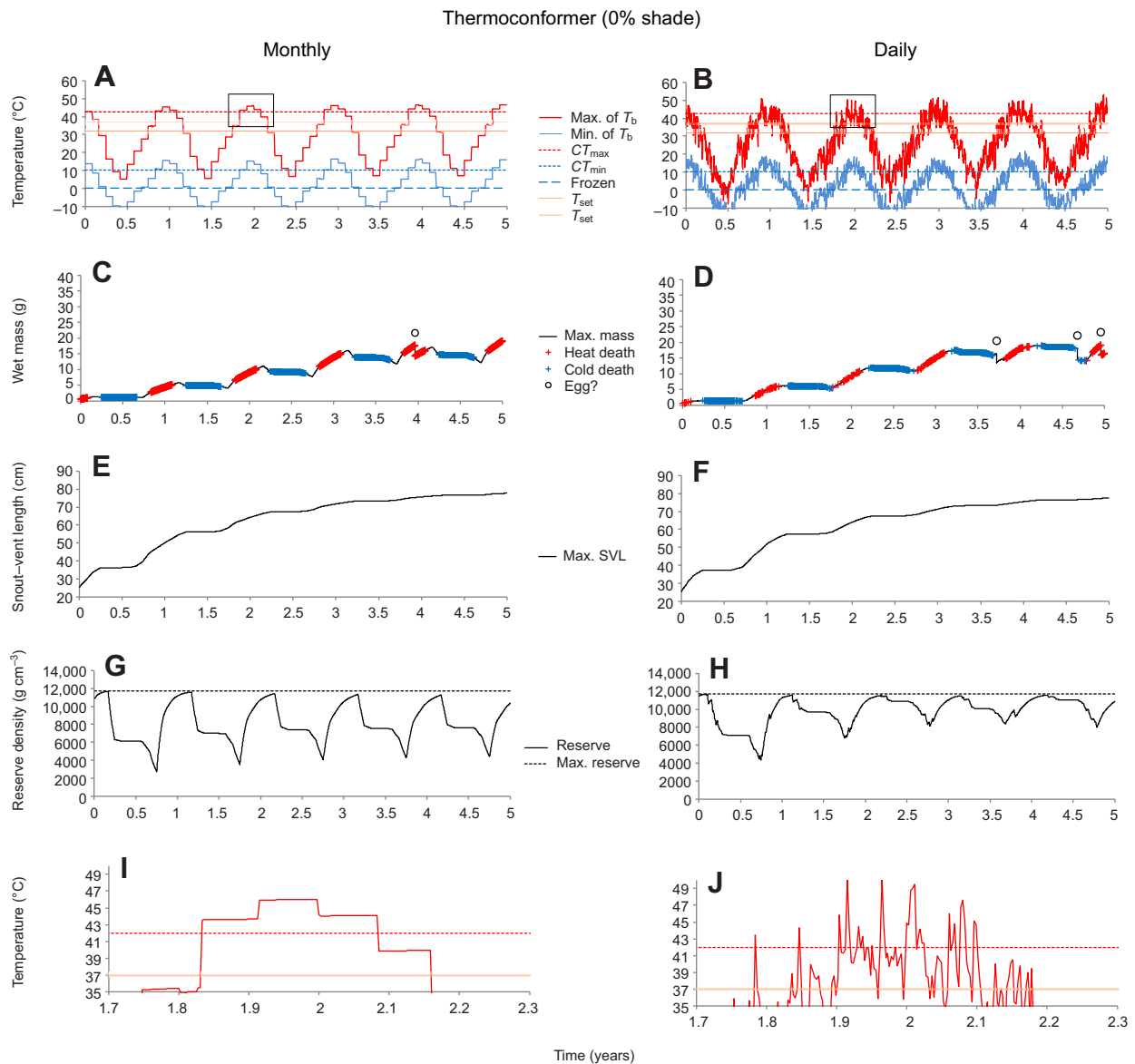


Fig. 1. Results of integrated thermoregulatory (Niche Mapper) and energy budget [dynamic energy budget (DEB) model] model simulations for daily body-temperature extremes (A,B), wet body mass (C,D), body size (E,F) and body condition (reserve density) (G,H) for a site in Colorado, USA. Simulations are driven either by monthly maximum and minimum climatic conditions averaged over the period 1973–1978 (A,C,E,G) or daily maximum and minimum conditions over the same time-period (B,D,F,H). Key thermal thresholds are depicted in the figures for daily body-temperature extremes (A,B). Sharp drops in body mass represent oviposition events for wet mass plots (C,D). These simulations assumed that the animal remained fixed on the surface in full sun throughout the simulations. Also shown are subsections of the maximum body temperature traces (I,J) that represent the regions of panels A and B delimited by the boxes.

the hourly measures into three categories. Values for ‘unlimited’ cover (arbitrarily 22,000 m in the dataset) were treated as 0% cover, values less than or equal to 250 m were treated as 100% cover and all intermediate values were treated as 63% (five-eighths) cover. Because of the patchy nature of the hourly data (frequently one or more hours were missing for a given day), we converted the data into daily maximum and minimum values. These data were then used to reconstruct hourly estimates of weather conditions using Niche Mapper, as described below.

The microclimate model

The standard configuration of the Niche Mapper microclimate model [described in detail previously (Beckman et al., 1973; Porter et al., 1973)] takes long-term average monthly maximum and minimum values for air temperature, wind speed, cloud cover and relative humidity as inputs, together with location data (latitude, longitude), terrain (slope, aspect, elevation), shade extremes and soil thermal properties. It then predicts environmental conditions on the hour for the average day of each month of a single year, calculating solar conditions for the middle day of each month. These outputs include air temperature, wind speed and relative humidity at the height of the animal, solar angle, solar radiation, ‘sky temperature’ (for incoming longwave

radiation) and soil temperature profiles from the surface down to 60 cm deep, at which point it is assumed that the diurnal temperature wave is completely extinguished. Soil temperatures are predicted through the numerical solution of a one-dimensional partial differential equation that requires two boundary conditions and an initial condition. The surface and 60 cm deep soil temperatures are the boundary condition for the transient soil temperature calculations; surface temperature is calculated by applying an energy balance equation, and 60 cm deep soil is assumed to represent the monthly mean air temperature (i.e. the average of the daily minimum and maximum values). The monthly cycle in soil temperatures is assumed to disappear at a depth of 2 m, where it is assumed that the temperature is equal to the annual average. The microclimate model commences each day with a uniform soil temperature profile equal to the monthly average value (i.e. the initial condition) and runs three iterations of each day to obtain a steady periodic of hourly soil temperature change at a set of user-specified nodes (we used 0, 2.5, 5, 10, 15, 20, 30, 40, 50 and 60 cm). Output is then provided for each hour of the average (middle) day of each month of the year for the two extremes of shade provided as input per month.

We reconfigured the microclimate model to accept five years of daily minimum and maximum air temperature, wind speed,

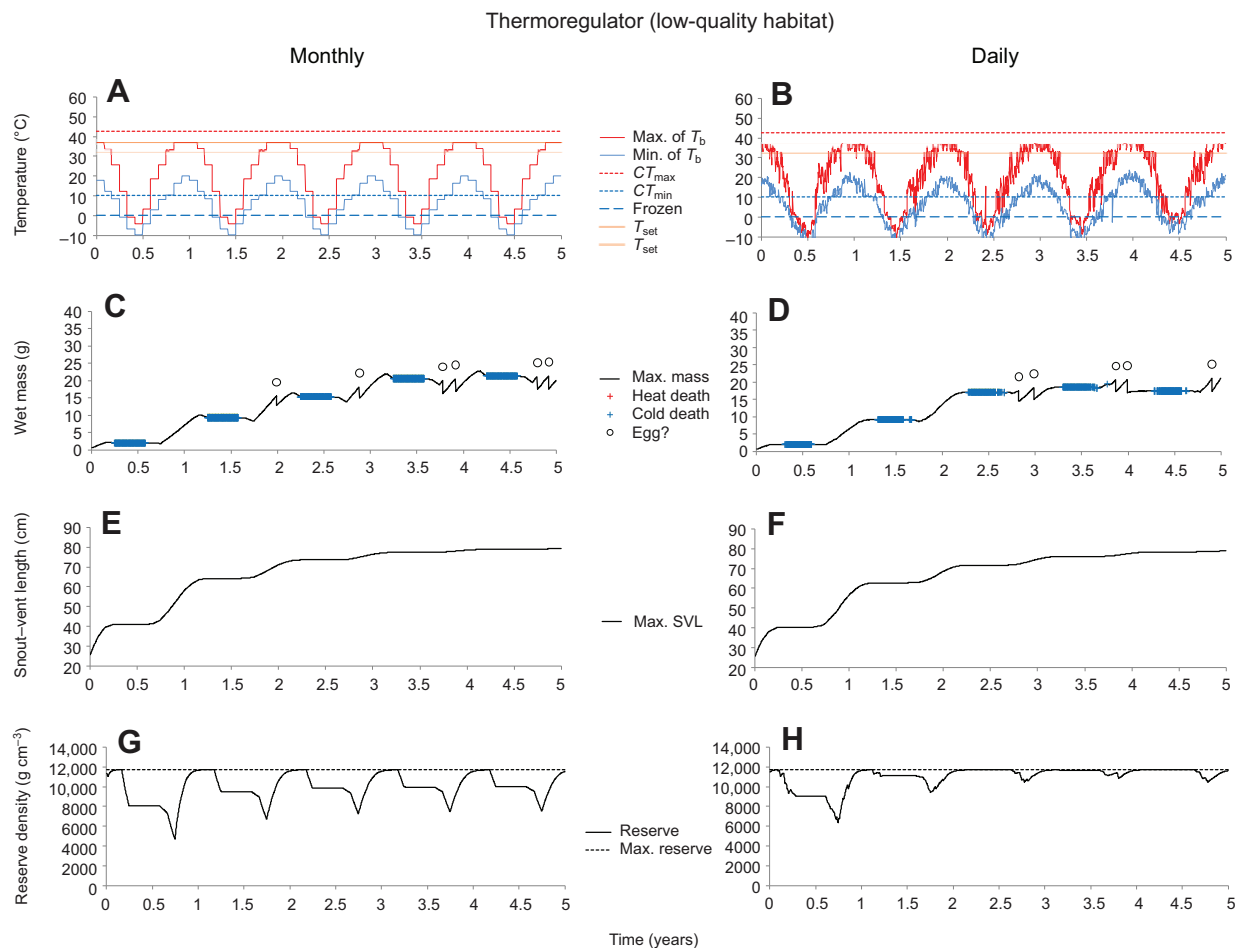


Fig. 2. Results of integrated thermoregulatory (Niche Mapper) and energy budget [dynamic energy budget (DEB) model] model simulations for daily body-temperature extremes (A,B), wet body mass (C,D), body size (E,F) and body condition (reserve density) (G,H) for a site in Colorado, USA. Simulations are driven either by monthly maximum and minimum climatic conditions averaged over the period 1973–1978 (A,C,E,G) or daily maximum and minimum conditions over the same time-period (B,D,F,H). Key thermal thresholds are depicted in the figures for daily body-temperature extremes (A,B). Sharp drops in body mass represent oviposition events for wet mass plots (C,D). These simulations assumed that the animal had access to 0–50% shade when active and burrowed down to 10 cm when inactive. SVL, snout–vent length.

cloud cover and humidity and to run one iteration of each day rather than three, with the starting soil temperature profile of a given day equal to that of the last hour of the preceding day. We calculated the running mean of the minimum and maximum air temperatures for the preceding 30 days (or the first 30 days if 30 days had not yet elapsed) and used that as the 60 cm deep boundary condition. Similarly, we calculated the running mean of the minimum and maximum air temperatures for the preceding 365 days (or the first 365 days if 365 days had not yet elapsed) as the 2 m deep soil temperature. Output was produced for every hour of every day over the five year period for the two extremes of shade levels.

Animal model and simulations

As with the microclimate model, the standard configuration of the ectotherm model of Niche Mapper is to run the average day of each month over one year. Calculations for each day are then summed over the number of days per month to obtain monthly and yearly totals, for example, of activity hours, water and energy requirements. Kearney developed a DEB model subroutine for the ectotherm model that is called every hour to estimate structural volume, reserve density and reserve allocated to reproduction, given the body temperature estimate and the thermal constraints of

activity periods on feeding (Kearney, 2012). The ectotherm model was reconfigured to repeat each simulation for the number of days in a given month, each time calling the DEB subroutine, and repeating this for up to 5 years. For analyses based on daily weather data in the present study, we simply adjusted the version of the ectotherm model used by Kearney (Kearney, 2012) so that it read in the 5 years of hourly output from the modified microclimate model described above, rather than repeatedly looping through the average day of each month.

As mentioned above, one of the justifications for using relatively coarse-resolution data in mechanistic niche models (e.g. 5 km² grid cells, monthly climate) is that animals behaviourally buffer themselves through habitat selection. The capacity for such buffering, however, depends on habitat quality – that is, the presence of microhabitats that allow the animal to remain within a preferred or at least nonlethal range of body temperatures. To assess the impact of varying degrees of behavioural buffering, we ran simulations for each site for monthly and daily data, assuming: (a) 0–100% shade available, burrows down to 2 m (high-quality habitat), (b) 0–50% shade, burrows down to 10 cm (poor-quality habitat) and (c) no burrows or shade available (corresponding to a thermoconforming animal in the open; this configuration also thus provides a model for a sessile organism). The Niche Mapper system

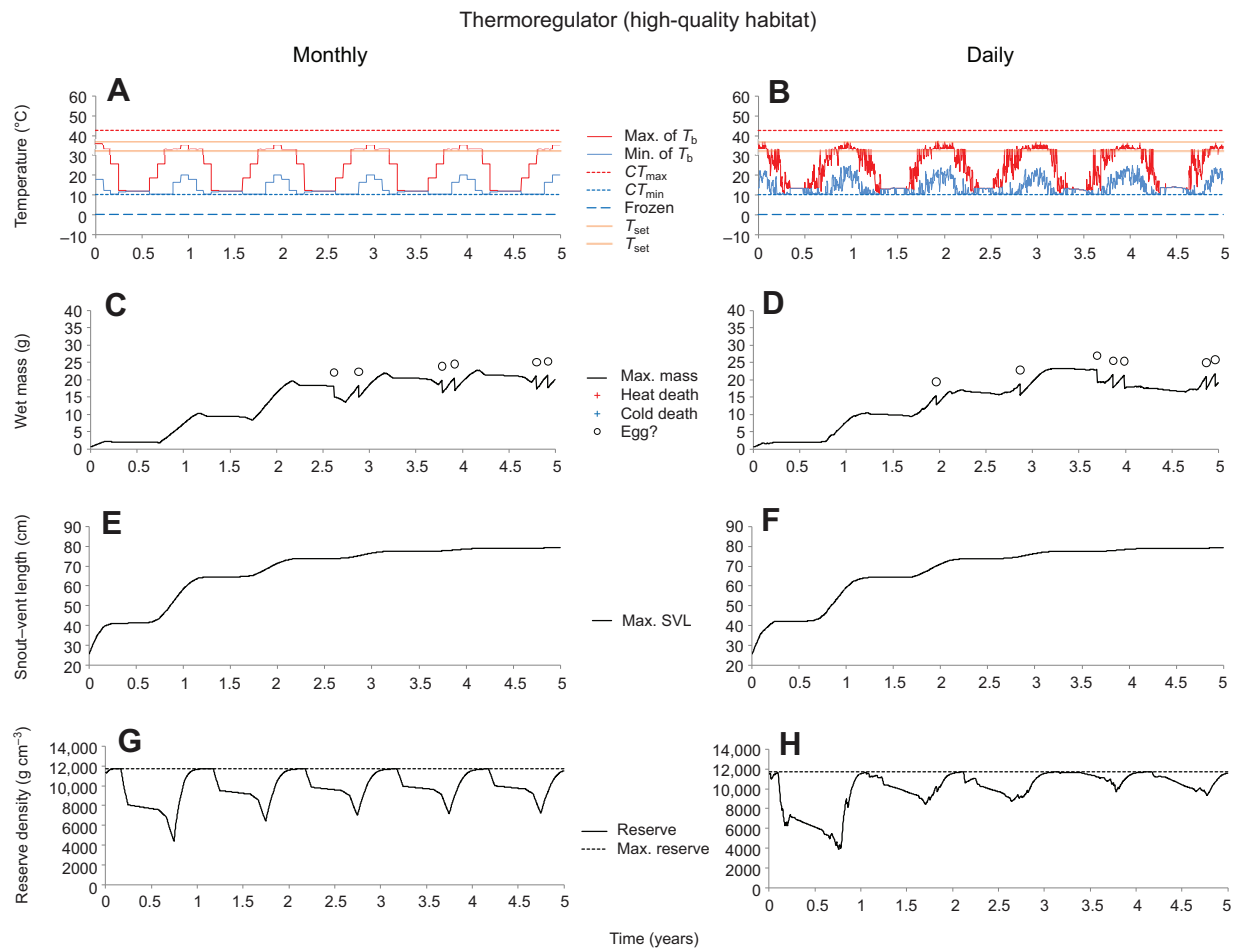


Fig. 3. Results of integrated thermoregulatory (Niche Mapper) and energy budget [dynamic energy budget (DEB) model] model simulations for daily body-temperature extremes (A,B), wet body mass (C,D), body size (E,F) and body condition (reserve density) (G,H) for a site in Colorado, USA. Simulations are driven either by monthly maximum and minimum climatic conditions averaged over the period 1973–1978 (A,C,E,G) or daily maximum and minimum conditions over the same time-period (B,D,F,H). Key thermal thresholds are depicted in the figures for daily body-temperature extremes (A,B). Sharp drops in body mass represent oviposition events for wet mass plots (C,D). These simulations assumed that the animal had access to 0–100% shade when active and burrowed down to 2 m when inactive. SVL, snout–vent length.

searched for the environment producing core temperatures closest to the specified preferred temperature, given these constraints.

We assessed the impact of these different behavioural buffering scenarios on five physiological metrics: (1) heat stress, when T_b was higher than the critical thermal maximum (CT_{max}) of *S. undulatus*, which ranges between 42 and 43°C (Ehrenberger, 2010) – we used a threshold of 42°C, assuming that 1 hour at this temperature is likely to be lethal, (2) cold stress, when T_b was lower than 0°C, which is very likely to be lethal for this species, although its critical thermal minimum is much higher at ~10°C (Ehrenberger, 2010), (3) fecundity, which refers to the number of clutches (of 8 eggs) produced per lifetime, (4) maximum size, which is the largest snout–vent length (SVL) attained by the end of the 5 year time-period and (5) minimum reserve density, which reflects the lowest

body condition level (i.e. the greatest level of starvation due to temperature-induced inactivity) experienced across the lifetime.

Results and discussion

Figs 1–3 show output from the simulations for the Colorado site for a 5 year block of time (August 1973 to July 1978, inclusive). All three behavioural buffering scenarios are depicted: no buffering (thermoconformer, on the surface in the open; Fig. 1), low buffering (low-quality habitat, 50% maximum shade, 10 cm maximum burrow depth; Fig. 2) and high buffering (high-quality habitat, 100% maximum shade, 2 m maximum burrow depth; Fig. 3). The equivalent figures for all other sites and time-blocks can be found in the supplementary material Figs S1–S4. From these figures, the substantial difference in daily core temperature variation between

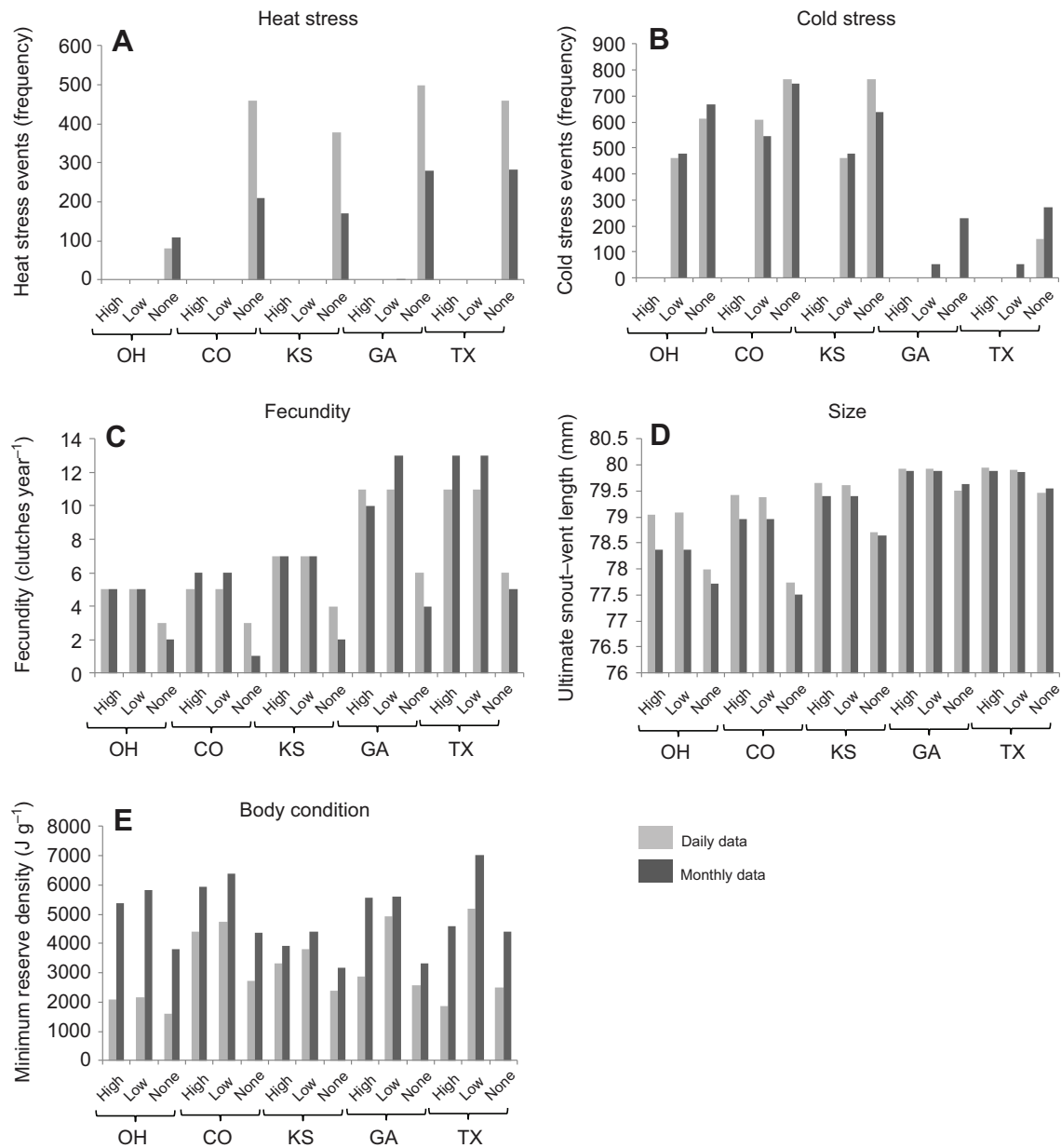


Fig. 4. Summaries of physiological metrics from simulations at sites in Ohio (OH), Colorado (CO), Kansas (KS), Georgia (GA) and Texas (TX). All results are for 5 year simulations as depicted in Figs 1–3, and all represent the years 1973–1978, except for Ohio, which represents the years 2004–2009 (1973–1978 was not available for this site). In each plot, results are shown for simulations driven by daily data (pale-grey bars) and monthly averages (dark-grey bars) over the 5 year blocks. Results are presented for the three behavioural buffering scenarios – high (100% maximum shade, 2 m maximum burrow depth), low (50% maximum shade, 10 cm burrow depth) and none (sessile, on the surface in 0% shade).

the monthly and daily simulations is highly evident, as is the buffering impact on body temperature of shade selection and burrowing underground (panels A vs B in these figures).

Fig. 4 shows the summarized impacts of the different sites and scenarios, for monthly and daily data, on the physiological metrics of heat and cold stress events, lifetime fecundity, maximum size and minimum reserve density. The sites are ordered from coldest (Ohio) to warmest (Texas). Heat stress events (Fig. 4A) were only an issue for the scenario of no behavioural buffering and were

minimal at Ohio, the coldest site. Surprisingly, heat stress events were predicted at substantially higher frequencies from monthly data than from daily data at all sites except Ohio. Daily data predicted higher magnitudes in body temperature extremes, whereas monthly data overestimated heat stress frequencies because the average day for each month produced conditions over the threshold we set for heat stress for the warmer months. In contrast, the higher variance in the daily fluctuations resulted in days with extremes much higher than this threshold but also much

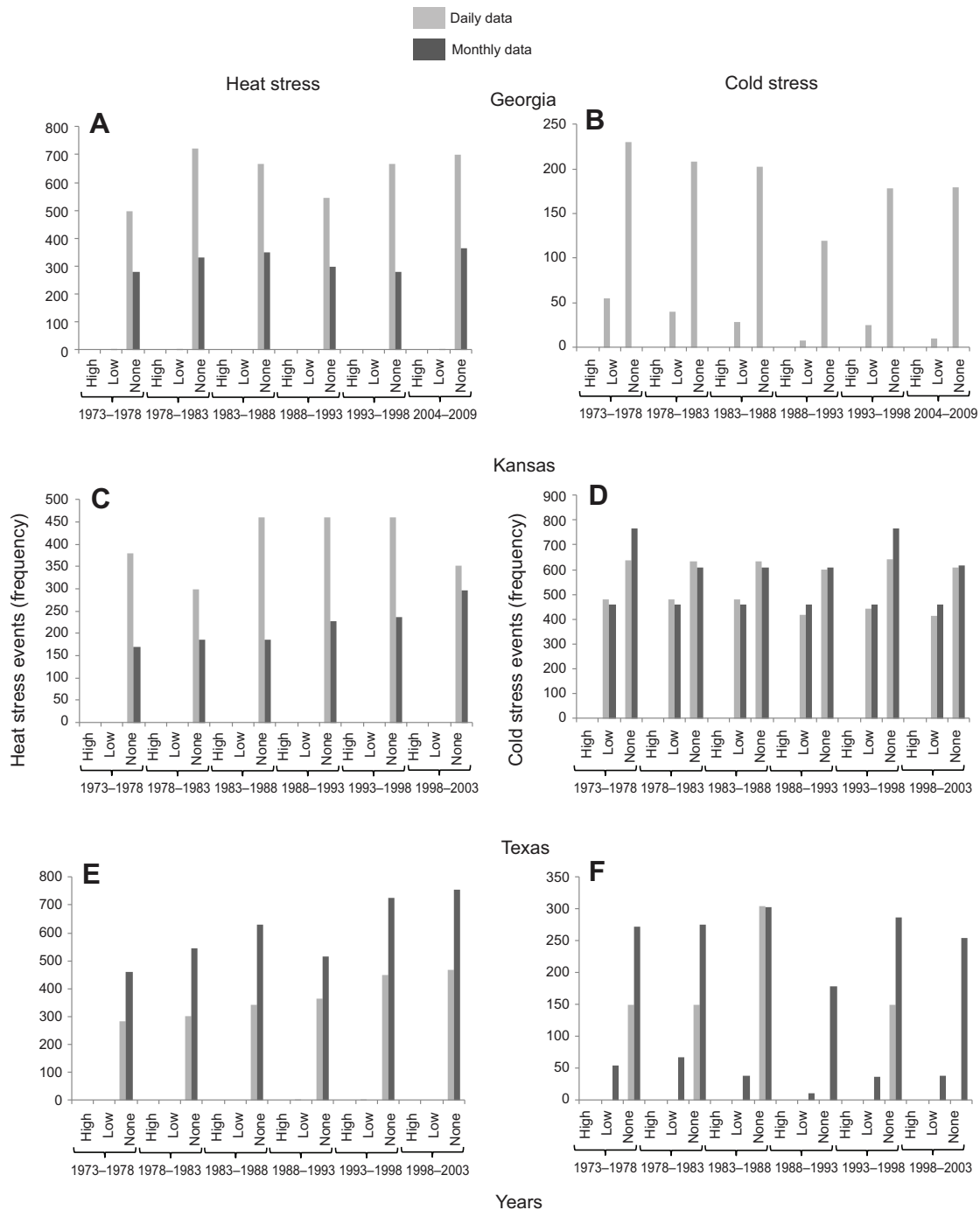


Fig. 5. Summaries of physiological metrics (heat and cold stress events) from simulations at three sites where climate data for 30 years were available. All results are for 5 year simulations, as depicted in Figs 1–3. In each plot, results are shown for simulations driven by daily data (pale-grey bars) and monthly averages (dark-grey bars) over different 5 year blocks. Results are presented for the three behavioural buffering scenarios – high (100% maximum shade, 2 m maximum burrow depth), low (50% maximum shade, 10 cm burrow depth) and none (sessile, on the surface in 0% shade).

lower over the same part of the season (see Fig 11,J); – that is, there was ‘spillover’ from extreme events in the monthly averages. No cold stress occurred under the scenario of high behavioural buffering for any site (Fig.4B). However, cold stress event frequencies were of similar, high frequency for the three coldest sites for the scenarios of zero and low behavioural buffering (Fig.4B). At the two warmest sites, cold stress events were of lower frequency and were only detected under the daily simulations for the scenario of low behavioural buffering.

For fecundity estimates (Fig.4C), there were no systematic differences between daily and monthly simulations, but the fecundity tended to increase in rank order with the temperature of the site and was consistently lowest for the scenario of no behavioural buffering. Ultimate size estimates were almost always biased upwards for monthly simulations relative to daily simulations and tended to be lower at colder sites and for the scenario of no behavioural buffering (Fig.4D). Growth trajectories

were very similar between daily and monthly simulations (Figs 1–3, panels E and F, and supplementary material Figs S1–S4). Finally, the minimum reserve density (i.e. body condition) was much greater under daily rather than monthly simulations, owing to periods of inactivity (and hence no feeding) being broken up more under daily simulations (Fig.4E). This permitted animals to refill their guts (*ad libitum* feeding was assumed whenever animals were active) and hence to run down their reserves less frequently under the daily simulations.

Recent studies have shown evident of physiological impacts of climate warming on ectotherms (Dillon et al., 2010; Sinervo et al., 2010). For three of our sites, Georgia, Texas and Kansas, we were able to examine long-term (30 year) trends in both body temperature and physiological metrics (Figs 5, 6). Results show statistically significant increases in the daily minimum and maximum air temperatures within the dataset for all three sites over the time-period considered (Table 2, Fig. 7), consistent with observations of

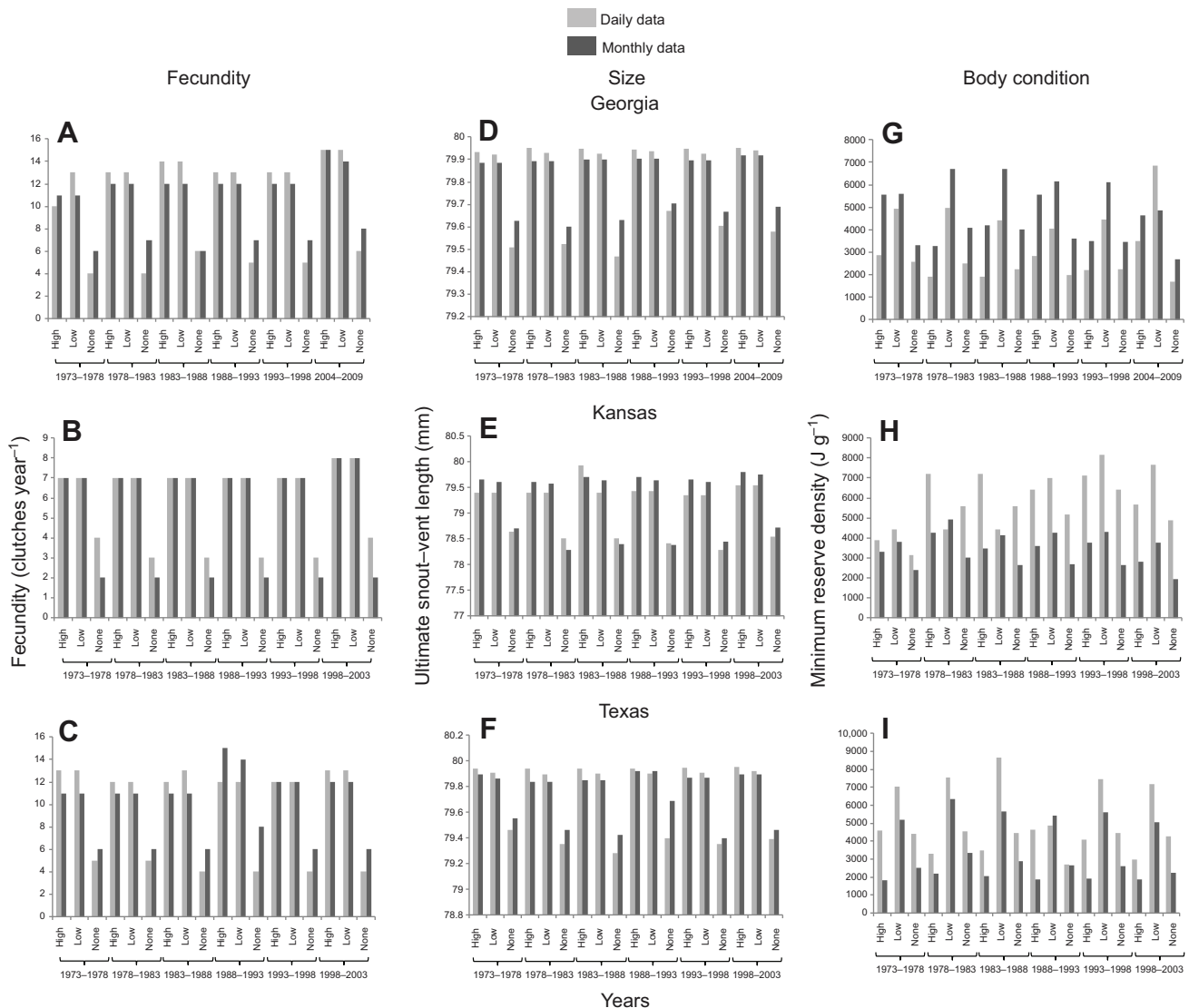


Fig. 6. Summaries of physiological metrics (fecundity, maximum body size and minimum reserve density) from simulations at three sites where climate data for 30 years were available. All results are for 5 year simulations, as depicted in Figs 1–3. In each plot, results are shown for simulations driven by daily data (pale-grey bars) and monthly averages (dark-gray bars) over different 5 year blocks. Results are presented for the three behavioural buffering scenarios – high (100% maximum shade, 2 m maximum burrow depth), low (50% maximum shade, 10 cm burrow depth) and none (~sessile, on the surface in 0% shade).

Table 2. Results of regressions of daily maximum (T_{\max}) and minimum (T_{\min}) temperature on time (days) across the 30 years considered in our analyses for three different sites

Site	Variable	N	R^2	Slope	P
Georgia	T_{\max}	10,953	0.001575	0.288	<0.001
	T_{\min}	10,953	0.001861	0.339	<0.001
Kansas	T_{\max}	10,957	0.000797	0.380	0.003
	T_{\min}	10,957	0.001417	0.475	<0.001
Texas	T_{\max}	10,957	0.001879	0.423	<0.001
	T_{\min}	10,957	0.000629	0.252	0.009

Note that all sites include the years 1973–1998, and Texas and Kansas continue until 2003 and Georgia jumps to the period 2004–2009. Slopes are reported in $^{\circ}\text{C}$ per decade.

anthropogenic warming over the same period. We thus considered how the physiological metrics we simulated have responded to this warming in the form of temporal shifts and how these shifts varied with the temporal resolution of the data.

While the general patterns in physiological response to this warming were remarkably consistent across years for most measures, in several cases statistically significant temporal patterns did indeed emerge (Table 3). Importantly, predicted responses were quite different, depending on whether daily or monthly data were used as inputs. For example, our model predicted a statistically significant temporal increase in fecundity at the Georgia site, regardless of what behavioural buffering scenario was used, but only when daily data were used as inputs. At the Kansas site, results suggested a temporal decrease in cold stress and an increase in energy reserves under low habitat quality scenarios, but again this was only detectable using daily data. At the Texas site (the hottest site), both monthly and daily data predicted a significant temporal increase in heat stress with no buffering, but the two data sets differed in their predictions of temporal trends in fecundity and maximum size under the different behavioural scenarios. These trends were all relatively minor in magnitude, with P -values not smaller than 0.01, and we did not apply adjustments for the number of tests. However, the point of the analysis is that temporal shifts

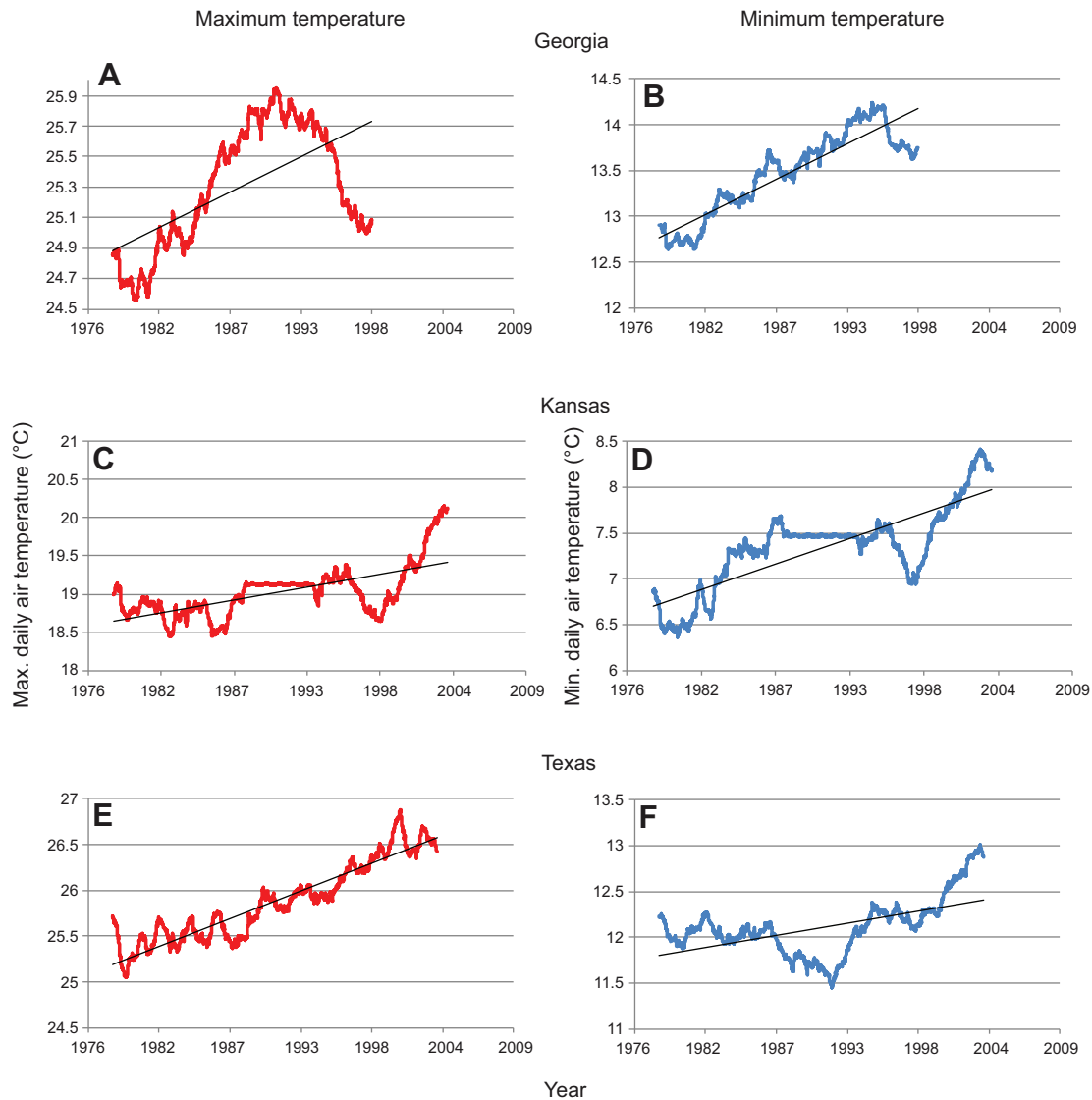


Fig. 7. Temporal trends (5 year running averages) in maximum (red lines) and minimum (blue lines) air temperature at the three sites for which long-term (30 years) climate data were obtained. Solid black lines are linear trend lines. A shorter time-series is presented for Georgia in these plots because there was a gap in data from 1998 to 2004, and hence a continuous 5 year running average was not possible over the whole time-period. See Table 2 for results of statistical analyses of temporal trends in these data.

Table 3. Results of regression analyses of physiological metrics against year for the different sites (30 year period) and behavioural buffering scenarios using daily or monthly data

	Georgia		Kansas		Texas	
	Daily	Monthly	Daily	Monthly	Daily	Monthly
No buffering						
Heat stress	n.s.	n.s.	+	n.s.	+	+
Cold stress	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Fecundity	+	n.s.	n.s.	n.s.	n.s.	-
Size	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Reserve	n.s.	-	n.s.	n.s.	n.s.	n.s.
Low buffering						
Heat stress	n.s.	x	n.s.	x	n.s.	x
Cold stress	-	x	-	x	n.s.	x
Fecundity	+	n.s.	n.s.	n.s.	n.s.	n.s.
Size	+	n.s.	n.s.	n.s.	n.s.	n.s.
Reserve	n.s.	n.s.	+	n.s.	n.s.	n.s.
High buffering						
Heat stress	x	x	x	x	x	x
Cold stress	x	x	x	x	x	x
Fecundity	+	n.s.	n.s.	n.s.	n.s.	n.s.
Size	+	n.s.	n.s.	n.s.	n.s.	+
Reserve	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Results are shown as either nonsignificant ($P>0.05$) 'n.s.', no data 'x' (i.e. no value recorded), a significant positive relationship '+' or a significant negative relationship '-'.

in physiological outcomes under warming might be artificially obscured or inflated if an inappropriate temporal resolution is used (Dillon et al., 2010).

Conclusions and recommendations

Increasingly sophisticated adaptation strategies are demanding quantitative, spatially and temporally explicit forecasts of ecological responses to climate change along with associated estimates of uncertainty (Williams et al., 2008). Importantly, these responses include not only mortality and changes in range edges but also nonlethal responses such as reduced growth and fecundity, or any other physiological or ecological response that can result in altered performance or the provision of ecosystem services (Mumby et al., 2011). The combination of biophysical models with energetics models provides a potentially powerful mechanism for providing this much-needed information, but it is vital that we match the scale of input data to the organism in question.

As shown here, fundamentally different results can accrue given the temporal resolution of input data used, and this is especially important for organisms with limited behavioural thermoregulatory ability (such as sessile or semi-sessile organisms) or organisms living in low-quality habitats. However, for species with significant capacity for behavioural buffering, including access to high-quality habitat with a suitable range of available microclimates, the impact of temporal data resolution declines. Thus, for physiologically based studies of coarse-scale species-distribution limits in thermoregulating species, where the spatial resolution is coarse enough that it likely captures some regions with suitable habitat (sufficient shade, places to burrow), coarse (monthly long-term) averages are likely to be sufficient (Buckley, 2008; Kearney and Porter, 2004). Given the increasing availability of spatially explicit data at fine temporal resolutions, however, we would recommend that mechanistic niche models be driven by fine (daily) resolution data wherever possible, especially when attempting to include the impacts of biotic interactions, when competition for high-quality habitat might play an important role in population dynamics (Huey, 1991; Huey et al., 1989).

Importantly, the use of fine-temporal-scale data unleashes the power of DEB theory and biophysical ecology to tackle questions operating over a diversity of different time scales, from growth to energy reserve dynamics to habitat choice and patterns of feeding. It also allows more detailed consideration of how the phenology of a species responds to environmental signals on different time scales, such as breeding events timed to temperature, day length or rainfall. Such analyses will produce more-nuanced predictions of the impact of environmental change on diverse organisms.

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